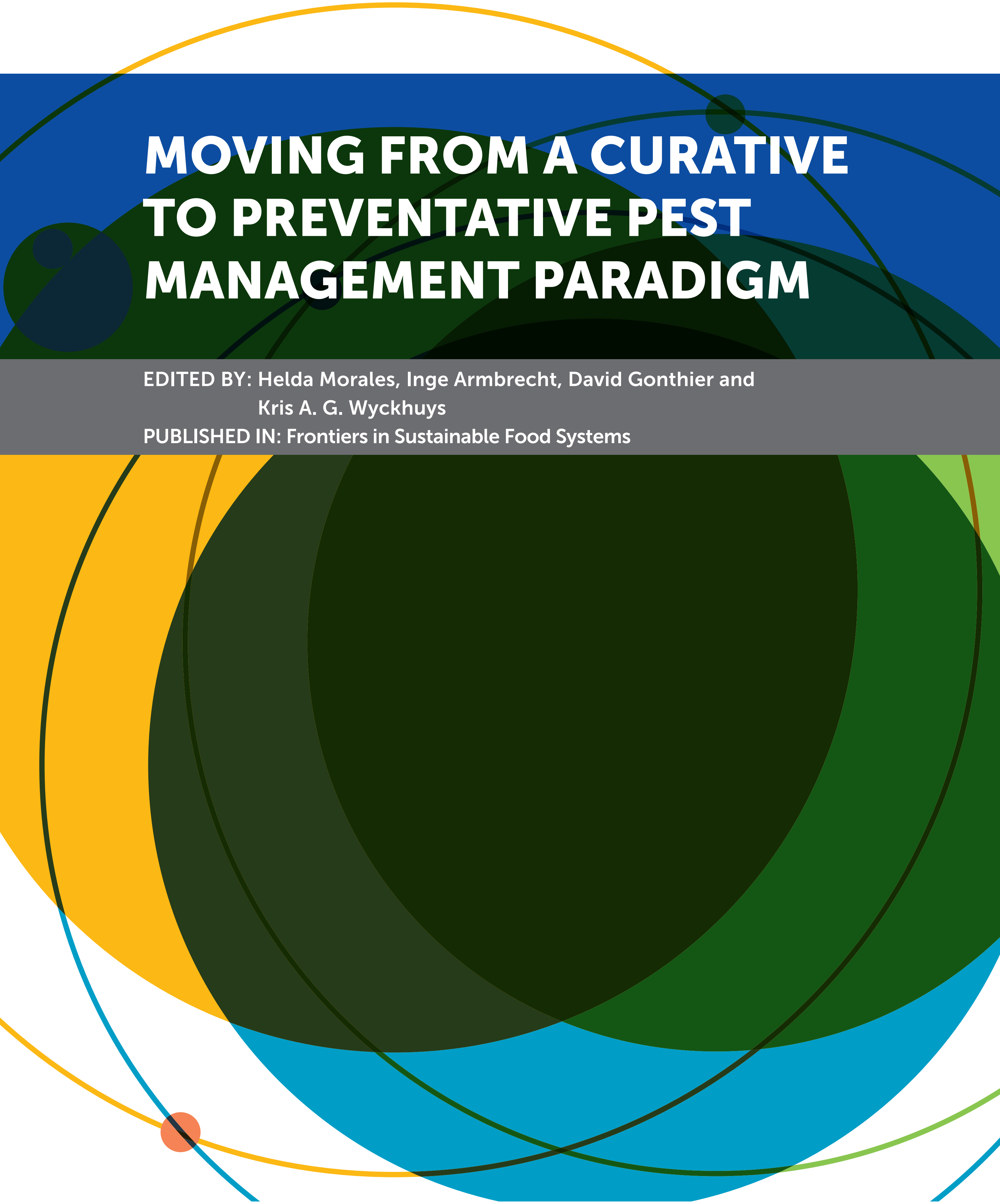

# MOVING FROM A CURATIVE TO PREVENTATIVE PEST MANAGEMENT PARADIGM

EDITED BY: Helda Morales, Inge Armbrecht, David Gonthier and
Kris A. G. Wyckhuys
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# MOVING FROM A CURATIVE TO PREVENTATIVE PEST MANAGEMENT PARADIGM

Topic Editors:
**Helda Morales,** The South Border College (ECOSUR), Mexico
**Inge Armbrecht,** University of Valle, Colombia
**David Gonthier,** University of Kentucky, United States
**Kris A. G. Wyckhuys,** Chrysalis Consulting, Vietnam

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EDITORIAL
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# Editorial: Moving From a Curative to Preventative Pest Management Paradigm

*Helda Morales*[1]*, *Inge Armbrecht*[2], *David Gonthier*[3] and *Kris A. G. Wyckhuys*[4,5,6,7]

[1] Departamento de Agricultura, Sociedad y Ambiente, El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Mexico, [2] Departamento de Biología, Univesidad del Valle, Cali, Colombia, [3] Department of Entomology, University of Kentucky, Lexington, KY, United States, [4] Chrysalis Consulting, Hanoi, Vietnam, [5] China Academy of Agricultural Sciences, Beijing, China, [6] University of Queensland, Brisbane, Australia, [7] Fujian Agriculture and Forestry University, Fuzhou, China

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***Edited and reviewed by:***
*Stacy Michelle Philpott,*
*University of California, Santa Cruz,*
*United States*

****Correspondence:***
*Helda Morales*
*hmorales@ecosur.mx*

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**Editorial on the Research Topic**

**Moving From a Curative to Preventative Pest Management Paradigm**

Over the past decades, crop protection research, education and outreach have increasingly focused on pest management as a reactive approach. Though the financial and human resources invested for that purpose are enormous, pests continue to be an increasing problem of global proportions—and are of particular concern in large-scale, simplified and chemically-intensified agroecosystems. This curative pest control strategy (and particularly farmer's over-reliance on synthetic pesticides) negatively impacts biodiversity, farmer and consumer health and farm profitability while directly contributing to global environmental change. Yet, first-hand experience of small farmers across the globe has shown that a preventative approach (e.g., crop and genetic diversification, tailored soil, water and fertility management, varietal resistance and conservation biological control) effectively defuses crop herbivores and proves to be far more efficient, cost-effective and environmentally-sound than conventional pest management strategies. A paradigm shift is urgently needed to help stall or revert the biodiversity crisis and to become a core component of initiatives that pursue agroecological transitions.

In this Research Topic we intend to collate the state of the art of research on pest prevention upon experiences from various agroecosystems around the globe.

Although agroecology promotes principles, not recipes, it is important to have empirical examples that serve as inspiration for other contexts. This special issue highlights how designing agroecosystems for preventative pest management can take many forms and functions and can be implemented across large and small scales. Specifically, several studies demonstrate that intentional selection of vegetative features can alter the natural behavior of pests, limit host finding, and dilute host-crop resources, ultimately limiting their ability to reach damaging levels. For example, intercropping blueberry orchards with peppermint, which release high levels of volatile organic compounds, deter spotted-winged *Drosophila* flies from ovipositing in berries (Gowton et al.). While diversifying field edges with woody habitat reduced yield loss by the sunflower moth 4-fold compared to bare, undiversified field edges (Kross et al.). Other studies highlight how diversified agroecosystems harbor more structural and trophic resources that allow natural enemies to better persist over time to limit pests preventatively (Iuliano and Gratton). For example, in shaded coffee farms of southern Mexico, where agroforestry practices provide ample resources for high densities of bird and bat species, removal of these predators results in increased abundance of herbivores on coffee (Schmitt et al.). Even in greenhouses, the most simplified agroecosystems, introducing prey resources to preventatively establish predators and parasitoids before the arrival of pests can improve the success of biological control programs beyond curative release strategies (Pijnakker et al.).

Agriculture is a dynamic, inter-connected socio-ecological system. While work along ecological or agronomic fronts is important to advance preventative pest management, its social facets cannot be disregarded. As a central premise of agroecology, farmer-scientist crosstalk and collaboration is crucial to empower country folk and to mobilize the wealth of traditional, indigenous knowledge. Meanwhile, by engaging anthropologists, one can pinpoint key knowledge gaps and identify needs for further awareness-raising—as elegantly shown for Peruvian *mestizo* farmers (Beltran-Tolosa et al.). Even within seemingly monotonous agri-food systems e.g., California urban community gardens, farmer knowledge is surprisingly diverse—molded by ethnicity, experience and gender (Liere et al.). In such settings, mental models can help to detect how particular beliefs obstruct farmers' ultimate adoption of biodiversity-based practices such as biological control (Bardenhagen et al.). Involvement of social scientists is also sorely needed to gauge the economic weight of preventative pest control—an exercise which is done in a mere 4% of instances in the Asia-Pacific (Wyckhuys et al.). Yet, these few economic assessments do show how monetary impacts are substantial; vegetable growers that harness biodiversity for pest control reap 78% higher profits and cut their (pesticide) expenditures by hundreds of dollars. Echoing recommendations by the 57 authors that underwrote our Special Topic, an interdisciplinary "Humboldtian" perspective is thus indispensable to bring about transitions toward sustainable food systems.

As presented in the overview, most research and funding is placed on conventional approaches to pest control, especially directed to agribusiness and formulas which could be easily applied at large scales. Given that widespread unintended consequences have already been documented, we need a drastically different philosophy. The articles published in this special issue witness the transition from this reactive approach to a preventive approach in terms of pest management. It is increasingly becoming more evident that the new agriculture for a sustainable future needs much more qualified science, given that its main input is knowledge. A new paradigm for agriculture is not an easy task. It implies the recognizing and sharing of traditional peasant/indigenous wisdom and scientific approach. Scientists should no longer ignore that there are efficient millenary ancestral practices in preventing pest outbreaks, which need to be put under scrutiny. Agronomists and agroecology practitioners need an ecological lens to develop autonomous ecosystem services to avoid pest losses. Multiscale and transdisciplinary working probably will be one of the keys to reach sustainable agriculture, but this will require profound changes in our institutions of higher education. We hope that this Special Topic will contribute to start those changes.

## AUTHOR CONTRIBUTIONS

HM proposed the idea of the Research Topic and invited the other editors and for the editorial wrote the introduction. DG wrote the ecological synthesis. KW the social sciences contributions. IA the conclusions. We all edited the manuscripts.

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

MINI REVIEW
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# Tropical Occurrence and Agricultural Importance of *Beauveria bassiana* and *Metarhizium anisopliae*

*Amy V. McGuire*[1] *and Tobin D. Northfield*[1,2]*

*[1] Centre for Tropical Environmental Sustainability Science, James Cook University, Cairns, QLD, Australia, [2] Tree Fruit Research and Extension Center, Washington State University, Wenatchee, WA, United States*

Entomopathogenic fungi are often relied on as important components of integrated pest management in tropical agriculture, either as biopesticides or as naturally occurring microbes conserved in the environment. Tropical abiotic conditions are often well-suited for microbial growth, and tropical habitats can be teeming with microbial biodiversity. However, competitive interactions with other fungi and the need to overcome defenses of hosts adapted to high fungal loads may inhibit the ability of insect pathogens to control tropical pests. Here, we review the current literature on *Beauveria bassiana* and *Metarhizium anisopliae* inhabiting tropical environments and their potential use as biological control agents. In some cases there is not a clear distinction between temperate and tropical agroecosystems, such as in the level of organic matter or soil texture in agricultural soils. Therefore, the effects of these soil characteristics in temperate agroecosystems are likely applicable to tropical systems as well. In contrast, factors such as microbial biodiversity and seasonal fluctuation in environmental conditions can differ dramatically between temperate and tropical systems. Therefore, we discuss literature that can be generalized to tropical systems. Where temperate and tropical systems are likely to differ we synthesize the literature specifically for tropical agroecosystems. We also provide hypotheses to stimulate future work on latitudinal gradients and the relative importance of biotic and abiotic factors in governing entomopathogen prevalence and community composition. These hypotheses provide a path forward to developing theory guiding the conservation and augmentation of entomopathogenic fungi to prevent pest outbreaks.

**Keywords: *Beauveria bassiana*, *Metarhizium anisopliae*, biological control, biopesticide, IPM, entomopathogenic fungi**

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**Edited by:**
*Kris A. G. Wyckhuys,*
*Chinese Academy of Agricultural Sciences, China*

**Reviewed by:**
*Maria L. Pappas,*
*Democritus University of Thrace, Greece*
*Ibtissem Ben Fekih,*
*Fujian Agriculture and Forestry University, China*
*Mark Goettel,*
*Retired, Lethbridge, Canada*

***Correspondence:**
*Tobin D. Northfield*
*tnorthfield@wsu.edu*

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## INTRODUCTION

Growing insecticide resistance and impacts on human and environmental health have encouraged entomopathogenic fungi (EPF) use for biocontrol (Inglis et al., 2001). Tropical environments support impressive microbial biodiversity (Thompson et al., 2017), including many parasites of arthropods (Mahe et al., 2017). However, by far the most common commercially available EPF in tropical and subtropical agroecosystems belong to two genera: *Beauveria* and *Metarhizium* (Ascomycota: Hypocreales) (Faria and Wraight, 2007; Li et al., 2010; Kumar et al., 2018; Mascarin et al., 2019). Here, we review literature focused on controlling arthropod pests with entomopathogens, with particular emphasis on these two genera.

*Metarhizium* and *Beauveria* have pan-global distributions revealing significant genetic diversification, with a wide insect host range and vast ecological niches (Driver et al., 2000; Rehner and Buckley, 2005; Zimmermann, 2007). Thus, many aspects of using these EPF to control pests span latitudinal gradients, and we discuss these generally. Environmental conditions and species compositions, however, can differ greatly between tropical and temperate regions, so we discuss these factors with specific reference to tropical studies and use general theory resulting from model systems to bridge gaps in the current literature and stimulate further studies.

EPF are generally formulated as biopesticides and applied in response to outbreaks. However, if the habitat is well-suited for the particular fungal strain to the environment it may be possible for fungal applications to serve as inoculative releases, where the EPF remain in the soil and prevent insect outbreaks. Here, we describe entomopathogenic fungal niche preferences to help inform EPF use to prevent pest outbreaks. We focus on two species *Beauveria bassiana* and *Metarhizium anisopliae*, but each most likely represents a broader range of species and strains that were previously grouped together. Therefore, the majority of cited papers regarding these fungal species refer to *Beauveria bassiana* and *Metarhizium anisopliae sensu lato*, due to recent taxonomic revisions (e.g., Driver et al., 2000; Bidochka et al., 2001; Inglis et al., 2019).

## *BEAUVERIA* AND *METARHIZIUM*

Entomopathogenic fungal species, *B. bassiana* and *M. anisopliae* control a wide range of pests (Kassa et al., 2004; Castrillo et al., 2010; Migiro et al., 2010; Singha et al., 2010; Skinner et al., 2012; Akmal et al., 2013; Wraight et al., 2016). These fungi can also inhabit the leaf surface of variety of plant species and environments (Meyling and Eilenberg, 2006a; Garrido-Jurado et al., 2015), inhabit soil as saprophytes (Evans, 1982), or grow endophytically (Greenfield et al., 2016). The apparently wide distribution and diversity of pathogen hosts attacked by these fungi, and persistence in the environment when hosts are rare suggest potential value in integrated pest management programs across diverse locations and conditions (Lacey et al., 2015).

Fungal propagule persistence and efficacy on plants is directly influenced by temperature, humidity, sunlight, and microbial activity on the phylloplane (Jaronski, 2010). Much of our knowledge comes from *in vitro* studies (Fargues et al., 1997; Luz and Fargues, 1997; Fargues and Luz, 2000; Devi et al., 2005; Shin et al., 2017). However, it is unclear whether *in vitro* data be extrapolated to field conditions (Keyser et al., 2017), due to environmental influence on processes such as infection potential, conidial persistence and complex abiotic and biotic interactions that are rarely duplicated in laboratory environments (Inglis et al., 2001; Lacey et al., 2015).

*Metarhizium* and *Beauveria* readily colonize plant rhizospheres, forming endophytic associations (Vega et al., 2009; Behie et al., 2015). *Beauveria* species associate with several tropical or subtropical plant species, including cocoa (Posada and Vega, 2005), banana (Akello et al., 2008), and coffee (Vega, 2008). Post-endophytic colonization, *Metarhizium robertsii* can even transfer insect-derived nitrogen to plants (Behie et al., 2012). *Beauveria* and *Metarhizium's* plant host affiliations in agriculture and ecosystem services (i.e., beneficial symbiosis in plants and control of insect pest populations) make them promising candidates for their application as biopesticides in tropical agriculture. The use of EPF as biopesticides in a variety of agroecosystems provides exciting and sustainable farm management opportunities, but in depth knowledge of endemic fungal species is crucial to identifying scenarios and environments when the insect pathogen will be most effective (Meyling and Eilenberg, 2007; Meyling et al., 2009; Perez-Gonzalez et al., 2014).

## LIFE IN THE SOIL

Soil can act as a reservoir for fungal inoculates (Castrillo et al., 2010), dispersing above-ground by wind, rain-splash and insect activity, or via infection of soil-dwelling insects and radial hyphal growth (Meyling and Eilenberg, 2007). Hypocrealean fungi efficacy and persistence is influenced by soil type, moisture levels, and microbial interactions (Inglis et al., 2001). While tropical soils may contain very high organic matter and microbial diversity, the agricultural levels for each depend primarily on farm management practices (Moeskops et al., 2010; Bai et al., 2018), and texture varies widely amongst tropical soils without clear distinctions from temperate systems (Pulla et al., 2016). Therefore, temperate studies describing soil physical characteristics effects on EPF persistence and efficacy are likely directly applicable to tropical systems.

Soils high in organic matter often teem with microbes, potentially allowing antagonistic interactions between microbes (Inglis et al., 1998; Pal and Gardener, 2006). In temperate studies, antagonistic effects of increased microbial activity in the soil contributed to the inhibition of *B. bassiana* (Studdert and Kaya, 1990; Kessler et al., 2003; Quesada-Moraga et al., 2007), *B. brongniartii* (Kessler et al., 2004), and *M. anisopliae* (Jabbour and Barbercheck, 2009). For example, high soil moisture content promoted occurrence of antagonistic organisms, suggesting soil moisture could either directly or indirectly reduce conidia survival (Lingg and Donaldson, 1981; Jabbour and Barbercheck, 2009). However, this has been refuted by other studies in temperate regions finding little or no relationship between soil moisture and EPF occurrence, potentially due to limited variation in sampled soil moisture levels or oxygen deficiency (Griffin, 1963; Ali-Shtayeh et al., 2003; Kessler et al., 2003).

Soil oxygen levels during infection can promote mycelial growth, thermal tolerance, germination, and virulence against insects (Garza-López et al., 2012; Miranda-Hernández et al., 2014; Garcia-Ortiz et al., 2015; García-Ortiz et al., 2018; Oliveira and Rangel, 2018). *In vitro* studies reveal a positive correlation between enriched oxygen concentrations (26 and 30% $O_2$) and conidial quality when compared to normal atmospheric oxygen levels (21% $O_2$) (Miranda-Hernández et al., 2014; Garcia-Ortiz et al., 2015; García-Ortiz et al., 2018). Similarly, at deprived oxygen levels, the same contrast in conidia growth and virulence applies, reducing under ambient oxygen concentrations (Garza-López et al., 2012; Oliveira and Rangel, 2018). Germination under hypoxic conditions is lower than at normal atmospheric levels (Garza-López et al., 2012), increasing as oxygen conditions become enriched (Miranda-Hernández et al., 2014). Thus, aerating soil during mycelial growth may facilitate optimal entomopathogenic fungal development and pest control.

Soil texture influences fungal propagule transmission and retention. Increasing clay content can promote entomopathogenic fungal persistence, likely due to smaller pore size and/or the adsorption of conidia to clay and organic particles (Ignoffo et al., 1977; Storey and Gardner, 1988; Quesada-Moraga et al., 2007). However, high clay content can also inhibit the ability of a potential host to encounter another, due to reduced porosity for conidial penetration to deeper soil layers and potential transmission (Vänninen et al., 2000; Fuxa and Richter, 2004). Therefore, mechanical filtration of the soil structure can be a major determinant of entomopathogenic fungal persistence and effectiveness when applied to soil (Storey and Gardner, 1988). For example, the efficacy of *B. bassiana* against the red fire ants *Solenopsis invicta* improved when applied to wetter soils, promoting conidia transmission and infection rates (Fuxa and Richter, 2004).

# NICHE PREFERENCE

## The Habitat Selection Hypothesis

Biotic interactions may alter tropical EPF persistence (Jaronski, 2010), particularly The habitat selection hypothesis for *Metarhizium* species suggests this is a key difference between temperate and tropical regions (Bidochka et al., 2002). Bidochka and Small (2005) suggested *Metarhizium* genotypes are associated with habitat types in temperate and polar regions and are more likely associated with certain host insects in (sub)tropical regions. The authors also suggested *M. anisopliae* originated in Southeast Asia but now comprises an assemblage of cryptic species, many of which traverse large geographical barriers. Temperate studies regarding *Beauveria* and *Metarhizium* have highlighted their preference for habitat selection over associations with insect hosts (Meyling and Eilenberg, 2006b; Meyling et al., 2009; Ormond et al., 2010). Any insect host associations of *M. anisopliae* at higher latitudes were attributed to the insect's habitat, suggesting that abiotic factors could potentially be driving the population genetic structure (Bidochka et al., 2001).

Takatsuka (2007) characterized *Beauveria* isolates from Japan using ISSR-PCR and found no evidence for long-term coevolution between the fungus and insect hosts, supporting the Bidochka et al. (2002) hypothesis that variation in persistence of the free-living, saprophytic stage of a facultative insect pathogen drives population genetic structure. In contrast, Bridge et al. (1997) suggested coevolution between tropical *M. flavoviride var. minus* isolates of a single genotype and those insects belonging to the superfamily *Acridoidea*. Tropical isolates of *M. flavoviride var. minus* with host-preference traits differed from those with a European derivation. Interestingly, the majority of isolates in the publications supporting the Bidochka and Small (2005) hypothesis regarding the association of *Metarhizium* spp. with insect host species have a tropical origin (Rombach et al., 1986; St. Leger et al., 1992; Bridge et al., 1993, 1997; Leal et al., 1994; Tigano-Milani et al., 1995). However, future analyses are needed to define these relationships.

*Metarhizium* strains have adapted to particular environments, supporting versatile life-history strategies (Lovett and St. Leger, 2015). Adjustments in environmental stress responses can arise from adaptation to environmental abiotic (e.g., temperature, UV radiation, and humidity) and biotic factors relating to infection of a host (e.g., antimicrobial and behavioral stressors) (Lovett and St. Leger, 2015; Ortiz-Urquiza and Keyhani, 2015). Conidia produced under abiotic and biotic stress can withstand a broader environmental range, and improve virulence against insects (Li et al., 2015; Rangel et al., 2015). For example, overcoming acridid host behavioral fevers during infection can produce more thermotolerant entomopathogenic fungal isolates (Fargues et al., 1997; Blanford and Thomas, 2000; Rangel et al., 2005). Behavioral defensive traits in grasshoppers can result in discrepancies between entomopathogenic fungal species and their effectiveness in controlling pest populations at different temperatures (Inglis et al., 1999). Grasshopper nymphs infected with *B. bassiana* and *M. acridum* experienced reduced levels of mortality when temperature was increased, and *M. acridum* substantially outcompeted *B. bassiana* in nymphal mortality at higher temperatures (Inglis et al., 1999).

From the evidence primarily presented for Metarhizium we propose two general hypotheses for EPF: (i) Abiotic factors are primary determinants of population genetic structure at higher latitudes, due to the insect pathogen's requirement to adapt seasonality and extreme environmental conditions. (ii) Conversely, biotic factors (interactions with other species and fungal-host associated infection pathways) are the primary regulators of EPF population genetic structure in lower latitudes. We evaluate these hypotheses in light of recent research below. To visually present our hypotheses, we constructed a conceptual model (**Figure 1**). This is meant to qualitatively describe our hypotheses to stimulate future research, rather than stand alone as a mathematical model.

## Abiotic Conditions and Adaptation

Fungi inhabiting higher latitudes experience a wider range of temperatures due to seasonality (Wielgolaski and Inouye, 2003). Thus, abiotic stressors (particularly temperature) at higher latitudes may predominantly drive population genetics and adaptability of EPF. In temperate regions, EPF must adapt to a broad range and greater levels of climatic intensities (Maggi et al., 2013; Wang et al., 2017), whereby abiotic factors primarily influence generalist pathogen's survival (Bidochka et al., 2001; Lennon et al., 2012). In contrast, we hypothesize that low latitude biotic factors such as species richness and pathogen-insect associations that drive coevolutionary arms races predominately influence EPF life history. Phylogenetic *B. bassiana* cluster by habitat type more at seasonally variable high latitudes (Ormond et al., 2010), although one study found no seasonal effect in regions of sub-tropical climates (Garrido-Jurado et al., 2015). Phylogenetically structured investigations suggest *B. bassiana* adapts gene regulation to environmental conditions, with habitat adaptation driving population dynamics (Bidochka et al., 2002; Xiao et al., 2012). Thus, differences in the magnitude of seasonal environmental conditions at different latitudes may contribute to

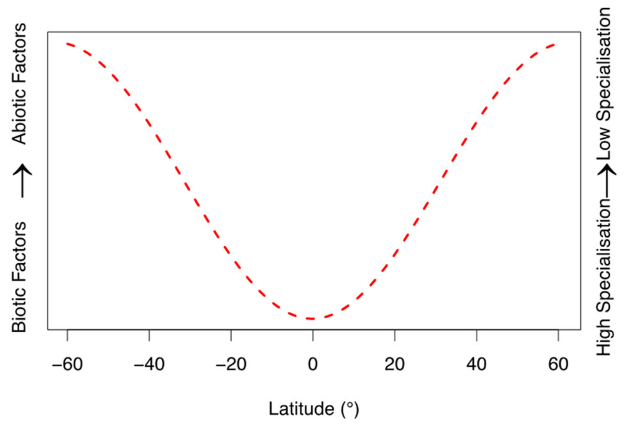

**FIGURE 1 |** Qualitative conceptual model based of our reviews developed hypotheses. Specificity of fungal entomopathogenic communities' changes with latitude, corresponding to biotic and abiotic factors. Biotic factors are related to interactions with the host and other microbes (i.e., coevolutionary arms races and infection pathways). Abiotic factors include environmental variables such as temperature, humidity, UV radiation, and oxidative and osmotic stressors. The latitudinal range was capped at 60°N and 60°S, as this figure does not account for the climatic extremes beyond these thresholds on fungal communities. We hypothesize that at lower latitudes entomopathogenic fungi inhabit more ideal environmental conditions, despite increased pressure from other fungal species, and greater host defense (see "Abiotic conditions and adaptation" and "Biotic interactions and adaptation" sections of main text for more information). This corresponds to an increase in specialization of entomopathogenic fungi.

the observed temporal dissimilarities in *B. bassiana* population dynamics between the studies.

Environmental conditions near entomopathogenic fungal survival limits can drive local adaptation when these limits are regularly experienced (Doberski, 1981; Vidal et al., 1997). The optimal temperature for growth and virulence against insect hosts of *Metarhizium* and *Beauveria* species is generally between 25 and 30°C (Luz and Fargues, 1997; Ekesi et al., 1999; Devi et al., 2005; Bugeme et al., 2009). However, significant variation exists in a fungal pathogen species' thermal preference and their effects on potential hosts, due to the environment in which the pathogens evolved (Fargues et al., 1997; Bugeme et al., 2009; Alali et al., 2019), and individual strains can differ in their thermal optima (Doberski, 1981; Thomas and Jenkins, 1997; Alali et al., 2019). *M. acridum* isolates obtained from a hot environment exhibited greater performance at higher temperatures than those derived from a much cooler climate (Thomas and Jenkins, 1997). Similarly, sub-tropical *B. bassiana* strains collected from hotter areas of Syria demonstrated greater thermotolerant ability than the outlier collected from a site experiencing lower temperatures (Alali et al., 2019). Regarding virulence against insects, temperate isolates of *B. bassiana* were significantly more effective against the elm bark beetle (*Scolytus scolytus* F.) at low temperatures (2 to 6°C) than isolates of *M. anisopliae* originating from tropical and sub-tropical latitudes (Doberski, 1981), although it is impossible to separate fungal species differences from differences arising from the geographical sources of the two fungal strains. *B. bassiana* and *M. anisopliae* are also sensitive to ultraviolet radiation, prompting UV protectant use in oil-based field sprays (Inglis et al., 1995; Shin et al., 2017; Kumar et al., 2018). UV tolerance often varies among isolates from different latitudes (Braga et al., 2001; Fernandes et al., 2008), and habitat types (Bidochka et al., 2001). Isolates of *B. bassiana* and *M. anisopliae* closer to the equator exhibit higher UV tolerance, and cold-adapted populations from higher latitudes generally experience optimal conditions in colder temperatures (Fernandes et al., 2008). In Canada *Metarhizium* isolates encountered in forested habitats are less tolerant to UV radiation and are more cold-active compared to agricultural landscapes (Bidochka et al., 2001). Thus, abiotic selection at high latitudes (e.g., UV exposure in a given habitat type) for specific genetic groups of fungal entomopathogens could influence their effectiveness in agriculture, particularly if isolates are sourced from forested or hedgerow habitats.

## Biotic Interactions and Adaptation

Tropical forests support high entomopathogenic mycotaxa diversity, where the teleomorphs (sexual stages) of hypocrealean fungi are mostly found and are often more specialized in their host range than asexual morphotypes (Evans, 1982; Vega et al., 2012; Hu et al., 2014). In contrast, asexually developing EPF (anamorphs) inhabit both tropical and temperate climates (Vega et al., 2012). Lab studies in model systems that increased biodiversity observed corresponding intensification of evolutionary arms races between hosts and parasites (Betts et al., 2018). Similarly, genetic diversity and host specificity of some fungal species suggests that host insects can exert strong selective pressures on pathogens through a cascade of defense and counter-defense mechanisms (Maurer et al., 1997; Evans et al., 2011; Mukherjee and Vilcinskas, 2018). For example, *Metarhizium* often evolved from specialist to generalist insect pathogens; an expansion in host range coinciding with fungal occupation of an expanding latitudinal range (Bidochka and Small, 2005; Hu et al., 2014). However, in high species-density rainforest areas, high fungal tropical diversity may experience stronger pressure from hosts and competitors that can favor the occurrence of pathogens such as the teleomorph genus *Cordyceps* (Evans, 1982; Sung et al., 2007; Aung et al., 2008), and specialist fungal entomopathogens of the genus *Ophiocordyceps* (Aung et al., 2008; Evans et al., 2011; Araújo et al., 2015). Phylogenomic analyses suggest *Beauveria* spp. is the asexual life stage of the *Cordyceps* lineage (Xiao et al., 2012). Despite *Beauveria* having direct genetic links to *Cordyceps*, generalist *Beauveria* and *Metarhizium* are less common within tropical rainforest habitats, and are more frequently encountered in agriculture (Rehner, 2005; Aung et al., 2008). The contrast in life-histories between these specialists and generalist fungi could be attributed to the loss of the repeat-induced point mutations in *B. bassiana* and *Metarhizium* spp. (infers the sexual cycle to be rare in both fungi), which was a prerequisite of these fungal pathogens for the expansion of gene families (Xiao et al., 2012; Lovett and St. Leger, 2017).

Given the probable southeast Asian origin of *Metarhizium* (the continent with the highest genotypic diversity) (Bidochka and Small, 2005; Lovett and St. Leger, 2017), and the subsequent evolutionary changes in specificity (Hu et al., 2014), a geographical range expansion to temperate regions may have corresponded to a more generalist host range. We hypothesize that this could be due in part to lower host species richness in temperate regions (Thompson et al., 2017), and a need to adapt to greater variation in climatic conditions focusing adaptation on abiotic conditions. A remaining question is how greater potential host diversity in tropical environments alters these selection pressures. Future research into how insect-pathogen arms races alter community composition with changes in latitude would improve management of entomopathogens in different latitudes. Additionally, empirical evaluations of fungi collected at different latitudes and laboratory experiments will improve our knowledge of endemic fungal species and their relevance within a particular system, alongside their appropriate use in biocontrol regimes.

## IMPROVING FUNGAL PERSISTENCE AND INSECT OUTBREAK PREVENTION

The ability of some fungal species to cross large geographical barriers (i.e., cosmopolitan in nature) does not imply that the application of fungal pathogens as an agricultural biopesticide will ensure fungal persistence. Rather, researching the appropriateness of a fungal pathogen specific to the target environment is required, including interactive effects of individual biotic/abiotic factors. Efforts should be directed toward focusing on endemic fungal communities and applied within its derived system. Regional differences between suitable fungal application type, host range (i.e., generalist vs. specialist) and the dominant environmental factors (biotic/abiotic) on pathogen performance can better predict the long-term success of entomopathogenic biocontrol and help prevent insect outbreaks.

## AUTHOR CONTRIBUTIONS

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# Effects of Field and Landscape Scale Habitat on Insect and Bird Damage to Sunflowers

**Sara M. Kross [1,2,3]*, Breanna L. Martinico [2], Ryan P. Bourbour [2], Jason M. Townsend [2,4], Chris McColl [3] and T. Rodd Kelsey [3]**

*[1] Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, United States, [2] Department of Wildlife, Fish and Conservation Biology, University of California, Davis, Davis, CA, United States, [3] The Nature Conservancy, Sacramento, CA, United States, [4] Department of Environmental Studies, Hamilton College, Clinton, NY, United States*

Agriculture-dominated landscapes harbor significantly diminished biodiversity. Woody vegetation along field margins can provide farmers with ecosystem services and benefit biodiversity. However, when crops are damaged by the biodiversity harbored in such vegetation, farmers are reluctant to incorporate field margin habitat onto their land and may even actively remove such habitats. We investigated how damage by both insect pests (sunflower moth, *Homoeosoma electellum*) and avian pests to sunflower (*Helianthus annuus*) seed crops varied as a function of field-margin and landscape-scale habitat, as well as by bird abundance and diversity. Surveys for insect damage, avian abundance, and bird damage were carried out over 2 years in 30 different fields. The mean percentage of moth-damaged sunflowers sampled was nearly four times higher in fields that had bare or weedy margins (23.5%; $877/ha) compared to fields with woody vegetation (5.9%; $220/ha) and was positively associated with landscape-scale habitat complexity. Birds damaged significantly fewer sunflower seeds (2.7%) than insects, and bird damage was not affected by field margin habitat type, landscape-scale habitat variables, or avian abundance, but was significantly higher along field edges compared to $\geq$ 50 m from the field edge. Avian species richness nearly doubled in fields with woody margin habitat compared to fields with bare/weedy margins in both the breeding season and in fall. These results indicate that the benefits of planting or retaining woody vegetation along sunflower field margins could outweigh the ecosystem disservices related to bird damage, while simultaneously increasing the biodiversity value of intensively farmed agricultural landscapes.

**Keywords: agroecology, crop damage, ecosystem services, farm, hedgerow, integrated pest management, pest control, landscape**

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*David Gonthier,*
*University Press of Kentucky,*
*United States*

**Reviewed by:**
*Alistair John Campbell,*
*Embrapa Amazônia Oriental, Brazil*
*Liming Ye,*
*Ghent University, Belgium*

***Correspondence:**
*Sara M. Kross*
*smk2258@columbia.edu*

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## INTRODUCTION

In the face of significant losses of both diversity and abundance of avian species (Rosenberg et al., 2019), farming agroecosystems represent a critical frontline for improving vast tracts of land for the conservation of biodiversity beyond the reserve system (Kremen and Merenlender, 2018; Grass et al., 2019). Establishing and protecting agroecosystems that harness functional diversity to provide ecosystem services at the farm and landscape level may simultaneously decrease chemical inputs and increase biodiversity (Daily et al., 2000; Bommarco et al., 2013; Weier et al., 2018; Kleijn et al., 2019). For example, establishing or maintaining strips of woody vegetation along field margins can increase the diversity, abundance, and corresponding ecosystem services of pollinators (Garibaldi et al., 2011; Sardiñas et al., 2016; M'Gonigle et al., 2015), arthropod predators (Eilers and Klein, 2009; Gareau et al., 2013), and birds (Heath et al., 2017; Gonthier et al., 2019). Likewise, higher amounts of natural habitat within agricultural landscapes (landscape-level complexity) can also increase biodiversity and associated ecosystem services (Chaplin-Kramer et al., 2011; Klein et al., 2012; Karp et al., 2018; Gonthier et al., 2019).

Increasing structural complexity within the working agricultural landscape can enhance the conservation value of larger tracts of protected land situated on the periphery of agricultural lands (Heath et al., 2017; Kremen and Merenlender, 2018). By integrating habitat complexity into agricultural landscapes, dispersal corridors, access to food sources, and greater genetic connectivity may occur across a wide diversity of taxa (Isbell et al., 2017). Such changes to the agricultural landscape could therefore have dual benefits for both landscape-scale biodiversity (DeClerck et al., 2010) and on-farm sustainability in the form of ecosystem services including biological pest control (Mitchell et al., 2013). However, natural habitat in agroecosystems can also harbor pests, which is true for avian pests of many seed and fruit crops worldwide (De Grazio, 1978; Gebhardt et al., 2011; Kross et al., 2012; Schäckermann et al., 2014). Farmers that perceive birds as detrimental to their crops will take action to deter birds (Kross et al., 2018), often by removing field margin habitat (Gennet et al., 2013) or utilizing commercially available bird deterrents such as gas guns, reflective tape, or netting (Baldwin et al., 2013), all of which can be costly for both farmers and non-target wildlife. Bird depredation of crops therefore not only has direct economic implications for growers, but can lead farmers to oppose conservation programs within agricultural communities and on their own properties (Kross et al., 2018).

Farmers are the primary decision makers for land management choices within agricultural regions, and their decisions, including those related to implementation of integrated pest management (IPM), are mostly based on direct economic returns (Kleijn et al., 2019). Ecosystem services, when enhanced by integrating habitat complexity into the working agricultural landscape, can serve as a part of IPM and contribute to a more sustainable and holistic preventative pest management paradigm (Stenberg, 2017). However, the effects of natural vegetation on biological control are complex and can vary with crop type, seasonality, farm management, and the demographic effects of interactions between natural enemies and pests (Karp et al., 2018; Settele and Settle, 2018). There is a strong need to provide clear, balanced empirical information to better inform habitat-modification based IPM strategies on the working, farm-scale level. This goal can be confused at times when, for example, studies into the detrimental behaviors of birds rarely focus on potentially beneficial impacts, and similarly, studies into beneficial pest-control services from birds rarely focus on damage that the same species may cause to crops (Pejchar et al., 2018; but see a few recent exceptions: Peisley et al., 2016; Gonthier et al., 2019). Therefore, disentangling the relationships between landscape- and field-level habitat complexity and crop damage from insect and avian pests has critical implications for both habitat management and preventative pest management in agroecosystems.

In California, one of the world's most productive and intensive farming regions, <4% of potential field margins have been planted with woody vegetation such as hedgerows (Brodt et al., 2009); field margins therefore have significant potential for increasing the biodiversity conservation value of California's working agricultural landscape. However, farmer surveys in California showed that major obstacles to hedgerow implementation included uncertainty around the potential ecosystem service benefits of hedgerows, along with concern that these hedgerows could harbor plant, insect, and vertebrate pests (Brodt et al., 2009). Research to provide empirical documentation of the costs and benefits of planting (and in some cases, retaining) such habitats is therefore critical to inform land management decisions.

Avian species and their abundance and diversity relationships to landscape structure can, in particular, create a still-unresolved conundrum in the analysis of costs and benefits to farmers (Pejchar et al., 2018). Local- and landscape-scale habitat influences both pests and their potential predators at varying scales and effect sizes (Karp et al., 2018). At the same time, some species of birds can provide ecosystem services, in the form of insect pest control, during the breeding season, and then can become major pests of the same crops when they switch to a more omnivorous diet in the fall (**Figure 1**).

In the present study, we analyzed the potentially conflicting roles of avian species within the unique sunflower (*Helianthus annuus*) seed growing region of California's Central Valley. We investigated the effects of both field-margin and landscape-scale habitat complexity on the occurrence of (1) potential benefits to farmers in the form of (A) avian insectivory leading to reduced occurrence of major invertebrate pests of sunflower seeds; and also (2) of potential costs to farmers in the form of (B) insect damage to sunflower seeds, and (C) bird damage to sunflower seeds.

## MATERIALS AND METHODS

### Study Area and Crop

California's Central Valley is one of the most productive agricultural landscapes in the world, producing over 25% of the fresh produce consumed in the United States (USDA 2015), and valued at over $45 billion (USD) per year. Over 95% of the Central Valley's riparian and wetland ecosystems have been replaced by highly intensive agriculture and urban development (Katibah, 1984; Frayer et al., 1989), with remnant native habitat existing only in fragmented and isolated patches. Nevertheless, some native biodiversity in this region persists despite the highly human-modified landscape (Heath et al., 2017).

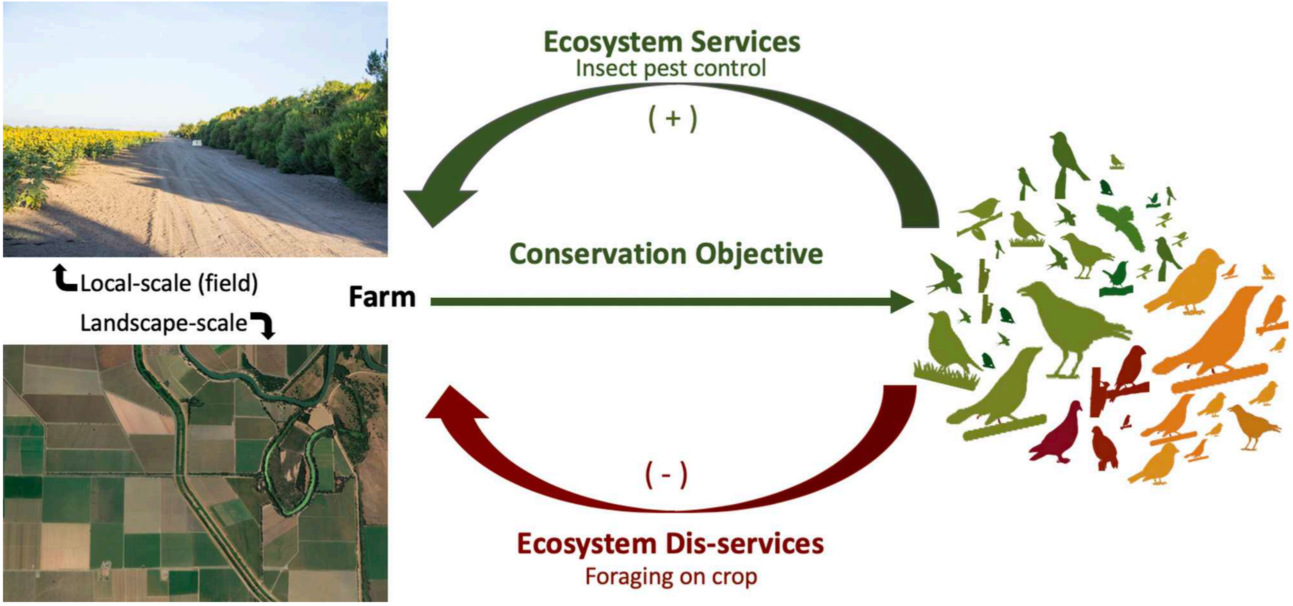

**FIGURE 1 |** A conceptual framework for the potential effects of landscape- and local-scale habitat complexity on avian diversity (represented by bird silhouettes), and potential benefits (ecosystem services in the form of insect pest control) or costs (ecosystem disservices in the form of bird damage to crops), which can also vary with seasonality and diet, that affect yields for farmers.

Each year, sunflower is grown for hybrid seed production on an average of 20,234 ha (50,000 acres) across California's Sacramento Valley, producing over 31,750 tons, valued at ∼\$70 million/year (Long et al., 2019). California's Central Valley produces over 95% of the United States' hybrid sunflower seeds, and over 25% of global sunflower seeds (Long et al., 2019). Sunflowers grown for seed are valued 5–10 times higher than the commercial oil crops for which they are used (Long et al., 2019), and growers therefore have a low threshold for damage. All sunflower fields in our study were grown for the same seed company and therefore were grown using the same standard sunflower production field-management practices (Long et al., 2019). This study was conducted within conventional fields (i.e., non-organic fields), but no growers reported utilizing insecticides on their fields over the duration of this study.

The sunflower moth (*Homoeosoma electellum*) is a major pest of sunflowers in North America and is the predominant insect pest of the crop in California (Long et al., 2019). Female sunflower moths lay eggs among the florets of sunflowers in early bloom, and eggs take 2–5 days to hatch. After hatching, larvae remain on the face of flowers for 8 days before boring into the developing seeds where they can cause losses of 30–60% of a crop (Long et al., 2019). Birds are the predominant vertebrate pest of sunflower crops around the world (De Grazio, 1978; Schäckermann et al., 2014; Ernst et al., 2019; Long et al., 2019). In North America, and in our study area, Icterid birds and the non-native European starling (*Sturnus vulgaris)* cause the most damage to sunflowers because of their omnivorous diets and behavior of foraging in large flocks. In Israel, bird damage to sunflowers is often concentrated to the edges nearest to habitat (specifically, large trees) that can act as shelter for birds, and can also be affected by landscape-scale habitat (Schäckermann et al., 2014), however flocking birds often cause damage within the interior of fields as well (e.g., European starlings in New Zealand vineyards; Kross et al., 2012).

## Habitat Complexity

### Local-Scale Habitat Complexity

The presence or absence of woody habitat along field margins has been demonstrated to affect avian diversity and abundance in our study area (Heath et al., 2017), and at the time of our study the effects of habitat on sunflower moth damage was not described. To quantify the influence of habitat complexity on the bird community and sunflower damage, we included fields with woody margin habitat ($n = 6$ in 2014 and $n = 12$ in 2015) and fields with bare or weedy field margins in ($n = 7$ 2014 and $n = 5$ in 2015), for a total of 30 fields (**Figure 2**). To quantify local (field) habitat complexity, at 5 evenly spaced locations along each 200-m long field margin transect (used for bird counts, see 2.6 below), we collected data on the maximum height of vegetation within 10 m of the of the transect, we estimated the number of canopy layers (out of a possible 7 predetermined canopy layers), and used satellite imagery to measure the width of field margin vegetation perpendicular to the focal field (see Heath et al., 2017 for details).

Because the variables describing field margin habitat (height, width, and number of vegetation layers) were highly correlated, we used a Principle Components Analysis (PCA) to reduce these into two orthogonal axes that explained over 95.5% of the variance among them. The two axes, PC1 and PC2, were included as predictor variables in our candidate models for sunflower damage and for bird abundance and richness. PC1

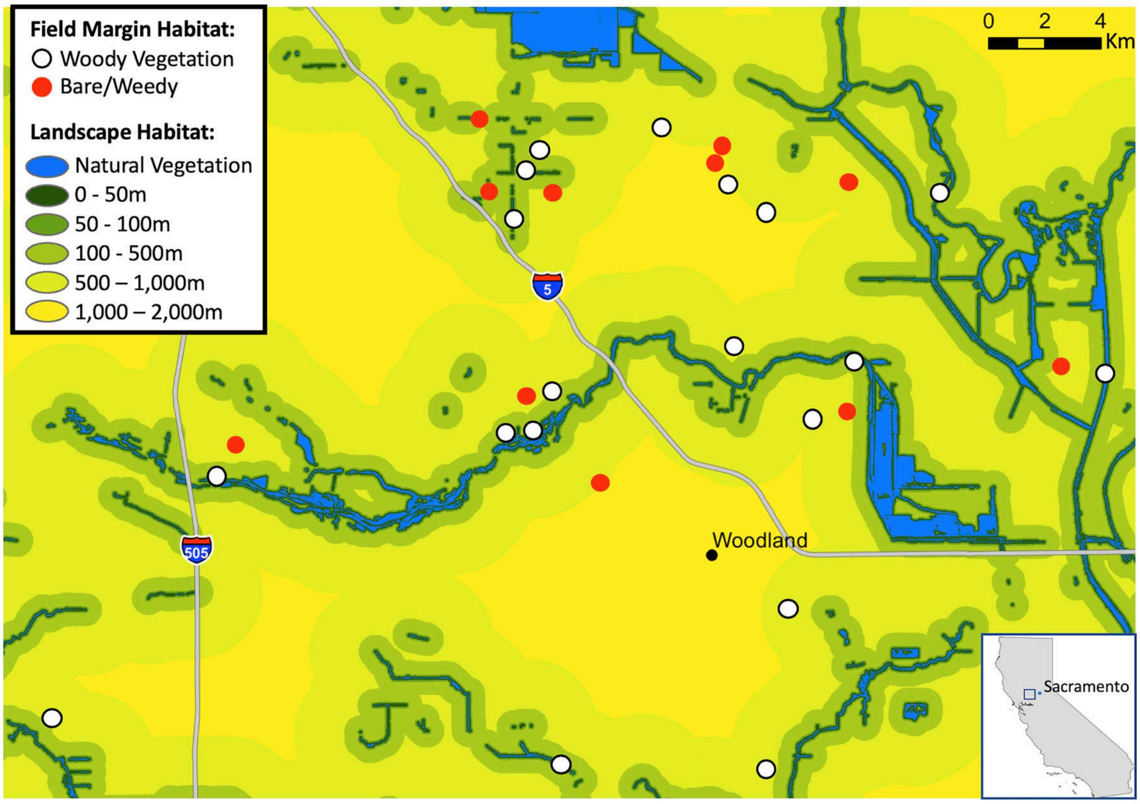

**FIGURE 2 |** Map showing sunflower field locations at varying distances from natural habitat (blue) across an intensive agriculture landscape. Sunflower fields had either bare/weedy field margin habitat (red points), or had woody vegetation field margin habitat (white points).

explained 86.2% of the variability among habitat variables and was negatively associated with all three variables, whereas PC2 was positively associated with habitat width and height, and negatively associated with habitat layers. Therefore, if PC1 is a positive predictor of damage, we would expect less damage at sites with habitat that is taller, wider and has more layers (because of the inverse relationship). If PC2 is a positive predictor of damage, we would expect less damage at sites with more habitat layers and more damage at sites with taller/wider habitat.

### Landscape-Scale Habitat Complexity

To quantify and incorporate landscape habitat complexity into our study design, we selected fields at varying distances from natural habitat, which in our study area consists mainly of remnant and restored riparian areas (**Figure 2**). We used pre-existing habitat data for our study area (CA DWR, 2008; Geographic Information Center, 2009), and added polygons for any trees within 800 m of each transect that were not included in the existing dataset (e.g., trees lining driveways, trees around homesteads). To calculate the distance to riparian areas, we first created a distance raster that encompassed the entire study area by using the Euclidean distance algorithm in ArcGIS 10.1 (ESRI, 2010). We used the riparian vegetation GIS dataset (habitats classified as native riparian, blue oak woodland, valley foothill riparian, fresh emergent wetland, saline emergent wetland, and valley foothill riparian) as the "source" input for the algorithm and set the output grid cell size to 10 m. Each field's transect center point was then buffered by 50 m, and we calculated the distance from each grid cell within the buffer to the nearest riparian vegetation polygon. The mean distance for all cells within each buffer was calculated as the distance value for each field. We also calculated the mean proportion area consisting of natural habitat at concentric buffer distances of 100, 200, 400, and 800 m, which have been shown to be relevant scales for riparian bird species in the Central Valley (Seavy et al., 2009).

To account for collinearity among landscape-scale habitat complexity variables, we ran separate models using the predictor variables for landscape-scale habitat complexity (either distance to the nearest natural habitat or percent natural cover at varying distances) for both the insect damage (**Table S1**) and the bird damage (**Table S2**) models.

## Vertebrate Exclosures

In 2015, we created exclosures to prevent vertebrates (birds and bats) from accessing sunflowers (see Maas et al., 2019 for a review of exclosure methods). Exclosures consisted of nylon bird netting (No-Knot Bird Netting ¾ polypropylene mesh, Bird B Gone Inc®, Irvine, CA) draped over an area 4 sunflowers in width and ∼20 flowers in length (for a total of ∼80 plants) and secured to cover the tops of the flowers to a height of ∼2–4 feet above the ground. Birds were never observed inside our exclosures. Exclosures were installed in late spring, prior to the onset of bloom (which is when sunflower moth typically lay eggs on the flowers), and were checked and maintained over the entire growing season until final damage estimates were made in August-September. We set up four exclosures in each field, with the closest end of each exclosure located 5, 10, 50, and 100 m from the edge of the field. Due to last minute changes in the harvest schedule at some fields, we were able to collect damage data from the exclosures at nine different fields.

## Sunflower Damage

We sampled from 10 sunflowers at distances from 0 to 200 m from the field edge. In 2014, we collected observations of both insect and bird damage from each site at 0, 10, 20, 30, 40, 50, 75, 100, 150, and 200 m from the field edge. In 2015, we collected observations from each site at 5, 10, 50, and 100 m from the field edge because we found in 2014 that bird damage dropped to close to 0 at distances beyond 50 m (see **Figure 3C**), and that insect damage was largely unchanged by distance from the field edge. Estimates for insect and bird damage in 2015 were taken from sunflowers within exclosures and from sunflowers that were ∼10 m from the exclosures (parallel to the field margin), but only data from non-enclosed sunflowers was used in our comparative analysis of insect damage.

We quantified both bird and insect damage by visually inspecting 10 sunflowers within each sampling area. Sunflowers were chosen by reaching out to select a plant stalk, so the seed-bearing area of each plant was not seen until after the plant was selected. Observers moved a few steps along and between rows to select each new flower. Bird damage was characterized by missing seeds. We were careful to avoid classifying wind-damaged seeds as bird damage. These seeds were generally removed from larger continuous areas of the sunflower head, whereas seeds removed by birds were in patchy sections or removed singularly. Insect damage was characterized by an area of visible frass (insect excrement and webbing) on the surface of multiple sunflower seeds. Seeds under the frass were often shrunken or visibly damaged. All areas that were under frass were classified as insect-damaged.

To estimate the percent of seeds on each sunflower that were damaged, we used a pre-cut circular piece of galvanized steel chicken-wire that was marked to allow for easy measurement of the flowers. Sunflower heads were classified into different size classes based on the diameter (to the nearest 1.3 cm, or 0.5 inches) of the seed-bearing area on each plant. We then estimated the number of hexagons on the wire (to the nearest ¼ hexagon) that was damaged by birds or damaged by insects on each sunflower head. Using the flower circumference and the known area within each hexagon of our grid, we were then able to calculate the percent of each sunflower head that was damaged by birds, and the total that was damaged by insects. For each sampling location, we aggregated the data from the 10 flowers for a single mean for percent damage. To estimate yield, damage from insects and damage from birds were summed for a total percent damage to each sunflower, since both types of damage result in a direct loss of yield for growers.

## Economic Estimates

We used published data on mean sunflower yields and economic value for the Sacramento Valley from 2015 to 2018 (Long et al., 2018) to calculate the reduction in gross earnings for farmers as a result of insect and bird damage in response to significant predictor variables. Mean sunflower yields were 1,260 lbs/acre (1,412 kg/ha; range 1,076–1,748 kg/ha) after seed companies cleaned and removed non-viable seeds and non-seed material from field harvests (Long et al., 2018). Seeds were valued at a

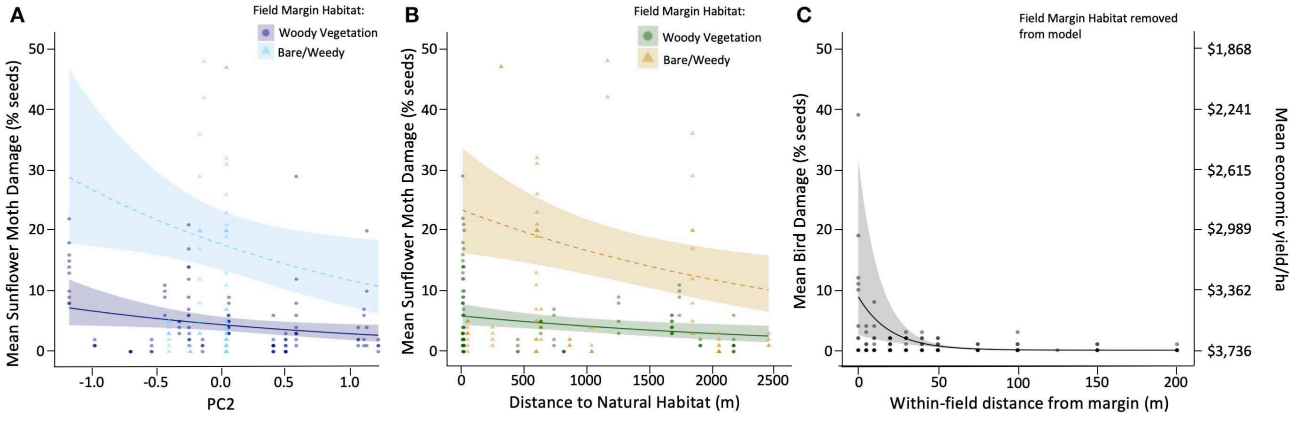

**FIGURE 3 |** Model estimates (and 95% confidence intervals) of percent of sunflower seeds damaged (primary axis) as a function of the presence (darker colored lines) or absence (lighter colored lines) of woody vegetation along field edges and, **(A)** increasing field margin height and width (PC2), **(B)** the distance to the nearest natural habitats; and **(C)** percent seeds damaged by birds as a function of the distance of sampling points within each field from the nearest field margin. Raw data points are shown, with darker points indicating multiple overlapping points. The secondary axis for economic yield (right side of figure) applies to all 3 panels and shows the mean value (from 2015 to 2018) of sunflower seed crop in the region ($3,736 USD) equivalent to 0% damage, and decreasing as percent damage increases on the primary axis.

mean value of \$1.2/lb [\$0.54/kg; range of \$0.41–0.68/kg (Long et al., 2018)]. We calculated the economic effect size of insect or bird damage by multiplying the scaled effect sizes from our model estimates with these mean values, assuming that yields were valued at \$3,736/ha if they sustained no bird or insect damage.

## Bird Counts

We conducted four bird surveys at each site, two in summer (June 9–July 2) and two in fall (August 5–September 16). All bird surveys were conducted by trained observers and timed to coincide with sunflower bloom in the summer (when sunflower moths typically lay eggs on the flowers), and immediately prior to the seed harvest in the fall. All counts were conducted between dawn and 10 a.m. and were not conducted in very cold (<3 C) or very hot weather (>24 C), in high winds, or in heavy precipitation. Counts were also re-scheduled if there were any farm workers or machinery in our focal field. The order in which fields were visited for counts was randomized within geographical groupings of fields. We conducted two counts per visit at each field: one to quantify the birds utilizing the field margin habitat, and another to quantify the birds utilizing the field interior. To count birds utilizing field margin habitat, observers walked a 200 m transect over 10 min, counting all birds detected by sight or sound within 20 m of the field margin, but not within the field itself. To count birds utilizing the field interior, observers returned to the mid-point of the transect, allowed 5 min for birds to settle, and then conducted a 10-min point count focused only on birds that were observed within the field (a half circle with an ∼200 m radius from our center point). We truncated the detection distance at field margins because margin habitat varied across sites. We assumed that intra-species detectability was the same within all sunflower fields, since sunflowers were at similar levels of maturation and height at the time of our surveys. Sunflowers are a tall (2–3 m) and densely planted crop, so most birds detected within the crop were of individuals flying into or out of fields, or singing/calling within a field.

## Statistical Analyses

For all statistical models, we included as predictor variables in our maximal models the continuous variables for the distance from the nearest natural habitat (or proportion natural cover within concentric distance bands), PC1, PC2, as well as the categorical variable for whether the field had a weedy or bare edge (simple edge habitat) or had woody field margin habitat (complex edge habitat). For insect and bird damage to sunflowers, we also included the distance into the field the sample was collected (as both a linear and quadratic predictor, to account for potentially non-linear effects of distance on insect and bird damage). We simplified the maximal models by removing interactions, then main effects, until no further reduction in residual deviance (measured using Akaike's Information Criterion) was obtained. For all regression analyses, we considered candidate models with $\Delta\mathrm{AIC} \leq 2$ and chose the most parsimonious model. All data was analyzed in R (R Core Team, 2015).

### Avian Consumption of Sunflower Moth

We used a Wilcoxon rank-sum test to compare the total insect damage observed inside exclosures and in adjacent non-exclosure locations.

### Bird and Insect Damage to Sunflowers

Only the data from the non-exclosure sampling locations were used for investigating the effects of habitat variables on sunflower damage. Sunflower moth damage and bird damage were analyzed in separate models. We assessed our data for appropriate model distributions using quantile comparison plots ("qqplot" in Fox and Weisberg, 2019), then the fitdistr function (Venables and Ripley, 2002). We also used likelihood ratio tests to compare the final models to alternative likely distributions. For both insect and bird damage to sunflowers, we used generalized linear models with a negative binomial family of errors ("glm.nb" in MASS package; Venables and Ripley, 2002).

### Seasonal Avian Species Richness and Abundance

We ran eight separate generalized linear regressions with a poisson family of errors for avian species richness and abundance along the field edge and within the field interior for data collected in summer and in fall (**Table S3**).

# RESULTS

## Vertebrate Exclosures

There was no significant difference between sunflower damage from insects inside exclosures (vertebrates excluded; mean = 3.40 ± 0.61% damage) compared to areas outside of exclosures (vertebrates present; mean = 3.08 ± 0.47% damage; $W = 67{,}828$, $p = 0.21$; **Figure S1**).

## Sunflower Damage

Sunflower moth damage was almost four-times higher at sites with bare or weedy field margin habitat (23.46 ± 1.41%) compared to sites with woody vegetation (5.89 ± 1.16%; $z = 7.12$, $p < 0.001$). There was a slight decrease in sunflower moth damage as habitat height and width (PC2) increased ($z = -2.75$, $p = 0.005$; **Figure 3A**). Model selection revealed that the variable for mean distance to natural habitat was the most parsimonious landscape-scale habitat variable in our insect damage models (**Table 1**) and had a significant reduction in damage as distance from natural habitat increased ($z = -2.25$, $p = 0.02$; **Figure 3B**).

The most parsimonious model for bird damage included the proportion of natural habitat within 800 m of the field as the landscape-scale habitat variable (**Table 1**) and had a marginally significant increase in bird damage ($z = 1.96$, $p = 0.05$). Bird damage was highest at the edge of fields, regardless of the presence of field margin habitat, and dropped quickly to near 0% within 50 m of the field edge (**Figure 3C**). This effect was driven primarily by distance from field edge, with the linear ($z = -4.38$, $p < 0.001$) and quadratic values ($z = 2.93$, $p = 0.003$) for distance from field edge retained in the final model.

## Economic Estimates

Our damage models estimate that the presence of woody field margin habitat results in significant changes to yield

**TABLE 1 |** Model selection for candidate models explaining sunflower moth damage to sunflower seeds using the distance to nearest natural habitat as a measure of landscape-scale habitat complexity, and for candidate models explaining bird damage to sunflower seeds using the proportion natural habitat within 800m of each site.

| | Model parameters | Residual df | Residual deviance | Δ AIC | $w_i$ |
|---|---|---|---|---|---|
| Insect damage | Field margin + distance to natural + PC2 | 190 | 218 | 0 | 0.48 |
| | Field margin + distance to natural + PC1 + PC2 | 189 | 218 | 1.7 | 0.2 |
| | Field margin + distance to natural + PC1 | 190 | 219 | 3.1 | 0.1 |
| | Field margin + distance to natural | 191 | 219 | 3.2 | 0.09 |
| | Field margin + distance to natural + distance into field + PC1 + PC2 | 188 | 218 | 3.3 | 0.09 |
| | Field margin * distance to natural + distance into field + PC1 + PC2 | 187 | 218 | 5.3 | 0.03 |
| | Null | 193 | 222 | 42.4 | 0 |
| Bird damage | Distance into field + distance into field$^2$ + prop. natural 800 m + fall field bird abundance | 189 | 115 | 0.00 | 0.30 |
| | Distance into field + distance into field$^2$ + prop. natural 800 m + PC2 | 189 | 118 | 0.32 | 0.26 |
| | Distance into field + distance into field$^2$ + prop. natural 800 m | 190 | 115 | 1.15 | 0.17 |
| | Field margin + distance into field + distance into field$^2$ + prop. natural 800 m | 189 | 115 | 2.06 | 0.11 |
| | Distance into field + distance into field$^2$ | 191 | 113 | 2.13 | 0.10 |
| | Distance into field + distance into field$^2$ + prop. natural 800 m + PC1 | 189 | 116 | 3.14 | 0.06 |
| | Null | 196 | 106 | 33.1 | 0 |

*We used a principle components analysis to consolidate field margin habitat complexity, with PC1 negatively associated with field margin height, width, and number of canopy layers; and with PC2 positively associated with field margin height and width, and negatively associated with number of canopy layers. Field margins for each site were categorically defined based on the presence or absence of woody vegetation along the field margin. The "Distance into Field" measure is the number of meters within the field for each sampling location from the nearest field edge, and Distance into field$^2$ is the quadratic term for this variable.*

and therefore economic value of sunflower crops. Multiplying these results by the mean value of sunflower seeds in the region ($3,736/ha) allows for a coarse estimate of the economic implications of damage to sunflowers. For example, at sites adjacent to natural vegetation, farmers would expect to lose $877/ha in yields due to sunflower moth damage at sites with bare/weedy vegetation along the field margin, compared to $220/ha in lost yields due to sunflower moth damage at sites with woody vegetation, but this difference would lessen with increasing distance from natural areas as overall insect damage also declined (**Figure 3B**, secondary axis). To put this into perspective, the mean cost of applying insecticides to treat for sunflower moth is $292/ha (the equivalent of losses of ∼7.8% damage), so our results suggest that fields with more complex, woody margins would be likely to remain under an economic threshold that would trigger growers to apply insecticides, whereas sites with bare/weedy margins mostly incur damage above that threshold (**Figures 3A,B**, secondary axis). Bird damage at the field edge would result in $100/ha in lost yields but that would decline to negligible damage within 50 m of the field edge (**Figure 3C**, secondary axis).

## Avian Species Richness and Abundance

We observed 70 different avian species during our summer counts, and 74 species during our fall counts. These included California 'Bird Species of Special Concern' (Shuford and Gardali, 2008) like northern harrier (*Circus hudsonius*), yellow warbler (*Setophaga petechia),* and California "Threatened" species like Swainson's hawk (*Buteo swainsoni*), and tri-colored blackbird (*Agelaius tricolor*, 13 individuals observed at one site). During our summer counts, 64 different bird species utilized sunflower field edges and 49 species utilized field interiors. During our fall counts, we observed 69 species utilizing sunflower field edges and 46 species utilizing field interiors. The most abundant birds observed in fields interiors during the fall were Icterid species including Brewer's (*Euphagus cyanocephalus*) and red-winged blackbirds (*Agelaius phoeniceus*), European starling (*Sturnus vulgaris)*, American goldfinch *(Spinus tristis),* house finch (*Haemorhous mexicanus*), and mourning dove (*Zenaida macroura*), all of which are species that are likely to damage sunflower seeds- although mourning doves most likely feed on seeds that have been knocked to the ground.

### Summer Avian Species Richness and Abundance

For our summer counts, avian species richness (**Figure 4A**) and abundance (**Figure 4B**) along field edges were positively associated with increasing field margin habitat complexity (**Table 2**, **Table S4**). Increasing field margin habitat was associated with lower avian species richness within fields in summer (PC1, **Figure 4C**, **Table 2**). For summer field interiors, avian species richness was negatively associated with increasing field margin habitat complexity (PC1, **Figure 4C**, **Table 2**). Avian abundance within field interiors in the summer was negatively associated with increasing height and width of field margin habitat (PC2, **Figure 4D**, **Table 2**). Model results for landscape scale habitat complexity, measured as the distance to nearest natural habitat, indicate that fields located further from natural habitat had lower avian species richness and abundance along field edges in the summer (but not field interiors, **Table 2**).

### Fall Avian Species Richness and Abundance

In the fall, avian species richness (**Figure 4E**) and abundance (**Figure 4F**) along field edges, and avian abundance within field interiors (**Figure 4H**) were positively associated with increasing field margin (local) habitat complexity (PC1; **Table 2**, **Table S4**). Avian species richness within field interiors in the fall was not

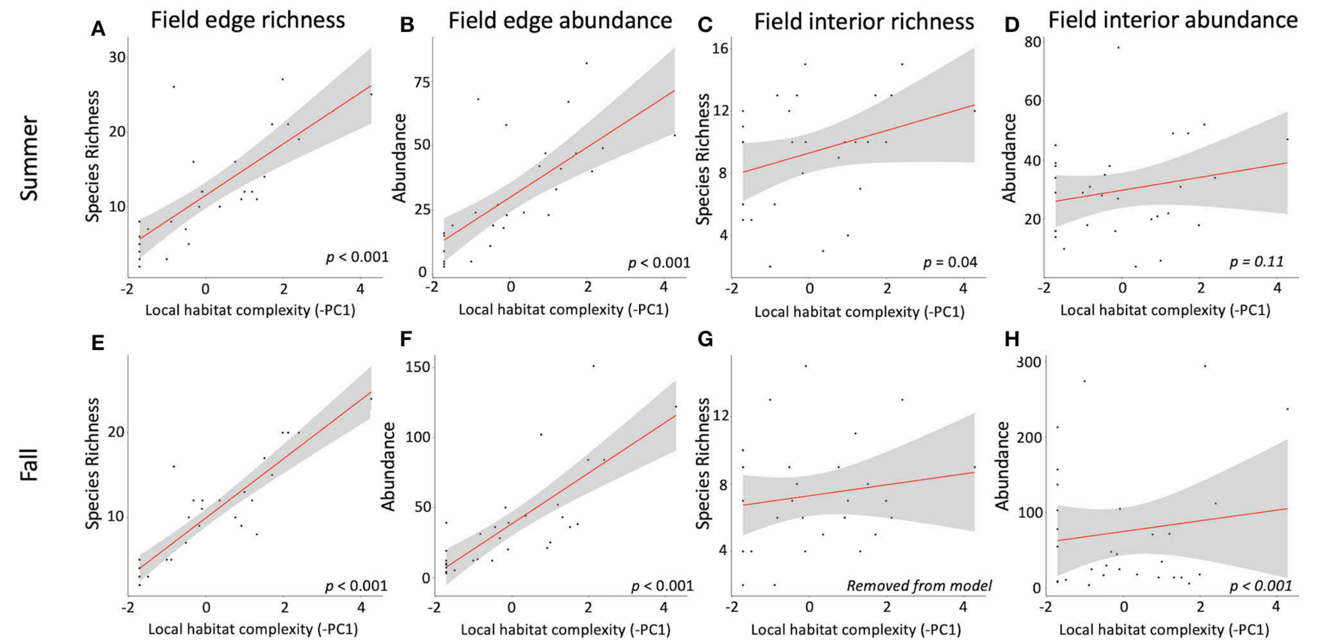

**FIGURE 4 |** Avian species richness and abundance along sunflower field edges and within sunflower field interiors in Summer (top row) and Fall (bottom row) as a function of increasing field margin habitat height, width, and number of canopy layers (-PC1). Statistical significance of PC1 variable as a predictor in a linear regression for each response variable is shown bottom right in each panel. Panels show **(A)** summer field edge richness, **(B)** summer field edge abundance, **(C)** summer field interior richness, **(D)** summer field interior abundance, **(E)** fall field edge richness, **(F)** fall field edge abundance, **(G)** fall field interior richness, and **(H)** fall field interior abundance.

**TABLE 2 |** Model estimates for each of eight models for avian species richness and abundance measured either along the edge of sunflower fields, or within the field interiors, in either summer or fall.

| | | | **Predicted difference from intercept per unit increase $p < 0.001$*** $p < 0.01$** $p < 0.05$*** | | | |
|---|---|---|---|---|---|---|
| | **Field location and avian diversity** | **Intercept** | **Field margin (bare/weedy)** | **PC1 (negatively associated with margin complexity)** | **PC2 (positively associated with margin height/width)** | **Distance to natural habitat (m)** |
| Summer | Edge richness | 12.09*** | – | −2.39*** | – | 0.00* |
| | Edge abundance | 35.95*** | −10.20** | −5.76*** | – | −0.01*** |
| | Interior richness | 9.24*** | – | −0.66* | – | – |
| | Interior abundance | 29.49*** | −1.14 | −1.63 | −5.30*** | 0.00 |
| Fall | Edge richness | 11.83*** | −4.44* | −2.00*** | – | 0.00 |
| | Edge abundance | 44.39*** | −21.23*** | −9.52*** | −6.34*** | −0.01*** |
| | Interior richness | 7.3*** | – | – | – | – |
| | Interior abundance | 56.63*** | 100.59*** | −9.55*** | −22.93*** | −0.02*** |

*Results show the most parsimonious model for each measure of avian diversity, location, and season (see **Table S5** for model selection), and blank spaces indicate parameters that were removed in model simplification. We report the intercept for each model, and the predicted difference per unit increase for each predictor variable (slope). Predictor variables include a categorical measure of "Field Margin" habitat (intercept level = woody vegetation), the results of a PCA for margin habitat complexity (PC1 negatively associated with field margin height, width, and number of canopy layers; and PC2 positively associated with field margin height and width, and negatively associated with number of canopy layers), and a measure of landscape-scale habitat complexity (distance to natural habitat).*

significantly correlated with PC1 (**Figure 4G**). However, avian abundance along field edges and within field interiors was negatively associated with PC2, which is associated positively with margin habitat height and width (**Table 2**). Fall avian abundance was significantly lower along bare/weedy field edges (estimated mean reduction of 21.23 birds/transect) compared to along edges with woody vegetation (estimated mean of 44.39 birds/transect), but the opposite was true within field interiors, where there was an estimated increase of 100.59 more birds per transect at sites with bare/weedy edges compared to fields with woody vegetation along their edges (intercept = 56.63, **Table 2**). Only the abundance of birds within field interiors was significantly driven by landscape-scale habitat complexity, with fewer birds in fields further from natural habitat patches (at a rate of ∼2 birds per 100 m, **Table 2**). Avian species richness in field interiors was not correlated with any of our predictor variables for local or landscape scale habitat complexity.

## DISCUSSION

Our results suggest that sunflower growers would benefit from planting or maintaining woody vegetation alongside their fields since insect damage was significantly higher at sites without field margin vegetation, while bird damage was not driven by field margin habitat. In fact, bird damage at our 30 fields was similar across sites with and without field margin habitat. Furthermore, within sunflower fields across all distances from the field margin, sunflower moth damage was significantly higher than bird damage, and was the main source of yield loss for sunflower growers in our area. The pest control service benefits that farmers receive from field margin vegetation therefore outweigh the potential ecological disservices associated with bird damage to sunflowers. Our results also indicate a clear benefit for biodiversity, with significantly higher species richness and avian abundance along field margins that had woody habitat. Combined, these results support the assertion that diversified farming systems can provide both farmers and broader society with multiple additive ecosystem services (Kremen and Miles, 2012).

Our exclosures did not reveal an effect of bird foraging on sunflower moth damage. This could be the result of small sample size ($n = 36$ exclosures in 9 fields), or these results could indicate that foliage-gleaning birds and bats are not a major predator of sunflower moth. We hypothesize that the patterns of sunflower moth damage we observed were driven by either increased predation pressure from invertebrates, or from aerially-hunting bats and birds (which would not have been affected by the exclosures). Because of their nocturnal nature, adult sunflower moths are likely to be targeted more by nocturnal arthropod predators and/or bats (both of which would not be affected by the presence of exclosures) than by the predominantly diurnal avian predators. Studies in California have shown that the presence of habitat along field margins is associated with increased diversity and abundance of beneficial insects including natural enemies (Eilers and Klein, 2009; Gareau et al., 2013; Morandin et al., 2014), and with increased bat activity (Kelly et al., 2016), suggesting that our results could be driven by either or both of these groups of predators. Alternative hypotheses to explain our findings could be that woody vegetation along field margins present physical barriers to sunflower moths, or that increasing sunflower resources further from natural habitat dilute concentrations (and therefore damage) of sunflower moths, especially if natural habitats are the source of sunflower moths (e.g., see Tscharntke et al., 2016; O'Rourke and Petersen, 2017). Further research is clearly needed in this system.

Our results demonstrate that both insect and bird damage increased with landscape-scale habitat complexity. California's Central Valley is largely dominated by agriculture, with few corridors of remnant natural habitat along riparian areas (**Figure 2**). In this landscape, such corridors of natural habitat may be a source of migrating sunflower moths, and may also provide roosting habitat for large flocks of icterid birds in the autumn. Natural areas may therefore be a greater source of pests than they are a source of natural enemies (e.g., Hypothesis 2 in Tscharntke et al., 2016). However, our results show that regardless of how complex the landscape a farm is embedded within is, retaining or planting woody vegetation along field margins leads to a decrease in insect damage, and has no effect on total bird damage compared to sites with low levels of local habitat complexity. Importantly, this is also the scale at which farmers make decisions about planting, and therefore has the largest implications for rapid changes on private lands. Native hedgerows, the primary method for farmers to plant new woody vegetation along field margins, are also an important sources of pollination services for sunflowers (Sardiñas et al., 2016) and support pollinator metacommunity dynamics (Ponisio et al., 2019).

Habitat loss, largely a result of agriculture, is a primary driver of alarming trends of decreasing avian abundance in North America (Rosenberg et al., 2019). Both local (e.g., Hinsley and Bellamy, 2000; Batary et al., 2012; Heath et al., 2017; Gonthier et al., 2019) and landscape (e.g., Railsback and Johnson, 2014; Heath et al., 2017; Karp et al., 2018; Gonthier et al., 2019) habitat complexity have been linked to increased diversity of avian communities in farmlands, and may boost the conservation value of intensive agricultural landscapes. We found that avian species richness was positively associated with local-scale and landscape-scale habitat complexity. The presence of woody vegetation also led to higher avian abundance along field edges, but was associated with decreased avian abundance within sunflower fields in the fall, although this did not drive a reduction in bird damage in our study.

Birds on farms can provide multiple, overlapping, and complex benefits and costs for farmers at multiple scales (Pejchar et al., 2018). Individual species can be beneficial to a crop in some seasons and detrimental in others, or may benefit one crop and cause damage to another. Birds may also disrupt other natural trophic cascades that benefit farmers (Grass et al., 2017). Importantly, while our results indicate a net benefit of woody vegetation along field margins for both sunflower yields and avian diversity in California, sunflowers in other regions (Peer et al., 2003; Schäckermann et al., 2014; Ernst et al., 2019) suffer from economically significant bird-damage to the same crop. Therefore, we caution that land managers and scientists should consider local climate, habitat availability, agricultural practices, and avian communities before translating our findings into management changes in other regions.

Increasing natural habitat in intensive agricultural landscapes can provide numerous ecosystem services and support biodiversity. However the risk of also attracting pests is a major cause of farmer reluctance to plant or retain such habitat (Brodt et al., 2009). Finding solutions that lead to landscapes that benefit both wildlife and farming is essential to ensuring food security and a thriving biodiversity in the future (Bommarco et al., 2013; Kremen and Merenlender, 2018). Our study demonstrates that while landscape habitat complexity leads to slight increases in insect and bird damage, but also increases bird diversity and abundance. Regardless of landscape-scale habitat, fields with local habitat complexity have higher yields compared to fields with bare or weedy edges, and fields with woody vegetation along field margins also harbor a greater diversity and abundance of birds. To move into a more preventative pest management paradigm, encouraging farmers in California to plant or retain woody vegetation along field margins will simultaneously increase sunflower seed yields and increase the diversity and abundance of birds.

## DATA AVAILABILITY STATEMENT

Data will be made available on the Columbia University Library Digital Repository, https://doi.org/10.7916/d8-k1sp-wd06.

## ETHICS STATEMENT

The animal study was reviewed and approved by Institutional Animal Care and Use Committee (IACUC #18033) at the University of California, Davis.

## AUTHOR CONTRIBUTIONS

SK, TK, and JT conceived the ideas and designed methodology. SK, BM, and RB field assistants collected the data. CM performed the landscape analysis. SK analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2020.00040/full#supplementary-material

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# Farmer Mental Models of Biological Pest Control: Associations With Adoption of Conservation Practices in Blueberry and Cherry Orchards

*Chris J. Bardenhagen*, Philip H. Howard and Steven A. Gray*

*Department of Community Sustainability, Michigan State University, East Lansing, MI, United States*

Conservation practices in agriculture—such as biological pest control, provision of pollinator habitat and cover cropping—may provide ecosystem services that are beneficial to both farmers and wildlife. Despite these benefits, however, their use is not yet widespread and the factors that may limit adoption are not well-understood. In this study we tested potential associations between farmers' beliefs about ecosystem services and their management practices using data collected from questionnaires and cognitive maps from 31 Michigan blueberry and cherry farmers describing their farming systems. We found that farmers who included key biological pest control concepts in their mental model representations reported the use of more conservation practices, and/or participation in conservation programs, than those who did not. In addition, the timing of management practices was a more central factor in the mental models of farmers who included both natural predators and beneficial insects than those omitting these factors. Finally, the farmers who included those two factors showed higher degrees of systems thinking based on mental model metric analysis. We suggest that outreach emphasizing the relationships between ecosystem services and the factors farmers view as most important may positively influence communication and potential of adoption of conservation practices and preventative pest management strategies.

**Keywords: conservation,ecosystem services, agriculture, ecological systems thinking, natural predators**

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*Kris A. G. Wyckhuys,*
*Chinese Academy of Agricultural Sciences, China*

**Reviewed by:**
*Hannah Torres,*
*Old Dominion University, United States*
*Randa Jabbour,*
*University of Wyoming, United States*
*Rica Joy Flor,*
*International Rice Research Institute, Philippines*

***Correspondence:**
*Chris J. Bardenhagen*
*bardenh1@msu.edu*

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## INTRODUCTION

Farmers are in a unique position to foster the conservation of natural resources and cultivate ecosystem services because their decisions and behaviors have a direct impact on the environment. For example, certain agricultural practices can positively influence crop production while also providing societal or ecosystem benefits such as preservation of wildlife and improved water quality (Swinton et al., 2007; Lindell et al., 2018). Such "ecosystem services" that benefit crop production include biological management of pests, increased pollination, and soil health through development of biota (Power, 2010; Park et al., 2018). On the other hand, failing to adopt such practices or engaging in certain practices that may have negative environmental influences and can have an impact on ecosystem services such as wildlife habitat (Foley et al., 2011). In order to expand the use of conservation practices for agricultural pest management, educational outreach is needed to increase farmer awareness of the ecosystem services benefits associated with specific practices (Kross et al., 2017; Salliou and Barnaud, 2017; Penvern et al., 2019). However, research into the factors affecting farmers' adoption of ecologically-beneficial practices is also critical (Halbrendt et al., 2014). Several studies have found associations between more "complex" thinking about ecosystems and the use of conservation practices (Vuillot et al., 2016; Teixeira et al., 2018) but understanding of how ways of thinking, behavior, and environmental outcomes are interrelated remains less characterized.

Farmers' decisions on whether or not to adopt a particular practice can be based on a variety of interests, some of which may conflict with each other. Personal goals and motivations for becoming a farmer can influence decision-making, creating barriers to certain practices but conduciveness toward adoption of others; for example, people who farm as a lifestyle choice might be more motivated toward conservation practices (Pannell et al., 2006; Greiner and Gregg, 2011; Prokopy et al., 2019). Like decision-makers in other natural resource management contexts (Stier et al., 2017), farmers might depend on university and industry experts when determining whether to take on a new practice or whether to continue with behaviors that are perceived to be working or otherwise beneficial. However, a barrier to adoption could potentially exist when knowledge about ecosystem services is not incorporated into a farmer's own thinking (Wyckhuys and O'Neil, 2007). This type of barrier has the potential to be overcome using appropriate information sharing techniques (Gray et al., 2014; Wilke and Morton, 2015) and, we propose, through incorporating ecological factors into their beliefs about farming dynamics.

A "systems thinking" approach to natural resource management considers, in a holistic manner, the way that important factors within a system interact with each other (Bosch et al., 2007). Instead of reducing a system to its parts, a systems approach examines how those parts fit into the whole (Gray et al., 2019). In a farming system, these "parts" include not only plants, soil, and farm inputs, but also soil biota, wildlife, water resources and runoff, and the farmers themselves. However, the degree to which farmers are engaging in ecological systems thinking, and how this influences their decision-making and on-farm behaviors, requires more research.

Knowledge about these farming systems, how factors are defined and the relationships between them can be developed through exploration of mental models, which are frameworks for thought that people use to understand their world (Jones et al., 2011). Mental models are used for making day-to-day decisions and are constructed through the acquisition of knowledge and through experience (Carley and Palmquist, 1992; Jones et al., 2011; Moon et al., 2019). For farmers, one manner in which this knowledge can be developed over time is through social learning processes (Reed et al., 2010), where information is shared back and forth with university extension agents, scientists, and other industry partners at meetings, outreach events, and informal situations such as farmer-to-farmer communications that influence their decision-making and preferences (Li et al., 2016).

Social learning processes may be a key to sustainability for natural resource management, by enabling the sharing of multiple stakeholder perspectives over a long term (Muro and Jeffrey, 2008). An iterative process where decisions are made, systems are affected, and mental models are consciously modified to reflect the new resulting perception of reality could assist in the development of more sustainable systems (Hjorth and Bagheri, 2006). For agriculture, when farmers have knowledge of how a particular conservation practice or its sub-parts fit into a farming system, it should be reflected in their mental models. External representations of the assumptions of these models could enable them to make more informed decisions about how their farming decisions potentially influence social or environmental outcomes. While recent research has discovered variations in farmers' mental models based on their style of management (Vuillot et al., 2016), less is known about the association between the presence and absence of ecological information on mental models, and the degree to which different mental models affect management practices.

To better understand how farmers think about their farming systems, and if differences in mental models are associated with the adoption of these types of conservation practices, we focused on the following questions:

- What are the general characteristics of farmers' mental models for pest management decision-making and how do these relate to conservation practices and behaviors?
- Are conservation practices more likely to be adopted by farmers who include biological control factors in these mental models?

In order to study these questions, we researched blueberry and cherry farmers' mental models related to pest management, including how farmers perceive natural predators to work within their pest management systems. We paid special attention to the practice of installing nest boxes to attract American kestrels (*Falco sparverius*), a natural predator of fruit eating birds, because nest box installation is a well-known management method used by a substantial number of blueberry and cherry growers in Michigan. Bird damage is a significant problem for fruit farmers (Anderson et al., 2013), and kestrels can help manage bird damage in blueberry and cherry orchards. Kestrels have been found to be effective at keeping fruit eating birds out of orchards when they are nesting in close proximity, thereby decreasing damage to cherries (Shave et al., 2018). Nest box installation has been found to be both inexpensive and effective for encouraging nesting near cherry orchards in Michigan, and their use could help to conserve and increase area populations of kestrels, particularly where natural nesting is limited (Shave and Lindell, 2017; Shave et al., 2018). For these reasons nest boxes are an ideal focus for studying the adoption of conservation practices within pest management programs.

## MATERIALS AND METHODS

Working with university extension and industry partners, we used purposeful sampling methods (Patton, 2015) to identify

Michigan blueberry and cherry farmers across a variety of categories, including age, generational experience, marketing strategies, and farm size. As perennial fruit crop farmers, blueberry and cherry farmers utilize similar pest management strategies. During in-person interviews averaging approximately 1 h for each farm, we worked with farmers to create maps of their mental models of interactions between factors in their farming systems. We also administered questionnaires inquiring about their farm characteristics and adoption of sustainable agricultural practices. The mental model and questionnaire data were combined in order to better understand potential relationships between ecological systems thinking and the adoption of conservation practices, and to test the hypotheses that conservation practice adoption will be associated with mental models that incorporate ecological concepts. We conducted interviews covering a total of 34 farms (usually with one individual representing the farm but in several cases there were two). This yielded 31 valid data sets (the first was not usable because of subsequent changes in the interview procedure, and two interviewees did not fill out the questionnaire). More specifics about data gathering and analysis follow below.

## Fuzzy Cognitive Mapping

FCM is a semi-quantitative method used to create an illustration or representation of a person's mental model about a particular topic or phenomena (Ozesmi and Ozesmi, 2004). FCM is increasingly used to aid natural resource management efforts (Hobbs et al., 2002; Meliadou et al., 2012; Vasslides and Jensen, 2016; Van der Sluis et al., 2018) and has also been applied to farming systems management and agricultural policy development (Fairweather, 2010; Christen et al., 2015; Pacilly et al., 2016). FCM is a useful tool for understanding the potential relationships between ecological thinking and adoption of conservation practices (Vermue, 2017); the mapping process may illustrate specific factors involved in farm production, and the relationships a farmer conceptualizes between those factors (Teixeira et al., 2018). Hence, the inclusion or omission of biological control factors, and the degree to which those factors are perceived to influence other aspects of the system, may provide insight into the degree of ecological systems thinking that a farmer employs.

The FCM mapping process consists of identifying factors or variables of importance in a system and then visually representing the connections between those factors, using a chalkboard, sticky notes, or other interactive and visual methods (Devisscher et al., 2016). The connections between factors on the map are typically given a direction (does A causally influence B, B causally influence A, or both), and a number between −1 and 1 is provided to signify the strength of the relationship between factors and whether it is positive or negative (van Vliet et al., 2010). The resulting map illustrates perceptions of the important factors in the system, and their direct and indirect relationships to each other. Importantly, most studies report a rapidly diminishing number of additional factors after conducting just five to ten interviews, due to a large number of shared concepts (Ozesmi and Ozesmi, 2004).

As graphical and "fuzzy" numerical representations of people's mental models, FCM structural elements may be compared among farmers and quantitatively analyzed. Structural characteristics such as the number of factors, number of connections between them, and the density of connections can be calculated and combined with other data sets for further analysis (Ozesmi and Ozesmi, 2004; Misthos et al., 2017; Konti and Damigos, 2018). Analysis can also examine "driving" or "transmitting" concepts—those that affect other concepts or factors in the map but are not themselves affected by other factors (e.g., in the case of farming "weather" would generally be considered a driver). "Receiving" concepts are those that are affected by, but do not affect, other concepts in the map. "Ordinary" concepts are those that both affect and are affected by other factors (Christen et al., 2015; Teixeira et al., 2018). We posit that including more ordinary concepts therefore suggests a mental model that represents a higher degree of systems thinking because a systems approach considers interactions between various types of factors (human, mineral, biological) at various scales (pest level scale, farm scale, larger ecosystem scale) (Bosch et al., 2007).

For this study, pre-interviews were conducted with two cherry farmers and one blueberry farmer in order to identify the key factors associated with pest management. Factors mentioned ranged from chemical methods of management to natural methods (including natural predators and beneficial insects), mammal, insect pests, and bird pests, weather, and markets. After testing and revisions, a total of 19 factors were identified and chosen for presentation to farmers during the mapping process. The concept "natural predators" is considered broadly to include insect natural enemies, predators of fruit eating birds, and predators of mice, among other agricultural pests. Because some beneficial insects are natural predators, there is some overlap between these concepts. Including these concepts in the mapping enabled us to understand how conservation practices fit into farmers' larger pest management mental models in a broad sense, which then provides a framework for understanding how a specific practice such as nest box installation is considered.

These factors were written on squares of magnetic paper and placed on a $2'$ by $3'$ magnetic dry erase board. Using a technique employed by Christen et al. (2015) and Li et al. (2016), participants were invited to add any more factors that they felt were important aspects of the system. In our case, they were offered blank magnetic paper squares that they could write on and place on the map. Farmers were then asked to evaluate whether relationships existed between each of the factors, and to draw those relationships using lines (**Figure 1**), noting the direction and the positivity or negativity of the relationship ("If A increases, does B increase as a result [positive] or decrease as a result [negative]?"). After the interviews, the individual farmers' FCMs were entered into Mental Modeler (mentalmodeler.org), a software program that allows the maps to be visualized in digital form; the program was also used to analyze the FCM data for structural metrics (Gray et al., 2013).

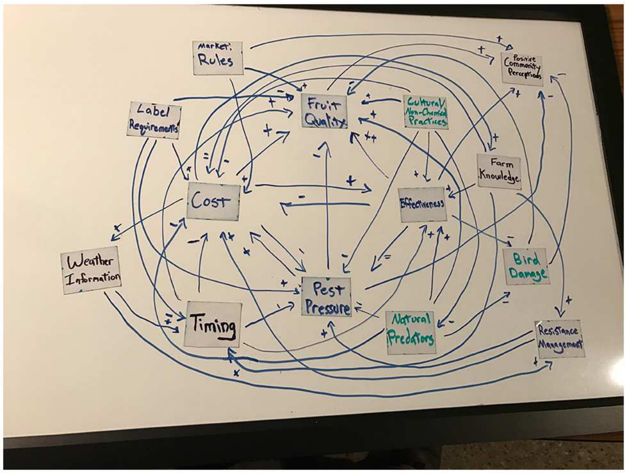

**FIGURE 1 |** Example of a cherry grower's mental map on the dry erase board. Arrows represent the causal direction (does A affect B or B affect A). "+" indicates a positive relationship (when A increases, so does B) and "–" indicates an inverse relationship (when A increases, B decreases.) A "++" or "– –" indicates a very strong effect.

## Questionnaire and Semi-structured Interviews

Our questionnaire was designed to elicit demographic information and farm characteristics, as well as to determine what types of conservation practices farmers have used, including installation of nest boxes to host natural predators. While this overall study was designed to better understand conservation practice adoption and ecological thinking broadly, the practice of installing nest boxes provides a well-known and promoted practice to use as an example. Therefore, we used the questionnaire to also inquire about different methods of bird damage control that farmers have used. Likert-type scale questions (Croasmun and Ostrom, 2011) assessed farmers' perceptions of the effectiveness of those methods [scale from 1 (not effective) to 5 (very effective)]. Farmers also were asked about their participation in three specific state and federal environmental and conservation programs. An early draft of the questionnaire was tested during pre-interviews, and the final version was administered during the in-person interviews to help insure completion and to allow for any clarification questions.

Three semi-structured interview questions were asked after the mapping process and questionnaire administration to capture additional relevant information from respondents (Reed et al., 2009). Two of the questions focused on the FCM process to gain feedback on the method, and to inquire if anything important pest management issues or interactions were missed due to the nature of the FCM method. The third asked whether the farm's pest management was affected by the proximity of neighboring fields or crops. The resulting in-depth data was analyzed for recurring themes and concepts in order to discover any potential data gaps. We focused on concepts/codes related to the timing of pest management actions, site issues such as the effect of woods and adjacent farmland (for example if abandoned blocks caused pest pressure increases,) items not captured by FCM and improvements that could be made to the research and mapping process.

## Adoption of Sustainable Practices Index

An index variable for adoption of sustainable practices was constructed by adding the self-reported use of 14 conservation-oriented practices (Cronbach's Alpha = 0.831). Here "adoption" is considered to be the farmer reported use of a practices with an intent to have beneficial environmental, conservation, and/or ecosystem service outcomes. The practices included the following: the use of wildflower strips to increase levels of food available for pollinators, cultivation or protection of beneficial insects, the maintenance of cover crops or other habitat for beneficial insects, scouting for beneficial insects during regular field inspections for pests, mowing orchard floors to manage rodents and arthropod pests, the use of Integrated Pest Management principles, and the use of hedgerows to reduce spray drift. The index was scored by giving one point for each practice that a farmer self-reported using. The index also included any reported participation in the following programs: the Conservation Stewardship Program (CSP), the Environmental Quality Incentives Program (EQIP), and/or the Michigan Agricultural Environmental Assurance Program (MAEAP). Each of these require the use of conservation and environmental quality-oriented practices (although we simply gave one point for participating in each program; we did not characterize specific practices within these programs.) For example, CSP and EQIP provide monetary incentives for engaging in particular conservation practices such as planting of cover crops or development of contour farming to mitigate erosion, improvement of forages and grazing land, and establishment of fish and wildlife habitat[1] MAEAP is a voluntary certification program focused on environmental outcomes[2], and it requires practices intended to lower rates of groundwater contamination by fertilizers and agricultural chemicals. A higher score on this index means that a farmer has participated in a higher total combined number of the programs and/or adopted more of the sustainable conservation practices identified in the questionnaire.

This index and other questionnaire data were then analyzed in IBM SPSS Statistics, along with FCM data, in order to evaluate trends across farmer types and conservation attitudes using *t*-tests, ANOVAs, and crosstabs (Lomax and Hahs-Vaughn, 2012).

## RESULTS

As **Table 1** shows, our final sample consisted of 16 cherry growers and 15 blueberry growers, all in Michigan's Lower Peninsula. Most farms were in the major fruit growing regions near the coast

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[1] For more information on the CSP practices see the list at: https://www.nrcs.usda.gov/wps/portal/nrcs/main/national/programs/financial/csp/ and for EQIP see: https://www.nrcs.usda.gov/wps/portal/nrcs/main/national/programs/financial/eqip/

[2] Information about MAEAP can be found at: http://www.maeap.org

**TABLE 1 |** Mean differences in mental model metrics and adoption of sustainable practices index by farm type.

| | **Blueberry farmers ($N = 15$) Mean ± *SD*** | **Cherry farmers ($N = 16$) Mean ± *SD*** | ***P*-value** | **Pick-your-own farmers ($N = 10$) Mean ± *SD*** | **Non-pick-your-own farmers ($N = 21$) Mean ± *SD*** | ***P*-value** |
|---|---|---|---|---|---|---|
| # of factors | 18.40 ± 2.8 | 16.88 ± 3.3 | 0.179 | 17.30 ± 2.1 | 17.76 ± 3.5 | 0.708 |
| # of driving factors | 8.33 ± 2.6 | 6.75 ± 2.6 | 0.106 | 7.30 ± 1.6 | 7.62 ± 3.1 | 0.766 |
| # of ordinary factors | 6.73 ± 2.6 | 7.75 ± 2.8 | 0.302 | 6.60 ± 2.6 | 7.57 ± 2.7 | 0.357 |
| # of receiving factors | 1.73 ± 0.9 | 1.31 ± 0.8 | 0.173 | 1.70 ± 0.9 | 1.43 ± 0.8 | 0.416 |
| # of Connections | 36.00 ± 13.6 | 37.19 ± 8.2 | 0.769 | 35.40 ± 16.3 | 37.19 ± 7.7 | 0.747 |
| C/N | 1.98 ± 0.8 | 2.25 ± 0.5 | 0.276 | 2.06 ± 0.9 | 2.15 ± 0.5 | 0.736 |
| Density | 0.118 ± 0.05 | 0.151 ± 0.06 | 0.110 | 0.129 ± 0.06 | 0.138 ± 0.06 | 0.679 |
| Complexity | 0.224 ± 0.13 | 0.239 ± 0.18 | 0.795 | 0.248 ± 0.15 | 0.224 ± 0.16 | 0.691 |
| Timing centrality | 3.06 ± 1.5 | 2.87 ± 1.2 | 0.696 | 3.02 ± 1.8 | 2.93 ± 1.1 | 0.858 |
| Sustainable practice adoption index[a] | 8.33 ± 3.9 | 11.07 ± 3.5 | 0.057 | 8.70 ± 4.4 | 10.16 ± 3.7 | 0.348 |

[a] *Two farmers are omitted from this outcome due to missing data.*

of Lake Michigan and had sandy soil profiles. Ten pick-your-own operations—farms that are open to the public where individuals can harvest fresh fruit themselves—were included in the sample. Five out of the 31 farmers were either certified organic or utilized organic practices for part or all of their farm. Total blueberry and cherry acres ranged from under a quarter acre to 800 acres, with a mean of 147. About half (15) of the farmers in our sample reported they were 1st or 2nd generation farmers, with the other half reporting longer farm legacies (3rd generation or more). A large majority, 81%, reported conducting some or all of the spraying for pest management on their farm, with 19% having employees exclusively do spraying. The percentage reporting current or past use of nest boxes to attract bird predators for pest management was 45%.

We first analyzed the structural characteristics of farmer's mental models to look for differences between groups, illustrated in **Table 1**. We found some differences between blueberry and cherry farmers, and between pick-your-own and non-pick-your-own farmers in our samples, but most were relatively weak. Mean Sustainable Practice Adoption Index scores, however, were approximately 3 points higher for cherry farmers than for blueberry growers ($P = 0.057$). We also analyzed other categories, including farm size, education level of the farmer, high vs. low spenders on pest management, organic vs. not organic, and found no strong differences based on these groups—we did not compare differences by gender due to the small percentage of women interviewed.

However, when we analyzed the content of the mental models, we discovered stronger differences based on farmer's inclusion or omission of key biological control factors in their mental maps. We found both differences in the structure of mental models and in practice adoption, as shown in **Table 2**, and qualitative differences based on the analysis of the most central factors in mental maps (more on this in the *Centrality of Factors* section below).

**Table 2** shows that farmers who included both natural predators and beneficial insects had the highest mean scores for the sustainable practice adoption index (11.55). Those who included neither had the lowest mean score on this index (7.29), and those who included just one of these factors scored in between. In other words, on average, farmers in our sample who included one biological control factor in their mental model had previously utilized 2 additional conservation practices in comparison to farmers who omitted them entirely, and respondent farmers who included two biological control factors had utilized 4 additional conservation practices than the farmers who omitted them entirely. Farmers who included both natural predators and beneficial insects were also likely to include more ordinary factors and connections than those who included just one, or neither. We did not find strong differences for inclusion/omission of the other two factors that were added after pre-interviews (cultural/non-chemical practices and bird damage), as nearly all farmers included them in their models (omission of cultural/non-chemical practices, $n = 0$; omission of bird damage, $n = 3$).

## Group FCMs Based on Inclusion of Biological Control Factors

Group maps were constructed for farmers who included both natural predators and beneficial insects (**Figure 2**), and those that included neither concept (**Figure 3**). The group maps illustrate only the factors that were included by multiple farmers in order to minimize idiosyncratic results (Fairweather, 2010; Vuillot et al., 2016). Most factors that farmers chose to add are therefore not represented on these group maps, with the exceptions of "yield" and "profitability." The group map for those including the biological control factors has more connections than those that omit both, illustrating the differences reported in **Table 2** (mean of 44 connections when including both factors vs. 32 when omitting both ($p = 0.012$). The map including both factors also had a higher complexity score, which is a measure of the ratio of receiver factors to driving factors (mean of 0.205 for farmers including both factors vs. 0.185 for those omitting biological

**TABLE 2 |** Mean differences for mental model metrics and adoption of conservation practices index by inclusion/exclusion of biological control factors in Fuzzy Cognitive Maps[1].

| | Both (natural predators and beneficial insects) included in map ($N = 12$) Mean ± *SD* | One (natural predators or beneficial insects) included in map ($N = 12$) Mean ± *SD* | Neither (natural predators nor beneficial insects) included in map ($N = 7$) Mean ± *SD* | *P*-value (ANOVA) |
|---|---|---|---|---|
| # of factors | 19.00 ± 1.9 | 17.00 ± 4.0 | 16.29 ± 2.6 | 0.129 |
| # of driving factors | 7.83 ± 1.9 | 7.33 ± 4.0 | 7.29 ± 1.0 | 0.882 |
| # of ordinary factors | 9.08 ± 2.2[a] | 6.08 ± 2.5[b] | 6.14 ± 2.2[b] | 0.007 |
| # of receiving factors | 1.42 ± 0.8 | 1.75 ± 0.8 | 1.29 ± 1.1 | 0.468 |
| # of connections | 43.67 ± 10.6[a] | 32.25 ± 8.3[b] | 32.00 ± 10.3[b] | 0.012 |
| C/N | 2.33 ± 0.7 | 1.98 ± 0.7 | 2.00 ± 0.7 | 0.387 |
| Density | 0.132 ± 0.04 | 0.138 ± 0.07 | 0.136 ± 0.06 | 0.975 |
| Complexity | 0.205 ± 0.16 | 0.285 ± 0.15 | 0.185 ± 0.16 | 0.317 |
| timing centrality | 3.56 ± 1.5 | 2.69 ± 0.9 | 2.38 ± 1.5 | 0.113 |
| Sustainable practice adoption index[2] | 11.55 ± 3.7[a] | 9.27 ± 4.1[ab] | 7.29 ± 2.4[b] | 0.067 |

[1] *[a]Groups differ significantly from [b]groups in rows where shown, based on Tukey's post-hoc testing ($p < 0.05$).*

[2] *Two farmers are omitted from this outcome due to missing data.*

control factors), although this difference was small. Interestingly, only farmers from the group omitting biological control factors considered "profitability" to increase fruit quality (discussed in more detail below).

## Centrality of Factors

An individual concept or factor in an FCM can be qualitatively analyzed for the degree of centrality it has in relation to other factors (Ozesmi and Ozesmi, 2004). A factor's "indegree" is defined as the total weight of relationships that are found to affect that factor, and the "outdegree" is the total weight of effect that the factor has on other factors; the absolute values of indegree and outdegree added together makes up a factor's centrality (Nyaki et al., 2014). Generally, the more central a factor is in a map, the more connections it has to other factors in the map, and/or the higher weight given to its connections.

The factors found to be the most central for the 31 farmers were cost, fruit quality, overall effectiveness of the pest management system ("effectiveness"), pest pressure and timing, in that order. However, as **Figure 4** shows, the farmers including both biological control factors in their mental models had much higher focus on "effectiveness" and "timing" and less concentration on "cost" and "fruit quality," whereas those who included neither factor had a greater focus on "cost," and especially on the quality of the fruit. The results for farmers including only one factor were in between the "both" and "neither" groups (except for "pest pressure," for which they had centrality scores similar to those with "both"). As **Table 2** indicates, the mean centrality of the factor "timing" was higher for farmers including both biological control factors compared to those omitting both (3.56 vs. 2.38, $P = 0.113$). In addition, **Table 1** shows no strong differences for the centrality of timing by farm type.

# DISCUSSION

The mental models of the farmers in this study were quite similar overall and did not show strong differences between blueberry or cherry growers, or whether or not they had pick-your-own sales. These commonalities may be due to the similar approaches that farmers take toward pest management as perennial fruit farmers operating in a Midwestern U.S. climate. For example, while there are differences between organic and conventional approaches, both are working to fight the same pest species in similar environments. Farming could therefore be viewed as a cultural practice, with ways of thinking that are highly convergent for larger or macro-areas of management.

Farmers who included biological control factors in their mental models, however, had higher rates of adoption of sustainable conservation practices. While all of the farmers in our sample had awareness of the factors of natural predators and beneficial insects, many did not see them as having a significant role, nor a reliable effect on, the farm system. Those farmers positing a higher level of interaction or connectivity between biological control factors and other factors in the map, however, had a higher number of factors in their model that both affect and were affected by other factors, and as a result, more connections between factors. This group of farmers also made more connections to the factor of "timing," suggesting an awareness of the temporal dynamics of farming systems that are not easily represented by a static FCM. The results therefore suggest that a higher degree of systems thinking may be associated with a greater likelihood of adopting

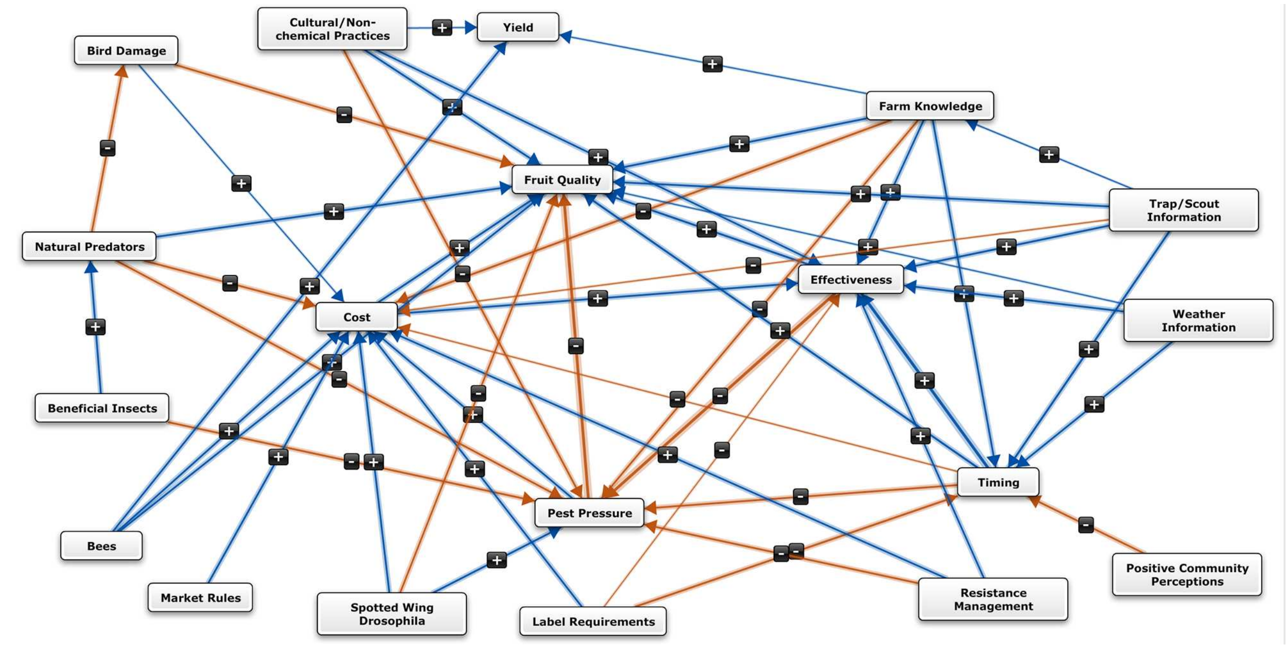

**FIGURE 2 |** Group map for farmers who included both natural predators and beneficial insects in their map. The blue lines indicate a positive relationship (if A increases, so does B) and the red lines indicate a negative relationship (if A increases, B decreases). The thickness of the line indicates the average strength of the relationship for the group of farmers, with thicker lines representing stronger effects, and thin lines representing lighter effects. The arrow indicated the direction of the relationship (A affects B).

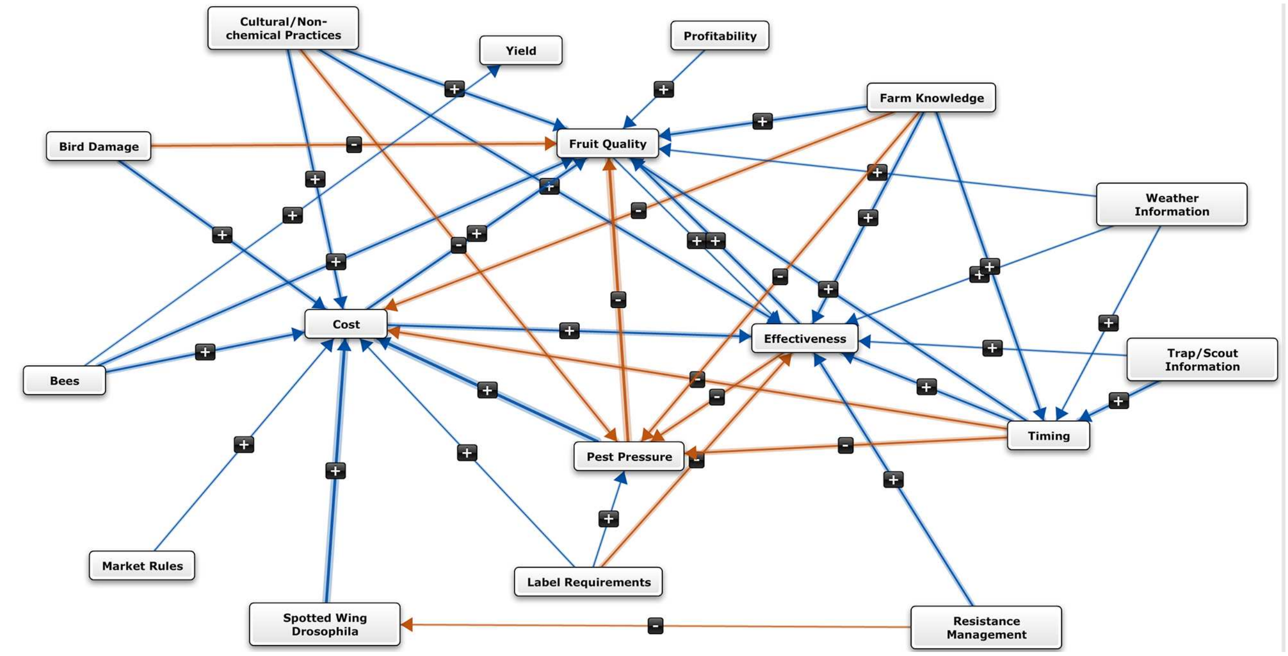

**FIGURE 3 |** Group map for farmers having neither concept (natural predators, beneficial insects) in their maps**.** The blue lines indicate a positive relationship (if A increases, so does B) and the red lines indicate a negative relationship (if A increases, B decreases). The thickness of the line indicates the average strength of the relationship for the group of farmers, with thicker lines representing stronger effects, and thin lines representing lighter effects. The arrow indicated the direction of the relationship (A affects B).

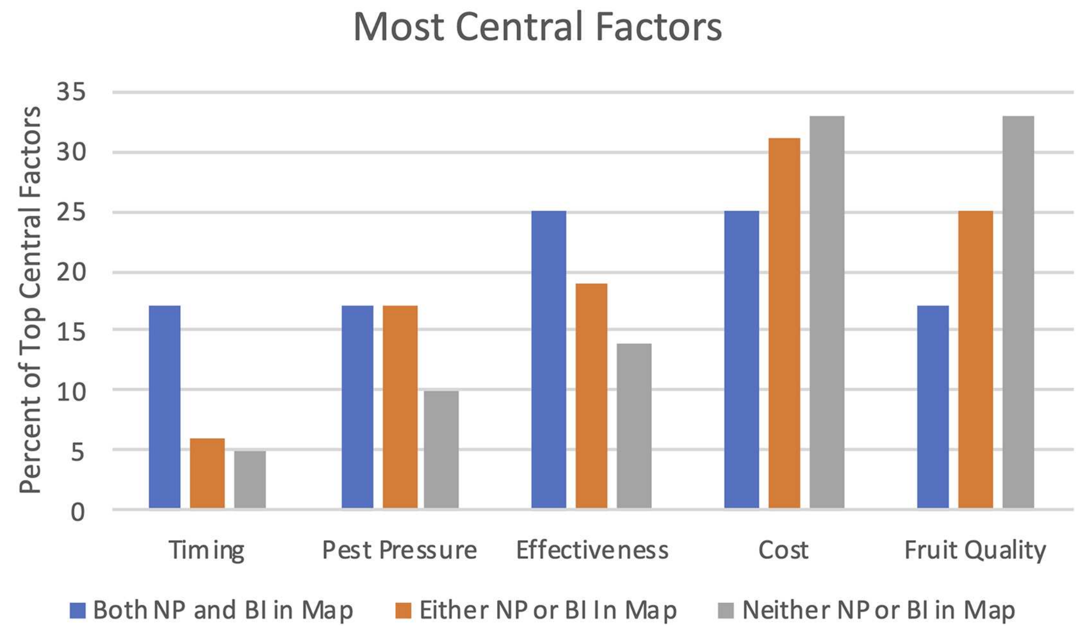

**FIGURE 4 |** The five highest-scoring factors according to their centrality, based on the inclusion or omission of the factors natural predators (NP) and/or beneficial insects (BI) in their maps. Percentages shown indicate the number of times a particular factor was included in the top three centrality scores for respondents divided by the total number of top three scores (therefore the highest possible score is 33%). For example, 12 respondents included both NP and BI in their maps: 9 had "effectiveness" in their top three scores; the total number of top 3 scores is 12 × 3 =36, and 9/36 = 25%.

more preventative pest management strategies and other conservation practices.

Although most farmers likely view fruit quality as having an effect on profitability (higher quality means higher value and/or less pick-outs), only certain farmers from the group omitting biological control factors considered the reverse—that "profitability" increases fruit quality. For these farmers, such a perception could relate to situations where fruit quality can be sacrificed to save costs if the fruit is intended for a lower-priced market than fresh markets, such as processor markets, because of varietal type or crop damage issues. Considering these cases, higher profit crops result in higher fruit quality because growers will spend more time and money to keep the quality high. While many farmers face such situations periodically, this difference between group mental models could reflect that these farmers employ a more linear pest management approach, one that is more focused on profit and cost, whereas those including biological control factors focus more on overall system effectiveness.

One limitation of this study that while the sample size is appropriate for assessing group mental models, it had less statistical power for analyzing potential associations with behaviors. In addition, the sampling strategy was not random and these farmers are not expected to be fully representative of blueberry and cherry growers in Michigan, therefore the results should be interpreted conservatively. Another limitation is that it was cross-sectional, therefore we were unable to clearly assess the direction of the associations between mental models and the number of conservation practices adopted. Does the adoption of more conservation practices lead to a greater degree of ecological systems thinking, or does an increase in ecological systems thinking encourage the adoption of more conservation practices, or is there an even more complex interaction between the two? Based on feedback regarding the FCM process in our interviews we hypothesize that direction of causality flows from changes in mental models to changes in behavior in most cases, although strong economic incentives for adopting a conservation practice may also lead to changes in mental models. Additional research is needed, however, to clarify these potential pathways.

Educational efforts that focus on bringing ecosystem services concepts into farmers' mental models, including through fuzzy cognitive mapping, may be helpful in increasing adoption of conservation practices. The semi-structured interview data provides evidence that for some interviewees, the fuzzy cognitive mapping process was helpful for better understanding the interrelatedness of different factors, for example the place or significance of natural predators. While more experiments and/or evaluations of systems thinking outreach efforts are needed to confirm the efficacy of this approach and to refine pedagogical methods, our results suggest that such efforts should assess farmers' current mental models to identify the degree to which they already converge and build upon those existing factors and relationships. For example, Michigan cherry and blueberry growers most frequently associated the factor "natural predators" with the level of bird damage, pest pressure, cost, and fruit quality, whereas "beneficial insects" were most frequently associated with the level of pest pressure, cost, and cultural/non-chemical farming practices. "Cost" was a central variable for all farmers, therefore outreach that emphasizes the connections and feedbacks between this factor and ecosystem service factors may facilitate more systems thinking. In addition, "timing" was a central variable for farmers that included biological control factors in their mental models. Providing information about the timing of tasks to farmers and other resource managers could be helpful for making informed decisions about conservation practice adoption, particularly for those who are already using more preventative approaches. Sharing such practical knowledge could increase awareness and even favorable perceptions of the practice, potentially leading to higher rates of adoption (Prokopy et al., 2019).

In addition, the process we used, and the greater use of FCM generally, could help researchers to characterize potential differences in mental models for other agricultural products and for regions outside of Michigan to better inform how "ways of thinking" and behaviors or behavioral intentions and attitudes are related. This could be done individually, as in our study, but group FCM workshops could provide a venue for group knowledge sharing (Voinov and Bousquet, 2010; Van der Sluis et al., 2018), and could stimulate discussion of ecosystem services between farmers who are using more conservation practices and those who are using fewer. This has the potential to shift the highly convergent mental models of farmers toward a more preventative approach to pest management. Greater use of FCM may therefore help farmers develop a better understanding of farm ecology and cultivate more ecosystems thinking (Devisscher et al., 2016), as well as bridge knowledge gaps between farmers and academic researchers (Garbach and Morgan, 2017; García-Barrios et al., 2017).

## CONCLUSION

This study analyzed mental models of blueberry and cherry farmers in Michigan and their associations with conservation practices and/or participation in conservation programs. Those who demonstrated more ecological systems thinking, as measured by more biological control factors in their model and more ordinary factors—those that both affect and were affected by other factors—were likely to report higher rates of adoption, as well as more connections to the dynamic factor of timing. Conversely, those who did not incorporate certain biological control factors in their model had a greater focus on cost and were likely to report lower rates of adoption of conservation practices. These results add to our understanding of the relationships between ecological systems thinking and differences in the use of preventative pest management practices. Although more research is needed to clarify the causality of these relationships, future work should emphasize connections and feedbacks involving the system factors that farmers already view as important.

## DATA AVAILABILITY STATEMENT

The datasets generated and analyzed for this study can be found in the openICPSR repository at http://doi.org/10.3886/E112171V2, with the exception of the semi-structured interview data which can be made available upon request.

## ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Michigan State University Human Research Protection Program. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

## AUTHOR CONTRIBUTIONS

PH conceptualized the study. Data collection was carried out by CB. All authors were involved in analysis, interpretation, writing, and methodological development.

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# Delivering on the Promise of Biological Control in Asia's Food Systems: A Humboldtian Perspective

**Kris A. G. Wyckhuys[1,2,3,4], Mauricio González-Chang[5]*, Evie Adriani[6], Annabelle B. Albaytar[7], Alice Albertini[8], Gonzalo Avila[9], Marie Joy B. Beltran[10], Ariel D. Boreros[11], Muhammad Z. Fanani[12], Duc T. Nguyen[13], Giang Nguyen[14], Ihsan Nurkomar[15] and Sundar Tiwari[16]**

*[1] Institute for Plant Protection, China Academy of Agricultural Sciences, Beijing, China, [2] Fujian Agriculture and Forestry University, Fuzhou, China, [3] University of Queensland, Brisbane, QLD, Australia, [4] Chrysalis Consulting, Hanoi, Vietnam, [5] Department of Sustainable Biosphere, Universidad de Aysén, Coyhaique, Chile, [6] Ichsan University, Gorontalo, Indonesia, [7] Institute of Weed Science, Entomology and Plant Pathology, University of the Philippines Los Baños, Los Baños, Philippines, [8] Institute of Life Sciences, Scuola Superiore Sant'Anna, Pisa, Italy, [9] The New Zealand Institute for Plant and Food Research Limited, Auckland, New Zealand, [10] National Crop Protection Center, University of the Philippines Los Baños, Los Baños, Philippines, [11] Regional Crop Protection Center XII, Tacurong City, Philippines, [12] Bogor Agricultural University, Bogor, Indonesia, [13] Vietnam National University of Agriculture, Hanoi, Vietnam, [14] University of Agriculture and Forestry, Hue University, Hue, Vietnam, [15] Universitas Muhammadiyah Yogyakarta, Yogyakarta, Indonesia, [16] Agriculture and Forestry University, Bharatpur, Nepal*

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**Edited by:**
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***Correspondence:**
*Mauricio González-Chang
mauricio.gonzalez@uaysen.cl*

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During the late twentieth century, the "Green Revolution" attained wide-ranging poverty alleviation, food security and improved nutrition across rural Asia. As these achievements were often reached at large environmental costs, "greener" trajectories urgently need to be traced for Asia's agri-food systems. In this sense, agro-ecological and biodiversity-based (ABB) farming systems can provide sufficient food, lift resource-use efficiencies and lower fossil-fuel dependencies while safeguarding the environment. Here, we systematically assess past progress and prospects for biodiversity-based pest management -or biological control (BC)- in five Asian countries. We characterize the extent to which BC science has matured, translated into practice and attained "real-world" outcomes within the prevailing farming systems of each country. To achieve this, we revert to the world-view of the eighteenth century naturalist Alexander von Humboldt. Doing so, we represent the extent to which BC science has progressed along a six-step "impact pathway" –from a description of on-farm biodiversity, over ecosystem service delivery to verifiable socio-economic outcomes. Our work pinpoints ways to strategize ABB science for an accelerated, evidence-based uptake by end-users within local agri-food systems. By entwining our Humboldtian "nature-culture" perspective with farmer-scientist co-innovation, bolstered awareness-raising and supportive policies, ABB farming transitions could be initiated that are prone to deliver concrete, desirable agro-ecological outcomes at local and regional scales.

**Keywords: agroecology, biodiversity, biological control, paradigm shift, holistic perspective**

## INTRODUCTION

In the early 1800's, the German naturalist, explorer and avid field scientist Alexander von Humboldt laid out his vision of nature as "a living whole" (Jackson, 2009; Wulf, 2015). Driven by a sense of wonder and devotedly measuring and tabulating innumerable phenomena, von Humboldt saw nature as a web of life in which fauna and flora, the elements, climatic processes, and human beings were all closely interconnected. Adopting a holistic, fused "nature-culture" perspective, von Humboldt tirelessly pursued a conceptual unification of Earth system sciences, planted the seed for agricultural sustainability or conservation ecology disciplines, inspired environmentalism and foresaw human-induced global change (Zimmerer, 2006; Jackson, 2009). This interdisciplinary "Humboldtian perspective," which speaks directly to pressing human concerns, is valued to mitigate today's global environmental crisis and to help redesign the world's agri-food systems (DeFries and Nagendra, 2017; Acevedo et al., 2018; Vandermeer et al., 2018; Yletyinen et al., 2019).

Conventional agriculture -as a dynamic, inter-connected socio-ecological system- entails land clearance, ecosystem mismanagement and chemical pollution, and is thus a major contributor to environmental change (Dirzo et al., 2014; Maxwell et al., 2016; Isbell et al., 2017). By depleting limited resources, adding to biodiversity loss and degrading ecosystem services over often extended spatial and temporal scales, many of today's agri-food production systems exert a pervasive influence on the "safe operating space" for global socio-economic development (Steffen et al., 2015; Springmann et al., 2018). The above phenomena are believed to be especially exacerbated in eastern Asia, a region that houses ∼50% of the world's agri-food production and which has experienced a steady 3.8% annual growth in agricultural output since the 1960's (Alston and Pardey, 2014).

Over the past 50 years, the "Green Revolution" (GR) has filled Asia's rice bowls, permitted a "quantum leap" in food production and defined much of the region's (agricultural) growth trajectories (Pingali, 2012). "Packaged" GR seed × chemical technologies and intensified farming schemes did secure a steady supply of nutrient-rich foods, but also degraded the resource base of local agriculture, imperiled farmers' health and imposed serious environmental costs across agro-landscapes (Tilman, 1998; Brainerd and Menon, 2014; Kleijn et al., 2019). As a GR hallmark, farmers' dependency upon synthetic pesticides didn't remain confined to rice settings but infiltrated other cropping systems, e.g., with present-day vegetable growers in Vietnam overspending as much as US$329/ha/cycle on pesticides (Schreinemachers et al., 2020) or Bangladeshi eggplant producers applying 150–200 chemical sprays per year (Pretty and Bharucha, 2015). As such, pesticide application regimes involve vast externalities for human and environmental health, estimated at up to $106/ha for Thailand's horticulture operations (Praneetvatakul et al., 2013; Jepson et al., 2020). These costs are likely to rise with the steady resistance development of prominent pests to "new generation" insecticides (Gorman et al., 2008; Jørgensen et al., 2018). Yet, experiences with "farmer first" training approaches in various Asian countries provide compelling evidence of how agro-chemical use in rice systems can be curbed while sustaining or even increasing yield, food output or farm revenue (Matteson, 2000; Pretty and Bharucha, 2015; Gurr et al., 2016). A tactical combination of agro-ecology science, targeted policies and carefully orchestrated extension campaigns achieved a full 70–75% reduction in pesticide use in Indonesia, Philippines or Vietnam's Mekong Delta during the 1990's, though these achievements have been largely undone in recent decades (Bottrell and Schoenly, 2012; Thorburn, 2015).

Concurrent with the rise of GR technologies, Humboldtian "systems approaches" have been increasingly advocated as a guiding premise for sustainable, ecologically-centered pest management (Ruesink, 1976; Altieri, 1984; Teng and Savary, 1992; Lewis et al., 1997; Coll and Wajnberg, 2017). In Asian rice systems, an integrative assessment of the full ensemble of drivers and determinants of pesticide use permitted an effective promotion of sustainable agriculture (Pretty et al., 2018). This involved a comprehensive appraisal of the resident biodiversity in rice ecosystems (Schoenly et al., 1998), quantification of associated ecosystem processes (Settle et al., 1996) and due attention to farmers as decision-makers and agents of change (Röling and Van De Fliert, 1994; van de Fliert et al., 2007). A central tenet of this "systems approach" was invertebrate biological control; an ecosystem service that is valued at $4.5–13.6 billion annually for US agriculture alone (Pimentel et al., 1997; Losey and Vaughan, 2006) and which can be bolstered through the in-field enhancement of beneficial, pest-killing organisms (Bale et al., 2008; Naranjo et al., 2015). As such, ecosystem services were effectively translated into farmer decision-making (Daily et al., 2009) and replaced chemically intensive GR technologies across Asian rice agro-landscapes.

However, as evident in historical pesticide use patterns (Pretty and Bharucha, 2015), the effective harnessing of biodiversity for (endemic) pest control was largely restricted to Asia's rice systems and its adoption proved transient in nature. In other systems, science on biodiversity and ecosystem functioning is regularly lagging, remains stuck in disciplinary "silos" and fails to deliver concrete outcomes (Daily et al., 2009; Chaplin-Kramer et al., 2019; Hines et al., 2019; Kleijn et al., 2019; González-Chang et al., 2020). A recently developed web-based tool (www.biodiversityfunction.com) outlines a "spiral approach" that provides an explicit pathway from the concept of biodiversity to produce agro-ecological outcomes at farm level (González-Chang et al., 2020). Thus, the spiral approach can help to identify the knowledge gaps that need to be filled for creating service-providing protocols (SPP; sensu Gurr et al., 2017; González-Chang et al., 2020) and to better understand the interactions and connectedness between the steps arising from the biodiversity concept. This approach provides the basic steps needed to devise agro-ecological and biodiversity-based (ABB) agri-food systems.

In this study, we provide a retrospective assessment of the extent to which biological control science has facilitated the necessary knowledge and tools to deliver such concrete, measurable agro-ecological outcomes in Asian farming systems. First, we conducted a systematic literature review of (published) biological control research in five Asian countries over the past 50 years. Next, we assigned each individual publication to one or more categories (and related sub-themes) within the spiral approach (González-Chang et al., 2020). Lastly, we visualized temporal dynamics in biological control science and plotted progress per geography and commodity. Our "Humboldtian" perspective permits identifying shortcomings in the integrative social-ecological research that revolves around ABB farming systems, and helps draw trajectories to foment transformational change in local agri-food systems.

## MATERIALS AND METHODS

Our assessment of historic biological control research progress was conducted in a step-wise manner. First, literature searches were run on different search engines to get a full set of scientific publications from different sources. An initial search was run on the Web of Science (WoS) Core collection database (1900–2020), thus covering over 21,100 peer-reviewed journals, conference proceedings and book data published globally. Studies that covered integrated pest management (IPM) without explicitly mentioning biological control in all fields were not taken into consideration. A core set of papers on insect biological control was consolidated by using the Boolean search string "ALL = country AND (field OR crop) AND ("biological control" OR biocontrol OR "natural enem*" OR predat* OR parasit*) AND (pest*)," as defined by the authors. Search strings were adapted to obtain results for each of five different Asian countries, i.e., Indonesia, Nepal, Philippines, Thailand, and Vietnam. For the latter country, separate searches were performed using the spaced and unspaced name, i.e., "Vietnam" and "Viet Nam." Queries were run using a University of Queensland staff subscription between February 15 and March 10, 2020, accessed through a regular internet connection from Hanoi, Vietnam. The above Web of Science search results were complemented with records obtained with the new scholarly database Dimensions (Thelwall, 2018) and with non-exhaustive queries of national journals, regularly featuring work in languages different from English. The latter searches yielded a fair number of scientific publications for the Philippines, Indonesia and Vietnam, but likely proved incomplete in Thailand and Nepal.

Next, abstracts of the resulting papers were screened and less pertinent studies were omitted from the analysis. This yielded a total of 430 publications covering different facets of biological control, across all five Asian countries. Publications solely comprised biological control interactions between invertebrate resource items (i.e., herbivorous prey, crop pests) and either invertebrate or vertebrate consumers (i.e., natural enemies such as carnivorous predators or endo-parasitoids). Publications that addressed biological control with micro-organisms (i.e., entomopathogenic fungi, bacteria, viruses, microsporidia) were not taken into consideration. Also, publications that solely described on-farm invertebrate biodiversity without explicitly listing either presence, abundance, or diversity of insect natural enemies (i.e., predators, parasitoids) were not taken into consideration. As such, literature records covered a range of research activities under the three subdisciplines of classical (or importation), augmentation and conservation biological control (Bale et al., 2008; Heimpel and Mills, 2017).

Within this extensive literature base, each individual publication was screened to determine the exact research focus. Published research was thus assigned to one or more themes within a six-step sequential "impact pathway" as adapted from concepts presented in González-Chang et al. (2020). More specifically, we considered the following six core thematic areas or categories: (1) biodiversity, (2) core attributes of the ecosystem service provider (ESP), (3) ESP population ecology, (4) service providing protocols (SPP), (5) delivery systems and implementation pathways, and (6) socio-ecological outcomes. The latter theme accounts for agro-ecological practices (e.g., flower strips, intercrops) that have a clear impact in the socio-economic domain, i.e., farmer income and farm-level revenue while including crop yield as an imperfect proxy of those measures. Although the concept of agro-ecological outcomes encompasses social, economic and ecological dimensions (González-Chang et al., 2020), here we have explicitly included economic aspects in the socio-ecological-outcomes step, as poverty in Asia has been recently associated with environmental degradation and pollution (Khan, 2019). The first theme refers to the discovery and description of the diversity of insect natural enemies that occur within farm settings. For the second theme, to assess the available knowledge on ESP core attributes, we considered different sub-themes that help anticipate the effectiveness of a natural enemy in population regulation, i.e., prey specificity, reproductive capacity, and environmental adaptability (DeBach and Rosen, 1991). As such, elements of the biology, life history, mass-rearing potential, or host acceptance behavior of a consumer item were covered (**Table 1**). Similarly, for the third theme on ESP population ecology, we logged studies that entailed either laboratory or in-field evaluations of biological control agents e.g., by using life table and mortality analyses, exclusion assays or dietary assessments (Fisher et al., 1999). Under theme four, we logged all published research that assessed how farmers can put functional biodiversity into practice (Gurr et al., 2017; González-Chang et al., 2020), e.g., by refraining from pesticide use, diversifying crop or farm settings, establishing flower strips (Barbosa, 1998; Landis et al., 2000; Gurr et al., 2016). Lastly, for theme five, we recorded the number of publications that involved end-user perspectives, e.g., farmer knowledge and decision-making, socio-political dimensions or agricultural extension strategies. By thus assigning published work to each these specific categories, it was possible to quantify the extent to which each research endeavor contributed to achieving concrete, verifiable agro-ecological outcomes.

For each literature record, we also logged the year of publication, focal commodity, target resource item (e.g., herbivorous prey, crop pest), consumer item (i.e., natural enemy) and noted whether the work involved field research, laboratory assays, mathematical modeling, farmer surveys or reviews. For resource and consumer items, the exact taxonomic classification was noted. Individual commodities were assigned to different crop categories as defined by the United Nations Food and Agriculture Organization (UN-FAO). Once pertinent literature records were classified within these six categories, a strategy is suggested to enhance ABB systems for each respective Asian country. Yet, in order to avoid a reductionist, pest-centric

**TABLE 1 |** Comparative extent of scientific attention to different themes along a six-step, outcome-oriented impact pathway.

| Theme/Sub-theme | Number of country-level records | | | | |
|---|---|---|---|---|---|
| | Indonesia | Nepal | Philippines | Thailand | Vietnam |
| **Biodiversity** | | | | | |
| Taxonomy | 4 | 1 | 7 | 4 | 3 |
| Genetic make-up | 2 | 3 | 1 | 2 | 0 |
| Insect diversity/pest-NE associations | 62 | 4 | 53 | 19 | 13 |
| **ESP attributes** | | | | | |
| Biology/life history | 24 | 1 | 31 | 9 | 12 |
| Pesticide susceptibility | 2 | 0 | 3 | 2 | 1 |
| Temperature-dept. development | 2 | 0 | 0 | 3 | 2 |
| Mass-rearing potential | 7 | 0 | 8 | 3 | 2 |
| Dietary range/host acceptance | 8 | 1 | 15 | 4 | 3 |
| Handling/searching behavior | 5 | 0 | 8 | 1 | 0 |
| **ESP population ecology** | | | | | |
| Functional response | 10 | 0 | 6 | 0 | 0 |
| Consumer-resource population model | 2 | 0 | 7 | 7 | 0 |
| Dietary assessment | 1 | 1 | 6 | 3 | 0 |
| Food-web dynamics | 20 | 0 | 19 | 2 | 3 |
| In-field dispersal | 1 | 0 | 4 | 0 | 0 |
| NE exclusion (e.g., cage assays, insecticide removal) | 8 | 0 | 1 | 2 | 4 |
| Habitat/landscape associations | 15 | 0 | 17 | 2 | 1 |
| Life table/mortality analysis | 4 | 0 | 0 | 0 | 0 |
| **Service-providing protocols** | | | | | |
| Pesticide avoidance | 15 | 0 | 11 | 3 | 2 |
| Fertilizer/organic matter addition | 3 | 0 | 2 | 0 | 1 |
| Plant spacing/irrigation | 1 | 0 | 3 | 0 | 1 |
| Cropping synchrony/fallowing | 1 | 0 | 1 | 0 | 0 |
| Crop genotype | 2 | 0 | 2 | 0 | 3 |
| Organic/IPM farming scheme | 5 | 0 | 1 | 2 | 0 |
| Crop diversification | 10 | 0 | 5 | 0 | 0 |
| Trap crop/banker plant system | 1 | 1 | 0 | 1 | 0 |
| Flower strip/beetle bank | 3 | 1 | 2 | 1 | 3 |
| Shade tree/canopy cover | 2 | 0 | 0 | 0 | 1 |
| Weed/understory/leaf litter | 3 | 0 | 1 | 1 | 1 |
| Supplementary feeding | 3 | 0 | 0 | 1 | 2 |
| Artificial nesting substrate | 1 | 0 | 0 | 1 | 0 |
| Natural enemy release protocols | 8 | 1 | 9 | 2 | 3 |
| **Delivery systems/Implementation pathways** | | | | | |
| Agro-ecological knowledge | 2 | 0 | 3 | 2 | 4 |
| Management decision-making | 4 | 3 | 6 | 3 | 9 |
| Socio-political interactions | 2 | 1 | 0 | 2 | 2 |
| Training/extension modules | 2 | 3 | 2 | 0 | 4 |
| **Socio-ecological outcomes** | | | | | |
| Environmental health/ecosystem integrity | 0 | 0 | 0 | 0 | 2 |
| Produce quality/yield | 11 | 1 | 9 | 6 | 6 |
| Farmer income | 1 | 1 | 6 | 4 | 6 |

*For each theme, sub-themes are listed that represent important research activities related to biological control. For each of five Asian countries, we list the number of scientific publications that have been generated per sub-theme, over a 50-year time frame.*

approach (Coll and Wajnberg, 2017), no pathways were drawn for individual crop × pest systems.

## RESULTS

Queries resulted in a total of 430 scientific publications, covering field studies (264), laboratory assays (118), reviews and management recommendations (34), farmer surveys (15), theoretical concepts and modeling exercises (14), and green- or screenhouse assays (9). Most records were obtained for Indonesia (159) and the Philippines (138), while for Nepal, Thailand, and Vietnam a respective 16, 62, and 54 publications were collated. A total of 144 publications covered cereals and other graminoids (112 of which including rice), while other well-researched crops were vegetables (86 literature records, 36 of which cruciferous plants such as cabbage or broccoli), orchard crops (66) and oilseed crops (42). Crop focus within each country differed substantially, with 52% of publications from the Philippines addressing cereals (**Figure 1**). With a first record dating back to 1976, literature output has risen over time with individual countries currently generating 10–87 publications per decade (**Figure 1**).

Resource items covered 11 different invertebrate orders and 69 families, with 159 organisms reported at the species-level (**Figure 2**). Most literature records were recovered for Hemiptera (152) and Lepidoptera (138); at the family level, Dephacidae, Cicadellidae (Hemiptera), and Agromyzidae (Diptera) were covered in a total of 62, 46, and 38 publications, respectively. Scientific attention was equally given to consumer organisms, with a respective 163, 173, and 85 publications reporting on either parasitoids, predators or both trophic guilds. Consumer organisms belonged to 18 different class- or order-level taxa (**Figure 2**) and 103 families. Most records were recovered for Hymenoptera (224) and Coleoptera (66); at the family level, Coccinellidae, Eulophidae, and Braconidae featured in 62, 56, and 55 publications, respectively. At the species level, resource organisms that were well-featured included the rice brown planthopper *Nilaparvata lugens* (37 records), the cruciferous pest *Plutella xylostella* (24), and the Asian corn borer *Ostrinia furnacalis* (16). For consumer organisms, ample scientific attention was given to the mirid bug *Cyrtorhinus lividipennis* (14), the leafminer parasitoid *Hemiptarsenus varicornis* (13), and the weaver ant *Oecophylla smaragdina* in orchard systems (13). Resource items comprised both native pests such as *N. lugens* or *O. furnacalis* and invasive pests, e.g., *P. xylostella*, the coconut hispid *Brontispa longissima* or the cassava mealybug *Phenacoccus manihoti*. Hence, biological control interventions included the use of endemic species in conservation (e.g., *O. smaragdina*) or augmentation (e.g., the predatory earwig *Euborellia annulipes*) schemes as well as a scientifically guided introduction of exotic natural enemies (often paired with augmentative releases) such as *Diadegma semiclausum* and *Cotesia plutellae* against *P. xylostella*.

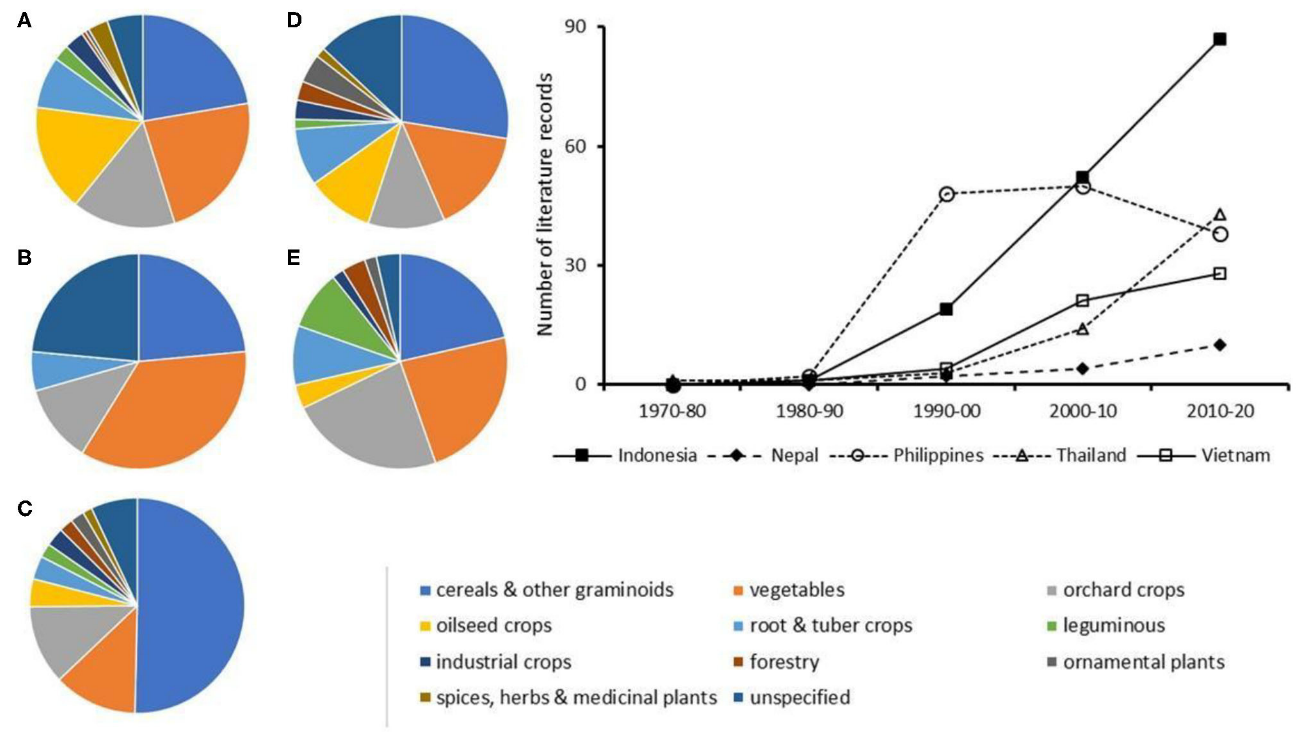

**FIGURE 1** | Temporal and commodity-specific trends in biological control science for selected Asia countries, as determined through systematic literature searches. The left panel comprises pie charts that reflect the relative scientific attention to different classes of agricultural commodities for Indonesia **(A)**, Nepal **(B)**, Philippines **(C)**, Thailand **(D)**, and Vietnam **(E)**. The right panel depicts interdecadal trends in the number of scientific publications covering biological control, for each of the above countries. Crop classifications are based on the United Nations Food and Agriculture Organization, UN-FAO.

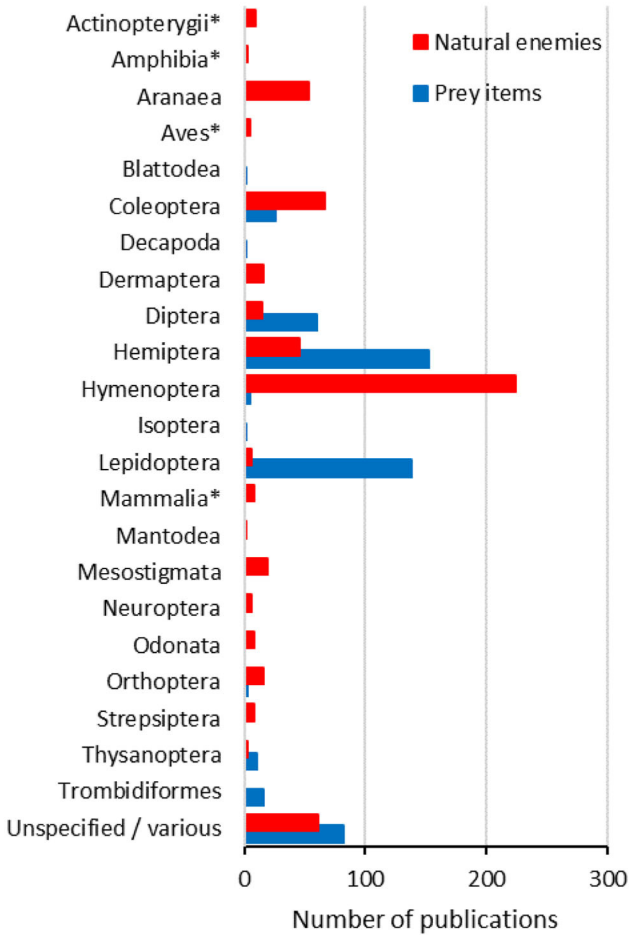

**FIGURE 2 |** Comparative extent of taxon-level scientific attention to prey items (e.g., herbivorous pests) and natural enemies. Bars represent the number of scientific publications covering a given taxon. Taxa include either consumer (i.e., natural enemy) or resource (i.e., prey) items. Taxa comprise different invertebrate orders within the phylum Arthropoda, while those with an asterisk belong to the phylum Vertebrata.

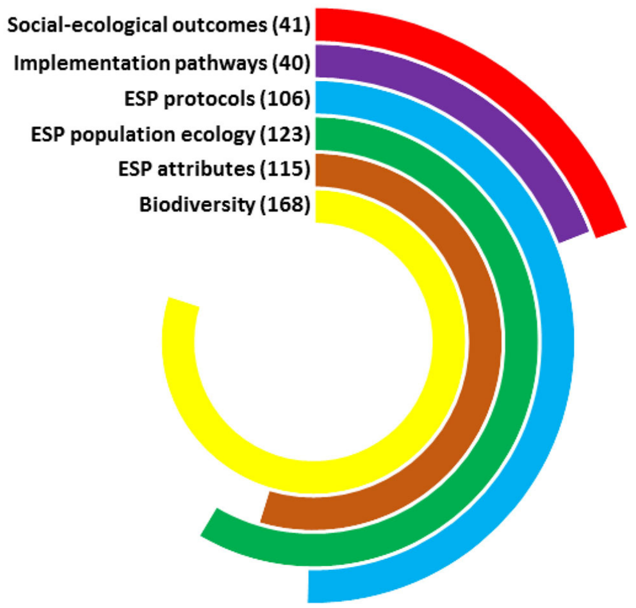

**FIGURE 3 |** Progress of biological control science along a six-step, outcome-oriented "impact pathway" for all Asian countries over a 50-year time frame. Within the concentric donut chart, the exact circumference of each loop mirrors the relative amount of scientific attention to a given research theme. For a given theme, the respective amount of scientific attention is expressed by the number of publications covering this theme. Themes include the measurement of farm-level biodiversity (inner-most circle) or a characterization of key attributes of ecosystem-service providers (ESP), to ultimately culminate in the envisioned social-ecological outcomes. Social-ecological outcomes also include crop yield (i.e., primary productivity) as imperfect proxy of farmer income or farm-level revenue, both important in achieving agro-ecological outcomes.

Along the six-step, outcome-oriented impact pathway, 168 (out of 430) publications covered the discovery and description of biodiversity in local ecosystems (**Figures 3**, **4**; **Table 1**). Lesser degrees of scientific attention were given to assess ESP attributes and population ecology, with up to 24–31 studies per country covering ESP biology and life history and up to 15 studies addressing host range and feeding patterns (**Table 1**). ESP population ecology was well-covered in Indonesia and the Philippines, with ample attention given to measuring functional response, characterizing in-field population dynamics or quantifying habitat- and landscape-level associations. Myriad experimental methods were employed to quantitatively assess natural enemies' interaction with resource items, with up to 4, 6, and 8 studies/country, respectively involving life table analysis, exclusion techniques and dietary assessment e.g., using behavioral observations or stomach flushing of fish and frogs. A total of 106 publications reported the field-level evaluation of service-providing protocols (SPPs), usually involving manipulative assays to record the impact of specific management changes (i.e., up to 15 publications/country reporting pesticide avoidance or fertilizer addition), habitat manipulations (i.e., up to ten records/country covering crop diversification or flower strips) or natural enemy additions. Work in Thailand and Indonesia assessed artificial nesting substrates for the predator ants *O. smaragdina* and *Dolichoderus thoracicus* in cocoa and fruit orchards (Anshary and Pasaru, 2008; Offenberg, 2014). Many SPP evaluation studies involved the concurrent in-field monitoring of pest and natural enemy populations but did not entail additional manipulative assays to quantify strength of biological control.

Comparatively low amounts of scientific attention were given to themes further along the BC impact pathway such as delivery systems, implementation pathways, and socio-economic outcomes (**Figure 3**; **Table 1**). In the former theme, most publications (25) either covered scientists' characterization of farmer management practices and decision-making processes underlying the uptake of biological control or outlined pest management recommendations—the latter routinely tailored to scientists instead of to farmer end-users. Publications

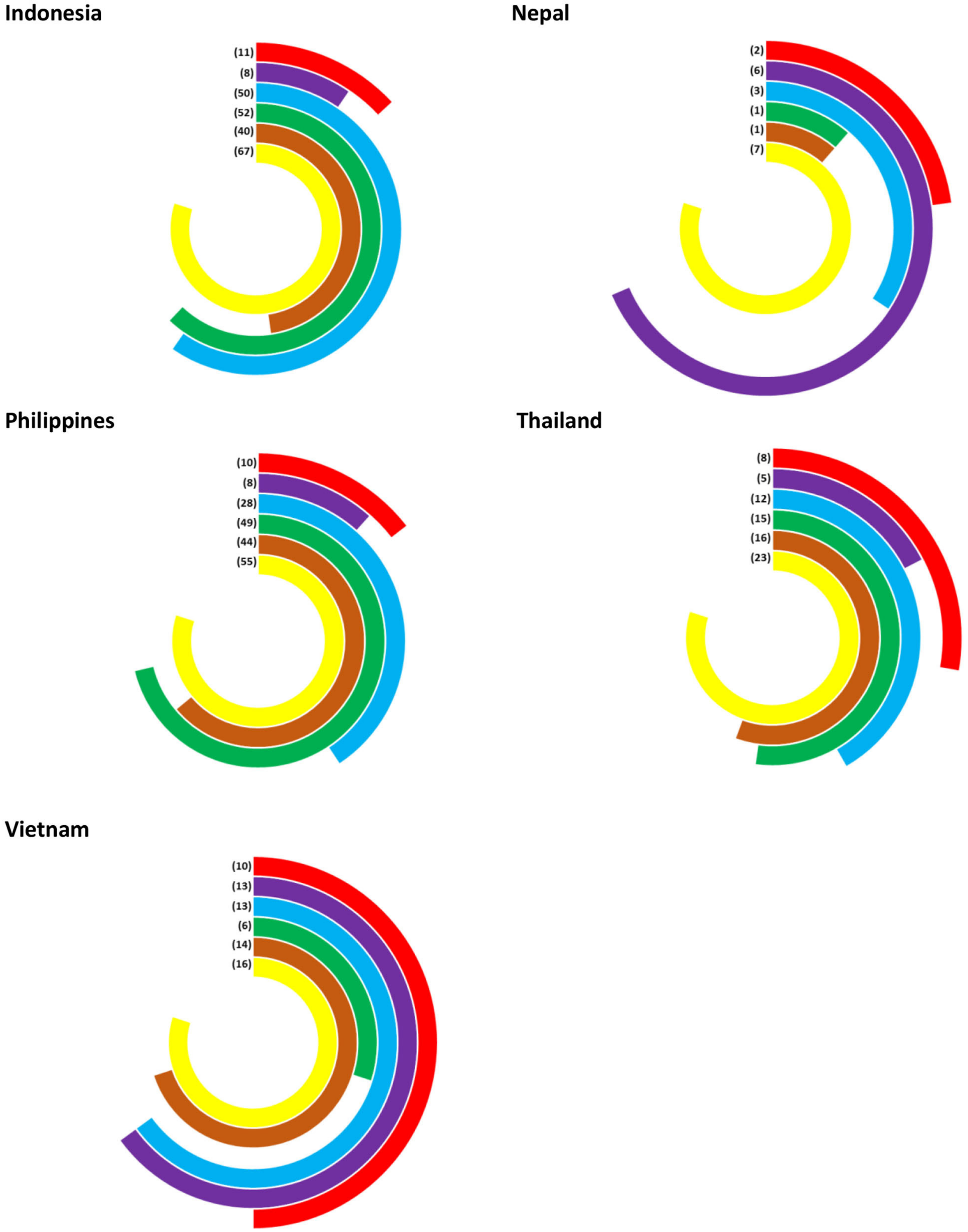

**FIGURE 4 |** Country-level progress of biological control science along a six-step, outcome-oriented "impact pathway." Within each chart, the number of scientific publications covering a given theme is indicated next to the respective loop. The inner-most circle reflects relative scientific attention to biodiversity assessments; the outer-most circle captures social-economic outcomes.

covering farmers' (agro-ecological) knowledge were equally limited in geographic and commodity scope, with 3–4 records each (out of 11) on Philippine rice or fruit orchards in Vietnam's Mekong Delta (but see Yanuwiadi, 2017). In terms of outcomes, though 33 different publications reported changes in crop yield, farm-level agricultural output or indices of product quality (i.e., sweetness, juiciness or oranges; Barzman et al., 1996), as few as 18 studies reported true socio-economic outcome measures such as farmer income. Also, social-ecological outcomes of biological control were only assessed in a comparatively small complement of cropping systems, i.e., fruit orchards, cassava, rice, and cruciferous crops impacted by the diamondback-moth *P. xylostella*. This lack of studies concerning socio-economic and socio-ecological parameters reflects a global challenge to reduce the gap between science and practice (Kleijn et al., 2019; Shields et al., 2019; González-Chang et al., 2020).

Biological control science in each of the five Asian countries progressed to variable extent along our six-step impact pathway (**Figure 3**). While the bulk of scientific publications from Indonesia or the Philippines covered the first three or four "basic" themes, reverse patterns were observed for Nepal. In Vietnam, scientific attention evenly covered the entire pathway, though crop and geographic focus for themes five and six was largely confined to rice, cassava, and fruit orchards (the latter in the Mekong Delta). Conversely, when considering crop-specific impact pathways, we recorded a lagging scientific attention to themes further along the pathway for grain cereals and oilseed crops such as coconut, oil palm, or soybean (**Figure 5**). For cereal crops such as rice, though ample scientific attention was given to the description of biodiversity, in-field population ecology and SPP validation, comparatively little advances were made in characterizing core attributes of ESPs, such as natural enemy communities and their environmental interactions.

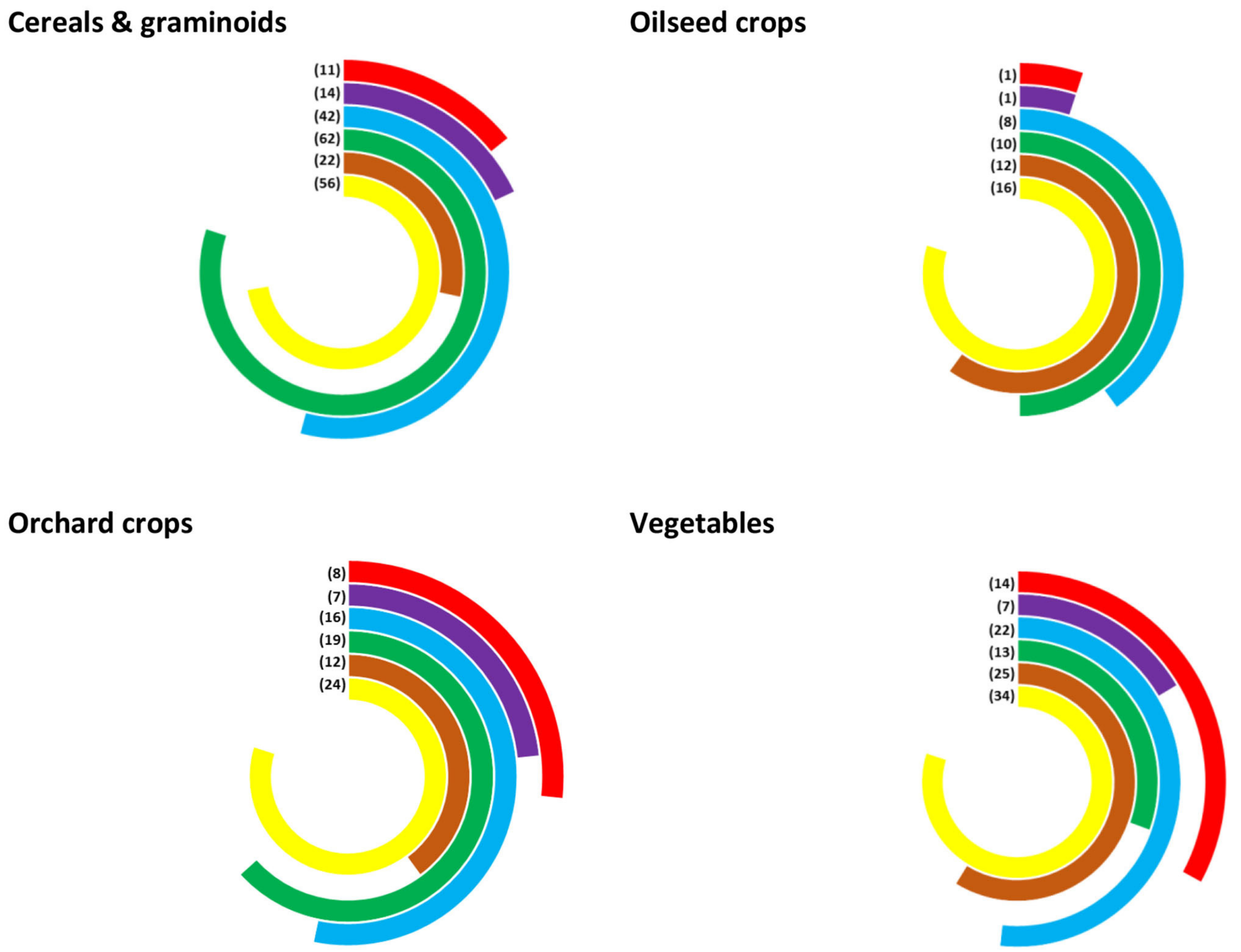

**FIGURE 5 |** Commodity-specific progress of biological control science along a 6-step, outcome-oriented "impact pathway." Within the concentric donut chart, the exact number of scientific publications covering a given theme is indicated next to the respective loop. Patterns are plotted for all five Asian countries, over a 50-year time frame. The category of "cereals and graminoids" includes rice, while "oilseed crops" covers coconut, oil palm, and soybean. Crop classifications are based on the United Nations Food and Agriculture Organization, UN-FAO.

# DISCUSSION

To mitigate the externalities of conventional, high-input agriculture, and to keep global food systems within environmental limits, transformative change –if not a "Greener Revolution" – must be pursued in current farming systems (Tilman, 1998; Poore and Nemecek, 2018; Pretty et al., 2018; Willett et al., 2019). Such transformation can be enabled through applied ecology (Bommarco et al., 2013), released through social science e.g., anthropology and economics (Hackmann et al., 2014; Naranjo et al., 2015) and brought about hand-in-hand with farmers and food producers (Altieri, 2004; MacMillan and Benton, 2014; Zhang et al., 2016; Mills et al., 2017; González-Chang et al., 2020). Biodiversity is the cornerstone of such revolution, featuring prominently in legume-based diversification and other practices to regenerate soil health (Snapp et al., 2010; LaCanne and Lundgren, 2018) or in the field-level conservation of biological control (BC) organisms (Dainese et al., 2019). Yet, in order for BC to achieve its full potential, scientists need to measure the correct variables and address the right questions (Geertsema et al., 2016; Jeanneret et al., 2016; Chaplin-Kramer et al., 2019). Here, fragmented research agendas, pest-centric approaches and disciplinary boundaries prevent the necessary holistic perspectives, obstruct collaboration and impede defining effective, integrative "action-oriented" solutions (Brondizio et al., 2016; DeFries and Nagendra, 2017; Yletyinen et al., 2019). Our "Humboldtian" perspective offers a structured quantification of the progress BC science has made in translating on-farm biodiversity into concrete, verifiable socio-ecological outcomes.

Our work complements earlier "culturomics" assessments of biodiversity and ecosystem services research (Hines et al., 2019) while drawing on recent advances in agricultural innovation science, e.g., transdisciplinary weed research (Jordan et al., 2016; Wigboldus et al., 2016). By doing so, this paper transcends the traditional "mono-disciplinary" field of applied insect ecology—in which, over the past century, innumerable dedicated scientists have laid a solid foundation for the technical facets of pest management science and biological control (e.g., Barbosa, 1998; Fisher et al., 1999; Landis et al., 2000; Gurr et al., 2017; Heimpel and Mills, 2017). Instead, through extensive literature searches and standardized analyses, we captured all BC published work irrespective of disciplinary boundaries, thus accounting for scholarly outputs that comprised biodiversity, ecological processes or farm management interventions but also decision-making among different stakeholders (e.g., scientists, farmers, extension personnel) at varying spatial scales (e.g., in-field, farm, agro-landscape, region). As such, we gain unprecedented insights into the extent to which BC innovations—under given Asian geographical or cropping system contexts–are "fit for purpose," technically ready to be used at scale and can thus contribute to agro-ecological transitions in agri-food systems (El Bilali, 2019; González-Chang et al., 2020; Sartas et al., 2020). Based upon our analyses, several BC interventions are ready for scaling e.g., farm- and landscape-level interventions to enhance conservation BC in rice (e.g., Westphal et al., 2015; Horgan et al., 2019), the century-long use of the weaver ant *O. smaragdina* in fruit orchards (Van Mele and Cuc, 2000), or the integrated use of *Bacillus thuringiensis* (Bt) and *C. plutellae* or *Diadegma insulare* parasitoid releases in cruciferous crops.

Our assessment, though comprehensive and interdisciplinary, is not without caveats. First, published work by national scientists in either domestic or Asia-regional academic journals was rarely picked up by WoS and Dimensions search engines. This data gap was filled to varying extent by running further in-country searches, e.g., covering national library databases. Second, though biological control constitutes a core component of integrated pest management (IPM), it is only intermittently listed as such in abstracts of IPM-related papers. Hence, publications that covered e.g., IPM farmer field schools and community IPM (Röling and Van De Fliert, 1994; Matteson, 2000; Pontius, 2002) outlined how participatory extension methods helped farmers identify and value natural enemies but often did not explicitly cover biological control. Hence, some of these papers equally were not included in our assessments. Third, we observe uneven reporting of BC socio-ecological outcomes between countries, crop × pest systems and scientific disciplines. While natural scientists sustain a steady publication output covering in-field dynamics or BC ecological outcomes (Cock et al., 2016), published ex-post assessments of BC interventions by social scientists remain rare—especially in Asian countries (Onstad and Knolhoff, 2009; Naranjo et al., 2015; Shields et al., 2019; Upadhyay et al., 2020). We recognize that future endeavors must account for the above issues, in order to paint a complete picture of BC science (and its resulting socio-ecological achievements).

Biodiversity-based interventions pay off; though only 4.2% of all BC publications found here reported monetary impacts, farm-level impacts are often substantial. One third of these studies specifically reported on the in-field conservation or augmentative release of *C. plutellae* and *D. insulare* wasps in cruciferous crops, which raised farmer income by up to 78% (Morallo-Rejesus et al., 2000) and cut pesticide expenditure with US$133-513/ha in various settings (Nga and Kumar, 2008; **Table 2**). Considering how 59–100% of farmers in Vietnam, Cambodia or Laos overuse pesticides at values up to $262/ha/cycle in leafy brassicas, BC constitutes a viable, practicable alternative to pesticide-based schemes. By lifting financial solvency of farming households, BC may even allow for incremental spending on consumer goods and potentially feed forward into the national economy (Haggblade et al., 2007). Farm-level monetary benefits however are not only restricted to cruciferous vegetables. In sugarcane, planted on >2.7 million hectares in Southeast Asia, scheduled releases of the larval parasitoid *Cotesia flavipes* raised profit by a staggering 208–315% (Maneerat et al., 2017). Simulation analyses further revealed how inoculative releases of the encyrtid *Anagyrus lopezi* may bring up to $1,714/ha increased revenue for cassava producers (Aekthong and Rattanakul, 2019), while conservation of the wrinkle-lipped bat *Tadarida plicata* annually yields US $1.2 million in dividends for Thailand's national economy (Wanger et al., 2014). This kind of economic valuation of ecosystem services is crucial -though not sufficient- to allow broader societal recognition, raise its stock with key stakeholders and ultimately attain outcomes at scale (Kronenberg, 2014; Naranjo et al., 2015). Considering how just 18 studies have attempted to value BC

**TABLE 2 |** Concrete monetary impacts of historic biological control interventions.

| Crop × pest system | Intervention | Country/year | Monetary impact |
|---|---|---|---|
| *P. xylostella* × cruciferous | Selective insecticides, decision thresholds | Indonesia/2001 | Costs−64–79% |
| | Parasitoid releases, Bt sprays[a] | Philippines/1994 | Net income + 40% |
| | | Philippines/1996 | Net income + 17% |
| | | Philippines/2000 | Net income + 5–78% |
| | | Philippines/2003 | ND[b]; enhanced profit |
| | | Vietnam/2008 | Costs–US$133–513/ha |
| Various × vegetables | Decision thresholds | Nepal/1997 | ND; lower costs and enhanced profit |
| Various × rice | Habitat manipulation | Philippines/2017 | ND; enhanced income |
| | Selective insecticides | Philippines/1996 | ND; enhanced income |
| | Habitat manipulation | Thailand/2016 | Net income + 7.5% |
| | Pesticide reduction, rice-fish integration | Vietnam/2017 | Gross income + 10–30% |
| *Sogatella furcifera* × rice | Bat conservation | Thailand/2014 | national economic value > US $1.2 million |
| Various × sugarcane | Parasitoid releases | Thailand/2017 | Net income + 208–315% |
| *Phenacoccus manihoti* × cassava | Parasitoid releases | Thailand/2019 | Net income + US$1,714/ha |
| | Parasitoid introduction | Vietnam/2018 | Stabilized commodity price |
| | Parasitoid introduction | Vietnam/2019 | Stabilized commodity price |
| Various × orchard crops | Ant conservation | Vietnam/2001 | Income unaffected |
| | Ant conservation | Vietnam/2013 | Net income +47% |

*Records cover all three subdisciplines of biological control (i.e., classical, augmentation, conservation) and are limited to those featured in the scientific literature, for five selected Asian countries over a 50-year time frame.*

[a] *Bt, B. thuringiensis; IGR: insect growth regulator.*

[b] *ND, not determined.*

services across Asian agro-landscapes over a 50-year timeframe, a step-change is clearly needed.

By assigning published work to specific steps along the outcome-oriented "impact pathway," regional progress in BC science became visible. Invertebrate taxonomy surely needs more "boots on the ground" in the tropics (Wilson, 2017), yet 39% of publication output covered the (morphological, molecular) identification of on-farm biota and entailed the description of pest × natural enemy communities in Asian agro-ecosystems. This emphasis on biodiversity discovery/description is manifest across crops and geographies (**Figures 2**, **3**) and catalyzed "downstream" applied ecology research across core domains—except for Nepal. For cereals and graminoids, the comparatively minor attention to ESP attributes is partially counterweighted by trials in other countries (e.g., on rice-inhabiting parasitoids and predators; Zhu et al., 2014) and extensive field-level community ecology and SPP assays. Limited attention was paid to life history trials on plant-derived, non-prey foods such as pollen (five studies), floral nectar (1), or honey as a substitute (6) (Lundgren, 2009); even though these assays underpin the development of effective SPPs (Gurr et al., 2017). Similarly, to quantitatively assess BC services, novel methods such as video surveillance, serological assays, or molecular gut content approaches have not been used (Phillips and Gardiner, 2015). Across cropping systems, studies were performed using a range of baselines, currencies and spatial scales (Hines et al., 2019). As such, ESP populations were studied along pesticide-use, soil fertility or land-use intensity gradients (Basedow, 1993; Klein et al., 2002; Wyckhuys et al., 2017). While field- or farm-level studies were common across settings, studies at broader spatial scale were primarily carried out in cocoa- or rice-based systems in Indonesia and the Philippines (Maas et al., 2013; Dominik et al., 2017). Aside from considering soil-based SPPs in six studies (**Table 1**), virtually no attention is given to the interplay between soil-dwelling and above-ground biota; a presumed driver of biological control (Veen et al., 2019). The shape of the commodity-specific impact pathways mirrors the BC subdisciplines that are primarily pursued. In oilseed crops such as coconut and oil palm, interventions targeted invasive pests such as *B. longissima* (6), *Aspidiotus rigidus* (4), or *Raoiella indica* (2), and primarily entailed biology and ecology studies, followed by guided releases of candidate natural enemies. Farmers and land managers were routinely bypassed and impact assessments were few (Andrews et al., 1992; Geertsema et al., 2016; Barratt et al., 2018), thus resulting in pathways in which categories five and six were critically under-represented. Conversely, for orchard and vegetable systems, BC science covered more "downstream" themes though this often resulted from the devoted work of few individual scientists or single institutions (e.g., Van Mele and Cuc, 2000).

Our exercise helps strategize science to fill key research gaps and to devise proper SPP protocols, thus improving the odds of achieving concrete outcomes. Out of the myriad ways to accelerate BC uptake across Asian agri-food systems, we spotlight three clear opportunities. First, predatory mites constituted the focus of 20 (largely laboratory-based) studies, with new species continuing to be described (Kreiter et al., 2020) while local farmers are still unaware about their existence and BC role (Wyckhuys et al., 2019). Further taxonomic surveys are warranted in Asia's biodiversity-rich agro-ecosystems, but applied socio-ecological research is also needed to ensure that conservation or augmentation BC with Phytoseiid mites is "fit for purpose" and properly valued by end-users. Second, Tephritid fruit flies are key pests of multiple fruit and vegetable crops, yet were only covered in 1.6% of BC publications. Given how fruit flies are vulnerable to predation during the larval and pupal stages (Bateman, 1972), generalist soil-dwelling predators can greatly enhance Tephritid mortality in orchards (Albertini et al., 2018). In this sense, the use of molecular tools is a promising strategy to unveil trophic interactions (González-Chang et al., 2016), identify key fruit fly predators (Albertini et al., 2018), and ultimately formulate suitable locally-adapted SPP. Third, invasive pests put a major drag on Asian economies (Nghiem et al., 2013) and pest targets have been prioritized for BC (Waterhouse, 1998). To exploit BC for invasive pest management, all steps along the "impact pathway," i.e., from biodiversity discovery in foreign exploration to an on-farm valuation of appropriate SPP such as release rates and densities (Shea et al., 2002), are important and can help disseminate BC knowledge amongst farmers (González-Chang et al., 2020). A proper *ex-ante* assessment of the dietary breadth of candidate natural enemies (e.g., as *in-vitro* description of ESP attributes) is essential to account for eventual risks, ensure biosafety and carefully anticipate eventual non-target impacts (Barratt et al., 2010; Barratt, 2011).

Our work rekindles the long-standing interest in systems thinking for pest management (e.g., Lewis et al., 1997), accentuates how BC science touches upon the multi-faceted socio-ecological dimensions of Asian agriculture, and draws science-based trajectories to enhance the likelihood of attaining concrete socio-ecological outcomes. As a true pioneer in systems thinking, Alexander von Humboldt straddled scientific disciplines such as ecology, climatology, and geosciences to pursue ground-breaking theories that shaped much of our current scientific understanding of natural phenomena (Jackson, 2009; Wulf, 2015). More than 200 years ago, Humboldt realized how human-mediated land-use change can disrupt the delicate ecological balance of nature and ultimately impact societal well-being. As such, Humboldt inspired our effort to devise strategies that harness biodiversity in farming systems and thereby realize the promise of insect biological control. Our "Humboldtian" perspective foment a transformational change in Asian agri-food systems, ultimately pursuing ABB farming systems that foster human well-being without sacrificing nature.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

KW and MG-C conceived the manuscript and organized the literature review process. All authors contributed to writing this article.

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REVIEW
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# Temporal Resource (Dis)continuity for Conservation Biological Control: From Field to Landscape Scales

**Benjamin Iuliano**[1]* **and Claudio Gratton**[1,2]

[1] Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI, United States, [2] Department of Entomology, University of Wisconsin-Madison, Madison, WI, United States

Conservation biological control (CBC) seeks to promote the occurrence of natural enemies of agricultural pests by managing habitat to provide key resources in and around farm fields. In particular, vegetation diversity may help ensure temporal resource continuity such that natural enemies are less likely to experience detrimental gaps or bottlenecks as they move through and use different habitats. While the conceptual value of resource continuity has long been recognized by CBC researchers and practitioners, empirical studies have tended to focus on snapshots in space and time. Here we review how continuity of trophic (food) and structural (shelter) resources affect natural enemy conservation and pest control outcomes within farm fields and across agricultural landscapes. Key trophic resources include alternative prey and non-prey food (such as floral nectar and pollen), which can bolster natural enemy nutrition when pests are scarce. Vegetative and non-vegetative structural resources can protect enemies when crop fields are disturbed and provide important overwintering habitat in temperate regions. Within fields, non-crop plantings such as wildflower strips or beetle banks are the most popular habitat management strategies, but temporal intercropping, asynchronous planting/harvesting, and the construction of artificial shelters have high potential to contribute to resource continuity. Analogously, semi-natural habitat at the landscape scale may contribute to resource continuity in some cases, but crop diversity, asynchrony, and urban habitat can also be important. Simultaneous consideration of resource diversity and continuity could generate better predictions and more targeted management interventions for particular pest and enemy assemblages. Future research should strive to expand our understanding of natural enemy resource requirements in space and time.

**Keywords: habitat management, natural enemies, agroecology, predator-prey interactions, landscape ecology, entomology**

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*Inge Armbrecht,*
*University of Valle, Colombia*

***Reviewed by:***
*Adrien Rusch,*
*Institut National de la Recherche Agronomique (INRA), France*
*Michael Garratt,*
*University of Reading, United Kingdom*

***Correspondence:**
*Benjamin Iuliano*
*biuliano@wisc.edu*

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## INTRODUCTION

Farmers, scientists, and policymakers are increasingly looking for ways to "ecologically intensify" agricultural production to meet the needs of human populations while minimizing negative effects on the environment and protecting biodiversity (Bommarco et al., 2013; Tittonell, 2014; Kleijn et al., 2019). Habitat management is often promoted as a promising strategy for managing insect pests while avoiding the downsides of indiscriminate insecticide use (Landis et al., 2000; Gurr et al., 2017). This typically entails diversifying fields and landscapes to minimize the occurrence of herbivores and promote their natural enemies, an approach known as conservation biological control (CBC; Begg et al., 2017). CBC constitutes a shift from the presently dominant "curative" approach to pest control, focused on the use of pesticides once pest problems arise, to a preventative paradigm that relies on biodiversity conservation to support agricultural production. Yet such a shift requires agroecological approaches supported by theoretical underpinnings and a technical infrastructure that enable ecological intensification in ways that are good for farming and the broader environment.

Many principles and practices associated with CBC are thousands of years old (Shields et al., 2019). For example, there are records of farmers in fourth century China manipulating weaver ant nests in citrus orchards to protect the fruit from pests (Huang and Yang, 1987), and indigenous farmers across the tropics engage in various cultural practices to avoid pest outbreaks (Morales, 2002). However, formal scientific investigations by ecologists and entomologists are relatively young (Shields et al., 2019). A classic paper by Root (1973) sparked significant interest in the "enemies hypothesis," which posits that predators and parasitoids should benefit more from plant diversity than their herbivore prey, increasing the ratio of natural enemies to pests and providing top-down control. This early formulation explicitly recognized the potential importance of resource continuity in time for natural enemies. Root (1973) writes:

> "A greater diversity of prey/host species and microhabitats is available within complex environments, such as most natural, compound communities. As a result, relatively stable populations of generalized predators and parasites can persist in these habitats *because they can exploit the wide variety of herbivores which become available at different times.*"

However, most studies and syntheses of CBC research have ignored temporal dynamics and focused on snapshots of insect populations in space (i.e., in focal crop fields) and at particular times (i.e., during the growing season of the focal crop). Furthermore, researchers frequently assume but rarely measure or directly account for the resource complementation in time that Root (1973) described.

While some studies have demonstrated that diverse fields (Letourneau et al., 2011; Dassou and Tixier, 2016) and landscapes (Chaplin-Kramer et al., 2011; Dainese et al., 2019) can promote more natural enemies and fewer pests than monocropped systems, it is by no means a guarantee (Tscharntke et al., 2016; Karp et al., 2018). Uncertainty about the effectiveness of habitat management, high risk aversion, and perception of non-crop habitat as a likely source of pests make farmers wary of adopting preventative pest management approaches (Salliou and Barnaud, 2017; Chaplin-Kramer et al., 2019; Shields et al., 2019). The challenge for agroecologists is to improve the scientific basis for habitat management while accounting for the context-dependency of pest and natural enemy dynamics (Settele and Settle, 2018). Temporal resource patterns are increasingly recognized as a crucial aspect of agroecosystem context, with many calling for more rigorous consideration in CBC research (Welch and Harwood, 2014; Schellhorn et al., 2015; Haan et al., 2020; Spiesman et al., 2020).

Here, we review the role of temporal resource continuity—and its opposite, discontinuity—for CBC in agricultural systems. While temporal resource patterns are likely to be important across agroecosystems globally, a persistent bias in CBC research toward the developed world (Wyckhuys et al., 2013; Peñalver-Cruz et al., 2019) makes examples from tropical regions scarce; thus, the empirical cases we draw upon come primarily from temperate regions, with a few key exceptions. We begin by outlining a conceptual framework for understanding how and in what instances temporal continuity may be important for facilitating desirable pest and enemy population dynamics. We then use this framework to summarize published studies that explicitly consider the temporal dimensions of different types of resources and habitat management strategies. Our systematic review of the literature focuses on top-down control by natural enemies, but we acknowledge that temporal resource patterns are also highly relevant to bottom-up processes (i.e., Root's "resource concentration hypothesis"; Root, 1973); accordingly, we include a brief discussion of these considerations. We conclude by proposing a new framework for predicting and evaluating the effects of heterogeneous resources on arthropods in agroecosystems that distinguishes temporal considerations from diversity *per se,* and offering recommendations for future research.

## CONCEPTUAL FRAMEWORK: DEFINING RESOURCES, CONTINUITY, AND SCALE

The collection of organisms that function as "natural enemies" of crop pests is incredibly broad and diverse, ranging from vertebrates to viruses. Even within the narrower grouping of *arthropod* natural enemies on which we focus here, species have considerable variation in their life history traits including diet breadth, mobility, voltinism, longevity, and habitat requirements. Accordingly, the particular resources in question, as well as the spatial and temporal scales relevant to patterns of resource continuity are highly context dependent. Nevertheless, the ecological processes underlying resource use and population dynamics are largely generalizable.

In simplified agroecosystems with just one or few annual crop types, resource scarcity is likely for significant portions of the year or growing season (e.g., before planting or after harvest), even if these resources may be occasionally abundant (i.e., a resource pulse; Ostfeld and Keesing, 2000; Yang et al., 2008). This situation creates *discontinuity* for organisms in need of resources over extended periods of time (**Figure 1A**). In contrast, complex, diversified, and/or perennial systems may include multiple types of crop or non-crop vegetation with different phenologies, providing more *continuous* resources over time (**Figure 1B**).

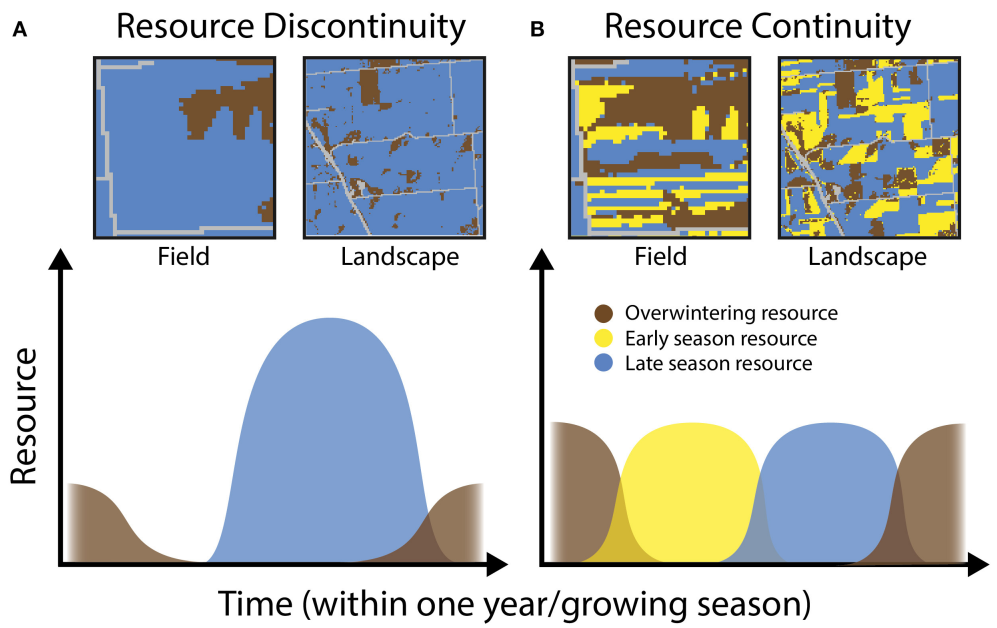

**FIGURE 1 |** Conceptual representation of how resources may vary through time in heterogeneous agroecosystems. **(A)** Depicts hypothetical low-continuity scenarios in a single farm field or an entire agricultural landscape. In these scenarios, natural enemy populations are limited by overwintering habitat and experience a resource gap in the early season. **(B)** Depicts high-continuity scenarios where enemies have sufficient resources available at all times.

Promoting the successful development and persistence of abundant natural enemy populations in agroecosystems thus requires "linking the resource chain" (Schellhorn et al., 2015) through time by ensuring that the appropriate trophic and structural resources are locally or regionally accessible—that is, within farm fields or in the surrounding landscape. This principle has been recognized for a different group of beneficial arthropods, wild and managed bees, and such "feast-famine" conditions have been shown to be important for pollinators and pollination services (Mallinger et al., 2016; Dolezal et al., 2019; Hemberger et al., 2020). Similar temporal dynamics are likely to be consequential for natural enemies and pest control (Schellhorn et al., 2015).

In the short term (i.e., the span of a single growing season), ensuring temporal resource continuity could be beneficial for promoting early recruitment of natural enemies to subsequent crops. The importance of early predation or parasitism for effective pest suppression is well-established in theoretical predator-prey population models (Ekbom et al., 1992; van der Werf, 1995). Thus, manipulating resources to attract and maintain natural enemies within crop fields could provide farmers with immediate pest control benefits. In the longer term, resource continuity is important for shoring up the stability of natural enemies by reducing gaps and bottlenecks that may result in the failed development of entire generations and ultimately reduced population sizes (Schellhorn et al., 2015).

Like all organisms, arthropod natural enemies rely upon two broad categories of resources in order to carry out their life cycles: food, or *trophic resources*, and shelter, or *structural resources*. In addition to crop pests, trophic resources include alternative prey as well as non-prey food such a floral nectar and pollen (**Figure 2**; section Trophic Resources). Structural resources include both short term refugia from disturbance as well as longer-term shelter such as overwintering sites (**Figure 2**; section Structural Resources). Because natural enemies are mobile, traversing multiple resource patches within and/or across generations, individuals, or populations may benefit from the ability to acquire resources from multiple patches of the same habitat type (landscape supplementation), while some may necessitate distinct resources from spatially segregated habitats (landscape complementation; Dunning et al., 1992). For many arthropods, particular trophic or structural resources requirements may vary across life stages or seasons. For example, a parasitoid wasp may feed and develop inside a caterpillar during its larval stage but benefit from nectar as an adult (varied trophic resources requirements). Alternatively, predatory beetles may forage in herbaceous vegetation as both larvae and adults during warm months but aggregate in wooded areas to overwinter (varied structural resource requirements). Proponents of CBC frequently recognize the relevance of organism movement from natural vegetation to crops, but spillover in the opposite direction is equally important from the perspective of continuous resource access and population persistence (Rand et al., 2006; Blitzer et al., 2012).

As mentioned above, the life history traits of the arthropod enemies in a particular agroecosystem will dictate the relevant spatial and temporal extents of resource access and use. For example, the distance over which a species is able to disperse or forage has substantial bearing on the scale at which habitat patches could feasibly contribute to temporal resource

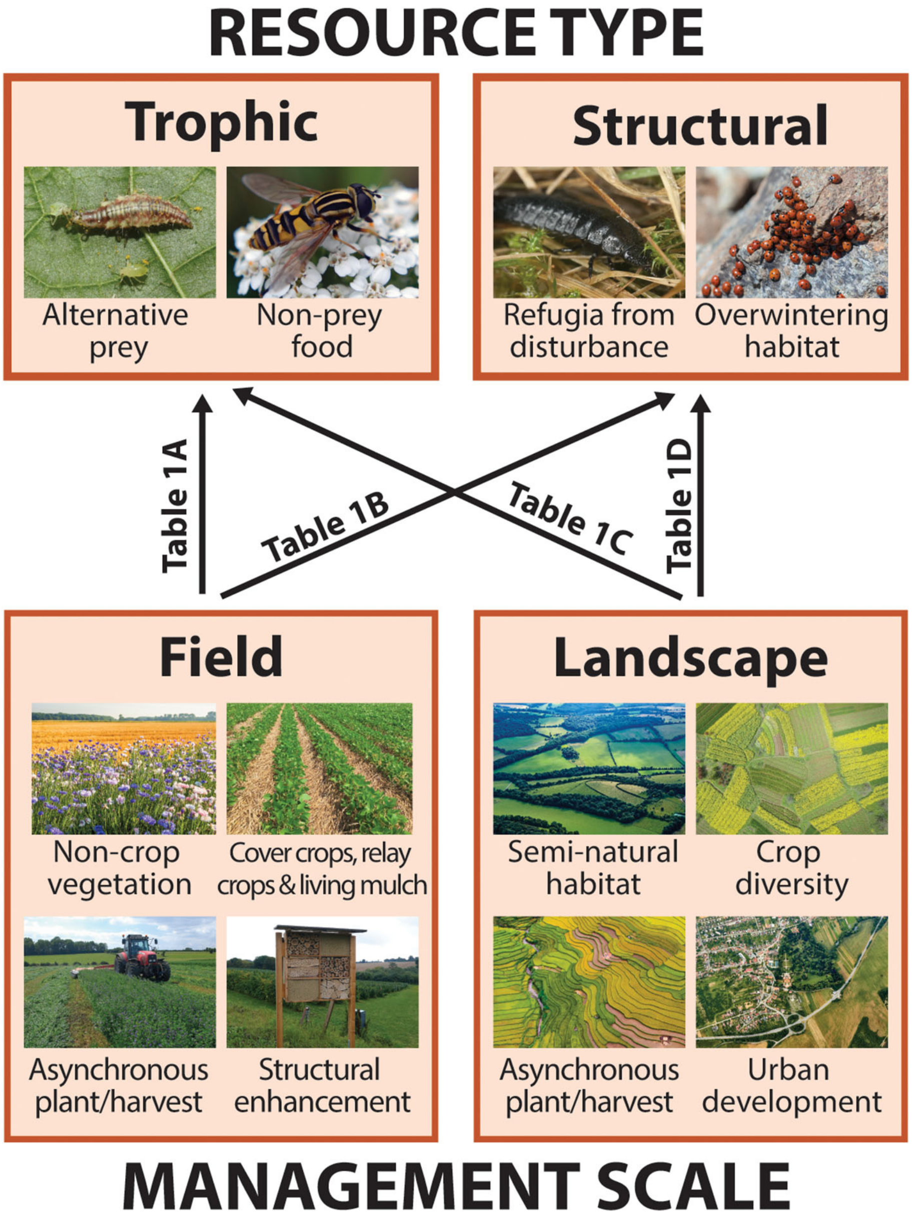

**FIGURE 2 |** Graphical schematic of the relationships between key natural enemy resources and habitat features that may contribute to their continuity or discontinuity at two management scales (described in section Conceptual Framework: Defining Resources, Continuity, and Scale). Boxes correspond to subsequent sections detailing how and in what instances different resource types, trophic (i.e., food) or structural (i.e., shelter), may be important for natural enemies (section Resources for Natural Enemies: Trophic and Structural), and management features that contribute to resource continuity both within-fields and across agricultural landscapes (section Creating Continuity: Habitat Features in Fields and Landscapes). Arrow labels refer to rows in **Table 1** listing examples of studies that describe each of four scale-by-resource interactions. Photos via Shutterstock, standard license.

continuity; large-bodied species with strong flight ability would be influenced by conditions at greater spatial extents than small, ground-dwelling species. Similarly, a long-lived species with a single generation per year would require a different duration of resource access in order for conditions of "temporal continuity" to be met than a short-lived species with many generations per year. In other words, it remains crucial to take an "organism's eye view" of the world when determining ecologically relevant scales of investigation and manipulation (Wiens, 1989).

At the same time, we identify two scales relevant to farmers and other land stewards for temporal resource management in agroecosystems: within a single crop field (field level) and across multiple fields and adjacent non-crop areas (landscape level). Field scale management features that have the potential to generate or increase temporal resource continuity for natural enemies include cover crops, relay crops, and living mulches, non-crop plantings, and structural enhancements such as overwintering shelters (**Figure 2**; section In-Field Features). In studies of the landscape ecology of predator-prey interactions, so-called "semi-natural habitat," or non-crop vegetation around farm fields, is the landscape-level feature most often considered to enhance natural enemy populations and pest control outcomes (Chaplin-Kramer et al., 2011; Karp et al., 2018; Dainese et al., 2019), but others may include landscape-scale crop diversity, asynchronous planting/harvesting, and urban development (**Figure 2**; section Landscape Features).

Importantly, resource type and management scale interact to affect natural enemy populations. That is, continuities or discontinuities can arise in both trophic and structural resources at field or landscape scales (**Figure 2** and **Table 1**). In the following sections, we explore each of these interactions by highlighting examples from a systematic review of the peer-reviewed literature that relate temporal resource continuity and natural enemies in agroecosystems. For simplicity, we describe resource type and management scale separately, with examples of particular scale-by-resource combinations throughout.

To conduct our review, we used ISI Web of Science to search peer-reviewed English-language literature through February 2020. To capture research on pest control, we used the topic terms "pest suppression" OR "pest control" OR "pest regulation" OR "biological control" OR "biocontrol" OR "natural enem*"; to capture temporal dimensions, we used "continu*" OR "complement*" OR "perennial" OR "tempor*" OR "asynch*" OR "early season" OR "late season" OR "overwinter*"; to capture habitat management features at multiple scales we used "habitat" OR "cover crop*" OR "relay crop*" OR "living mulch" OR "fallow" OR "landscape diversi*" OR "landscape complexity." This search returned 752 results. We then reviewed titles and abstracts for relevance, resulting in a final set of 55 papers. From these we extracted the geographic location (country or U.S. state) in which field work was conducted, the cropping system, the scale(s) (field or landscape) of manipulation or observation, the habitat feature(s) observed or manipulated, the resource type(s) (trophic or structural) considered, the pest and natural enemy group(s) studied, and a brief summary of the main findings (**Supplementary Table 1**).

## RESOURCES FOR NATURAL ENEMIES: TROPHIC AND STRUCTURAL

### Trophic Resources

For the purpose of pest control, the most relevant trophic resources that natural enemies consume are the pests themselves. While facilitating larger or more continuous pest populations could provide an ample food supply for enemies, this is obviously an undesirable situation for crop production. On the other hand, secondary pests or non-pest prey may contribute to the stability of biocontrol without increasing crop damage. The presence of alternative prey is sometimes shown to disrupt effective biocontrol if generalist predators prefer to consume alternative prey compared to pests (Koss and Snyder, 2005). Yet, it has also been hypothesized that the early presence of alternative prey (i.e., a temporally complementary resource for enemies) could build up predator populations to such an extent that large population size compensates for reduced individual predation (Harwood and Obrycki, 2005). In other words, temporal separation in the presence of alternative prey and primary pests may contribute to "apparent competition" between prey species (Langer and Hance, 2004; Blitzer and Welter, 2011), mitigating the negative effect of preferential feeding on non-pests. Similarly, a modeling study by Spiesman et al. (2020) showed that fields or landscapes that

**TABLE 1 |** Representative studies of temporal resource continuity for natural enemies in agroecosystems across trophic and structural resource types (sections Trophic Resources and Structural Resources) and landscape and field scales (sections In-Field Features and Landscape Features).

| | Management scale | Resource type | References |
|---|---|---|---|
| A | Field | Trophic | Langer and Hance, 2004; Litsinger et al., 2006; Schmidt et al., 2007; Yoo and O'Neil, 2009; Unruh et al., 2012; Segoli and Rosenheim, 2013; Villegas et al., 2013; Derocles et al., 2014; Damien et al., 2017; Nelson et al., 2018 |
| B | | Structural | Halaj et al., 2000; Sorribas et al., 2016; Boinot et al., 2019; Ganser et al., 2019 |
| | | Both/Unmeasured | Hossain et al., 2002; Men et al., 2004; Prasifka et al., 2006; Dong et al., 2012; Koch et al., 2015; Ramsden et al., 2015; Tsutsui et al., 2016; Pellissier and Jabbour, 2018; Toivonen et al., 2018; Bowers et al., 2020 |
| C | Landscape | Trophic | Settle et al., 1996; Prasifka et al., 2004; Pfannenstiel et al., 2012; Heimoana et al., 2017; Bertrand et al., 2019 |
| D | | Structural | Öberg et al., 2007; Royauté and Buddle, 2012; Roume et al., 2013; Sarthou et al., 2014; Raymond et al., 2015; Hanson et al., 2017; Gallé et al., 2018; Mestre et al., 2018; Ng et al., 2018; Sutter et al., 2018; Knapp et al., 2019 |
| | | Both/Unmeasured | Alignier et al., 2014; Bianchi et al., 2015; Macfadyen et al., 2015; Duflot et al., 2016, 2017; Ardanuy et al., 2018; Aviron et al., 2018; Sann et al., 2018; Yang et al., 2018; Nardi et al., 2019 |

*Letters correspond to arrows in **Figure 2**.*

contain resource patches with non-overlapping phenologies and distinct specialist prey communities could avoid the build-up of large pest populations by providing continuous food for mobile generalist predators at the landscape scale.

Temporally complementary alternative prey can occur in the focal crop itself or in adjacent vegetation. A study in Indiana (USA) soybean fields found that minute pirate bugs benefited from the presence of thrips early in the growing season and prevented soybean aphid outbreaks later (Yoo and O'Neil, 2009). Prasifka et al. (2004) used stable isotope analysis to show that lady beetles feeding on aphids in grain sorghum emigrated to nearby cotton fields when the sorghum senesced, and remained in cotton even in the absence of aphids; when aphids were present in cotton they switched their diets, enhancing biocontrol. Similarly, leafroller parasitoids in Washington (USA) fruit orchards benefited from rose and strawberry plantings that provided a key overwinter host (Pfannenstiel et al., 2012; Unruh et al., 2012). Adjacent vegetation may also provide alternative prey that keep natural enemies near crop fields during periods of disturbance such as harvest (Villegas et al., 2013) or pesticide application (Heimoana et al., 2017). Nevertheless, in some cases the prey species found in adjacent vegetation may be inadequate alternative prey for agriculturally-relevant natural enemies, and therefore fail to contribute to temporal resource continuity and improved pest control outcomes (Derocles et al., 2014).

Non-prey foods such as nectar, pollen, seeds, and fungi may also be vital to the energetic and nutritional requirements of natural enemies, with some species even requiring non-prey food to complete their life cycles (Wäckers et al., 2005; Lundgren, 2009). Plant- and fungus-derived foods can be especially important for predator and parasitoid subsistence when prey are scarce (e.g., Eubanks and Denno, 1999). Floral resources such as nectar and pollen have been well-studied in the CBC literature, especially for parasitoids (Tylianakis et al., 2004; Lee and Heimpel, 2005, 2008), but temporal dimensions are not often considered explicitly. Continuous access to floral resources has been shown to benefit parasitoids (Segoli and Rosenheim, 2013) and hoverflies (van Rijn et al., 2013) in lab settings, with implications for how flowers are managed in the field. For example, Segoli and Rosenheim (2013) show that leafhopper parasitoids in wine grape vineyards are sugar-limited, especially in autumn, and suggest that planting late-season flowers could enhance their biocontrol potential.

The importance of phenologically complementary floral resources has also been demonstrated recently for natural enemies at the landscape scale. Bertrand et al. (2019) quantified pollen use by a lady beetle and lacewing species throughout the course of a growing season in German and Swiss agricultural landscapes. They observed a clear shift from tree-derived to herbaceous pollen over time, and found that the majority of pollen came from non-crop plants even in areas dominated by farmland. This indicates that diverse, temporally continuous non-prey food is a key resource for natural enemy populations in agricultural landscapes.

Finally, natural enemies themselves may function as "alternative prey" in some cases (i.e., intraguild predation or cannibalism; Rosenheim et al., 1995). Although theory predicts that such antagonistic interactions between enemies should have negative consequences for biocontrol, this prediction is infrequently borne out in practice (Janssen et al., 2006; Rosenheim and Harmon, 2006). From the perspective of temporal resource continuity, intraguild predation could be beneficial if the presence of intraguild prey acts as an additional trophic resource that enables the persistence of the intraguild predator during times of extraguild prey scarcity; however, we did not encounter any examples of this phenomenon in our literature search.

## Structural Resources

In addition to food, natural enemies require appropriate habitat structure for growth & development, sheltering from predation and disturbance, reproduction, and in temperate climate zones, overwintering (Landis et al., 2000). Gontijo (2019) recently reviewed the engineering of natural enemy shelters to enhance CBC in crop fields, highlighting the importance that vegetative and artificial structures can have in providing suitable microclimatic conditions and protection from intraguild predation and pesticide exposure, in addition to providing supplemental food resources (discussed in section Trophic Resources above). While sheltering can improve conditions for predators in the middle of the growing season—such as protecting them from desiccation in high sun conditions (Diehl et al., 2012)—it may be especially important during periods when crop fields are bare or sparse. For example, Tsutsui et al. (2016) found that spiders in Japanese rice agroecosystems relied on the complementary use of irrigation and drainage ditches during periods when paddies were dry, suggesting that providing essential microhabitats could be important at particular times of the season.

Because highly intensified crop fields provide little suitable substrate outside of the growing season, overwintering habitat is likely to be a key limiting structural resource for natural enemies in temperate agroecosystems. In studies from European oilseed rape landscapes, overwintering spider density was found to be significantly higher in natural areas than crop fields (Mestre et al., 2018), and ground beetle-to-pollen beetle ratio was greatest in forest edges, especially those with high litter cover and compact soil (Sutter et al., 2018). In the absence of semi-natural landscape features, in-field enhancements (see section In-Field Features) have the potential to provide supplemental overwintering habitat to natural enemies. In one study from Switzerland, perennial wildflower strips were found to host significantly more overwintering spiders, ground beetles, rove beetles, and hoverflies than adjacent wheat fields, but plowing strips during the overwintering period reversed any benefits they provided (Ganser et al., 2019). In an alley cropped agroforestry system, Boinot et al. (2019) found that more predators, and disturbance-sensitive ground beetle species in particular, overwintered in understory vegetation strips than crop alleys, suggesting that the structural complexity created by the trees could enhance biocontrol services during the growing season. Finally, even in perennial systems where cropland itself may be a suitable overwintering habitat for some natural enemy species, supplementary habitat may be valuable for others. For example, several species of lacewings in Spanish fruit orchards tended to overwinter in nearby shelterbelts and disperse to fruit trees the following spring, while others remained on fruit trees year-round (Sorribas et al., 2016).

In summary, both trophic and structural resources within and outside of crop fields that complement the availability of prey are essential for sustaining long-lived, mobile natural enemies in agroecosystems. Agricultural systems that retain such temporally complementary resources are likely to have a greater potential for pest suppression within a crop by supporting robust natural enemy communities through periods of low pest abundance.

## CREATING CONTINUITY: HABITAT FEATURES IN FIELDS AND LANDSCAPES

### In-Field Features

Within individual farms or crop fields, there are a variety of habitat features and management techniques that could provide natural enemies with temporally continuous trophic and structural resources. Within a farm, local non-crop vegetation has long been studied for its potential value to beneficial insects and may be especially important before crops begin growing and after they are harvested. Grassy field margins, wildflower plantings, and beetle banks, are common examples of such non-crop features. This vegetation can often simultaneously offer both food and shelter for natural enemies. Ramsden et al. (2015) evaluated the relative importance of alternative prey, floral resources, and overwintering habitat provided by managed field margins to flying natural enemies of aphids in winter wheat by manipulating the type of vegetation present. They found that floral resources had the strongest effect, significantly increasing wheat aphid parasitism rates, as well as the abundance of hoverflies, lady beetles, and lacewings, particularly at the beginning of the growing season. Perennial wildflower strips have also been documented to support ground dwelling predators early in the season and facilitate their subsequent movement to adjacent barley better than non-flowering grasses (Toivonen et al., 2018). Yet in some cases, vegetation phenology may be more important than floral resources *per se*. Comparing the value of riparian buffers planted with cool- vs. warm-season grass mixes for natural enemies in maize and soybean, Nelson et al. (2018) expected the warm season plantings to perform better due to the greater abundance of flowering species included in the seed mix. However, they found that cool season grasses promoted earlier, more abundant ground- and canopy-dwelling enemies in crop fields. They attributed this to phenological differences between plantings, positing that the cool season grasses provide more continuous substrate and beneficial microhabitat for prey and predators early in the season. It is important to note that while managed non-crop vegetation frequently promotes early-season natural enemy abundance in the planting itself, benefits do not always spill over to the adjacent crop (Pellissier and Jabbour, 2018).

Cover crops, relay crops, and living mulches are within-field vegetation management strategies that could also promote temporal resource continuity. Cover crops are regularly promoted for their soil-building (Blanco-Canqui et al., 2015) and weed suppression (Osipitan et al., 2018) properties, but may also provide valuable habitat for beneficial insects outside of the focal crop growing season. Bowers et al. (2020) show that rye and clover cover crops increase early season recruitment of natural enemies to Georgia (USA) cotton fields and decrease thrips abundance, while rye cover crops also decreased boll injury by stink bugs. In France, flowering brassica cover crops increased parasitism rates of aphids in adjacent cereals, likely attributable to the early nectar resources they provide (Damien et al., 2017). Even when cover crops fail to enhance natural enemy recruitment to crop fields (Fox et al., 2016), they have been shown to depress pest populations by other mechanisms in some cases (Hooks et al., 2013; Koch et al., 2015).

In relay cropping systems, crops that have different phenologies are planted in the same field, and the first (early season or fast growing) crop is harvested before the second (late season or slow growing) crop. This strategy has proven especially effective in promoting early recruitment of lady beetles to control aphids in wheat-cotton (Men et al., 2004) and rye-wheat (Dong et al., 2012) relay cropping systems in China, as well as soybean planted into an alfalfa living mulch in Iowa (USA) (Schmidt et al., 2007). Alfalfa-clover living mulch has also been effective in increasing ground beetle abundance and predation of the European corn borer in an Iowa maize-soy-forage rotation (Prasifka et al., 2006).

For crops that can accommodate multiple harvest dates, such as alfalfa and other forages, asynchronous strip harvesting may promote the persistence of natural enemy populations in the field throughout the harvest season. This practice was popularized in California alfalfa fields (Stern et al., 1964; Summers, 1976) and its benefits for enemy conservation and pest suppression have been extensively documented in Australian production systems (Hossain et al., 2000, 2001, 2002). Similar results have been found in other parts of the world (Samu, 2003; Rakhshani et al., 2010).

Finally, non-vegetative within-field enhancements have the potential to provide resources for natural enemies and keep them around in the absence of crops. Halaj et al. (2000) note that the establishment of straw shelters in crop fields is a millennia-old practice used by Chinese farmers to create a refuge for spiders during periods of disturbance. They found dramatic increases in predator abundance and diversity in shelters compared to open fields, as well as one-third less insect damage to soybean seedlings near shelters. The use of artificial shelters for structural resource continuity is generally uncommon but has received particular attention in orchard systems (Horton et al., 2002; Horton, 2004; Kawashima and Jung, 2010; Yanik et al., 2011).

### Landscape Features

At the landscape scale, semi-natural habitat (i.e., non-crop vegetation patches) is perhaps the most investigated feature presumed to benefit natural enemy conservation and biocontrol services through its combined effects on both trophic and structural resource continuity for natural enemies. Semi-natural habitats are expected to improve temporal continuity because they are comprised of long-lived, perennial species that undergo minimal disturbance. Studies often measure the proportion of semi-natural landcover in a given area (e.g., 1 km radius) surrounding a crop field and relate this attribute to pest or enemy responses. The amount of surrounding semi-natural habitat sometimes correlates with the early-season abundance of natural enemies in crop fields (Alignier et al., 2014; Bianchi et al., 2015; Raymond et al., 2015; Wilson et al., 2017), suggesting its function as overwintering habitat and potential contribution to temporal resource continuity. Semi-natural habitat here is inferred to be a proxy for some limiting trophic or structural resources at low levels within crop fields themselves. However, these potentially limiting resources are rarely measured directly. When resources are measured, there tends to be substantial local heterogeneity in the quality of semi-natural habitat (Sarthou et al., 2014; Holland et al., 2016; Bartual et al., 2019), and this discrepancy could partially explain why it is an inconsistent predictor of CBC outcomes (Karp et al., 2018).

In addition to habitat amount, landscape configuration strongly affects pests, enemies, and crop yield, though temporal dimensions remain largely under-explored (Haan et al., 2020). One robust finding across temperate agricultural landscapes is that habitat edges tend to support more diverse, abundant ground beetle (Roume et al., 2013; Duflot et al., 2017; Ng et al., 2018; Knapp et al., 2019) and spider communities (Öberg et al., 2007, 2008; Royauté and Buddle, 2012; Mestre et al., 2018) in and around cereal fields, particularly early in the growing season. This observation demonstrates the contribution of semi-natural vegetation in patchy landscapes to overwintering habitat and timely recruitment of predators to crop fields (Bertrand et al., 2016; Gallé et al., 2018).

Non-crop habitat is not the only landscape feature that may promote desirable pest and enemy dynamics in agricultural landscapes. The heterogeneity of farmland itself is increasingly recognized for its relevance to biodiversity conservation (Perfecto et al., 2019; Sirami et al., 2019) and ecosystem service provisioning (Vasseur et al., 2013; Cohen and Crowder, 2017; Redlich et al., 2018). In particular, crop diversity at the landscape scale could offer temporally complementary resource patches to mobile generalists that can make use of different habitats throughout the growing season, as well as "bridge" semi-natural habitat and annual cropland by providing connectivity in time and space. For example, Nardi et al. (2019) used network analysis to show that while forest habitats hosted spider communities distinct from those in annual crop fields, perennial crops and meadows played a key role in facilitating dispersal across agricultural landscapes. Studying ground beetles in maize, Aviron et al. (2018) found that the presence of semi-natural areas did not enhance farmland species, but connectivity to winter cereal crops promoted short-winged species, whereas Duflot et al. (2016) saw no evidence of complementation between cereal and maize fields. In some cases, spatio-temporal resource complementation may benefit generalist pests but not predators (Macfadyen et al., 2015; Ardanuy et al., 2018). Finally, diverse crop types can act as temporally complementary sources of natural enemy population from distinct functional groups throughout the growing season. One study illustrating this point in Swedish agricultural landscapes found that predators emerged and dispersed early in the season from sugar beet fields, while later in the season grasslands were an important spider source and wheat fields were an important rove beetle source (Hanson et al., 2017).

In regions with year-long growing seasons, asynchronous planting of a focal crop can be an effective way to ensure resource continuity for natural enemies across the landscape. There is a longstanding debate in theoretical models and pest management policy about the value of synchronous vs. asynchronous planting for pest control, with the classic example coming from tropical rice systems (Ives and Settle, 1997). Settle et al. (1996) demonstrated that generalist predators were more abundant, and pest suppression was improved, with asynchronous planting and in the presence of alternative, detritivorous prey that provided continuous trophic resources and boosted their early population size. Subsequent work in tropical rice systems has corroborated these results, showing that asynchronous planting is sometimes more beneficial for natural enemies of rice pests than crop diversity or semi-natural habitat (Litsinger et al., 2006; Dominik et al., 2018; Sann et al., 2018).

Recently, an additional landscape element that has received scientific attention and which has the potential to affect resource continuity and pest control is the presence of developed or urban habitat. Long written-off as irrelevant to conservation, cities are increasingly recognized as remarkably complex, heterogenous patchworks that harbor abundant and diverse insect communities (New, 2015) and have the potential to support insect-mediated ecosystem services (Gardiner et al., 2013; Lin et al., 2015). Urban habitat features are important for pest and enemy dynamics within small urban agroecosystems (Gardiner et al., 2014; Egerer et al., 2017; Gardiner and Harwood, 2017; Philpott and Bichier, 2017), but may also influence nearby natural (Spear et al., 2018), and agricultural areas. Yang et al. (2018) found that lady beetle abundance in wheat fields was correlated with the proportion of dwellings in the surrounding area, but only in the early season, likely because human structures provide valuable overwintering habitat to beetles. Urban warming may also contribute to earlier emergence and faster development times in cities, but these effects seem more pronounced for pests than natural enemies (Dale and Frank, 2014; Meineke et al., 2014).

Overall, a variety of habitat features at both the field and landscape scales could promote or interfere with natural enemies' continuous access to key resources. Beyond the non-crop or semi-natural vegetation present in agroecosystems, crop diversity, management schedules, and non-vegetative structures may also be advantageous targets for manipulation to improve conservation and pest control.

## BOTTOM-UP PROCESSES AND RESOURCE DISCONTINUITY FOR PESTS

The research summarized above primarily focuses on the value of resource continuity for predators and parasitoids, beneficial species whose presence is desirable in agroecosystems. However, it is worth noting that temporal resource patterns can also be manipulated to generate resource *discontinuities* for undesirable species. One example of this is practiced at the field scale, where the rotation of annual crops has been used for thousands of years to disrupt the inter-annual life cycles of pathogens and insect pests (Bullock, 1992). Longer, more diverse crop rotations have been shown to decrease insect pest pressure in a variety of crops including canola (Harker et al., 2015), maize (Brust and King, 1994), and potato (Hare, 1990; Kabaluk and Vernon, 2000). In some cases, pests may evolve resistance to simple rotation schemes (e.g., corn rootworm in North America; Gray et al., 2009). Although crop rotation could potentially disrupt resource continuity for top-down control within crop fields, some studies have found neutral or positive effects on natural enemies (O'Rourke et al., 2008; Dunbar et al., 2016). The consequences of crop rotation for pests and enemies at the landscape scale are poorly characterized, but nevertheless a potentially important temporal consideration for CBC (Rusch et al., 2013; Bertrand et al., 2016).

Other cultural controls can interfere with the habitat requirements of insect pests. For example, plastic or biodegradable mulches can be used to alter the microclimate within crop canopies and on the soil surface, deterring or killing insect herbivores (Kasirajan and Ngouajio, 2012). Similarly, the isolation or removal of infested fruits can interrupt resource access for pests (Chouinard et al., 2016; Leach et al., 2018). Non-crop vegetation could also be managed to disrupt resource continuity for pests, such as by removing alternative host plants in the landscape. For example, Parry et al. (2019) demonstrate that exotic weeds in found in alfalfa fields and pasture in Australia act as early season hosts for a native hemipteran pest, the Rutherglen bug, and suggest that reducing weeds in these habitats could disrupt temporal resource continuity and facilitate better landscape-scale management. Similarly, soybean aphids and their overwinter host European buckthorn constitute two key pillars of an "invasional meltdown" North America; removing buckthorn in the landscape could promote the suppression of soybean aphid as well as other co-invaders (Heimpel et al., 2010).

# DISCUSSION

## Diversity and Continuity: The "What" and "When" of Resources in Agroecosystems

In Root's (1973) initial formulation of the enemies hypothesis, improved temporal resource continuity for natural enemies is a corollary to plant diversity. In other words, one reason agroecosystem diversification is presumed to be beneficial for natural enemy conservation and top-down pest suppression is because it decreases the likelihood enemies will encounter a period of resource scarcity, allowing populations to persist and grow. This is one among several potential mechanisms by which diversification may benefit natural enemies (e.g., nutritional enhancement provided by more diverse diets; Root, 1973; Russell, 1989). Disentangling the contributions to natural enemy response of resource diversity *per se* and resources continuity could be a fruitful direction for CBC research. For example, natural enemy diets could be manipulated in a factorial experiment crossing high and low temporal continuity with high and low nutritional diversity, measuring physiological, developmental, or survivorship outcomes. Clarifying the mechanisms by which diversification is likely to benefit enemies in specific contexts could inform more useful habitat management schemes that address relevant resource deficiencies.

When considering resource continuity and resource diversity separately, four broad types of agroecosystems are apparent (**Figure 3A**). In low diversity systems such as crop monocultures, resources may be either ephemeral (as is the case for the commercial production of many annual crops around the world) or long-lasting (as in orchards or perennial forage crops, for example). Similarly, high diversity systems can encompass mixtures of plants with similar phenologies ("synchronous polyculture," such as many classic companion plants) or temporally distinct phenologies ("asynchronous polyculture," such as relay or cover crops). Given the findings from studies on resource pulse-consumer interactions in natural ecosystems (Ostfeld and Keesing, 2000; Yang et al., 2010), we would predict that the nature of the effects of resource patterns in agroecosystems will depend on the specific life history traits and resource requirements of relevant pest and enemy species. Accordingly, resource continuity and/or diversity could in some cases be manipulated to facilitate optimal pest management outcomes. We describe the application of this framework for three relevant traits: habitat/diet breadth (generalists vs. specialist; **Figure 3B**), voltinism (univoltine vs. multivoltine; **Figure 3C**), and mobility (high vs. low mobility; **Figure 3D**).

We expect that habitat generalists are likely perform better relative to specialists in cropping systems with heterogeneous, temporally complementary resources (**Figure 3B**, top right quadrant) because, all else being equal, they have the ability to move and exploit a diversity of resources in habitats that become available at different points in time. In contrast, specialists are more likely to perform better in simplified systems (**Figure 3B**, bottom left quadrant) because they are well-adapted to such ephemeral environments (Wissinger, 1997). Results in diverse but fleeting (**Figure 3B**, top left quadrant) or homogenous perennial systems may be more variable (**Figure 3B**, bottom right quadrant). This suggests that effective management of pests with field or landscape diversification practices would be more likely under scenarios in which the targeted pests are specialists (and only occur in the crop or limited number of alternative habitats) that are attacked by generalist natural enemies which can bolster their populations by accessing resources in a diversity of habitats. In contrast, diversification may be less effective if key pests and enemies have similar habitat or diet breadths.

An organism's voltinism, or the number of generations it completes in a year, is also relevant to how a population may respond to changes in resources over time. For univoltine species, adequate capture of resources may in some cases be achieved even when trophic resources are fleeting—as long as food is available during the organism's phenological growth and development window. Individuals may remain in their dormant life stage for the rest of the year (provided adequate structural resources) when trophic resources are not available. Multivoltine species, on the other hand, require host plants (in the case of pests) or prey

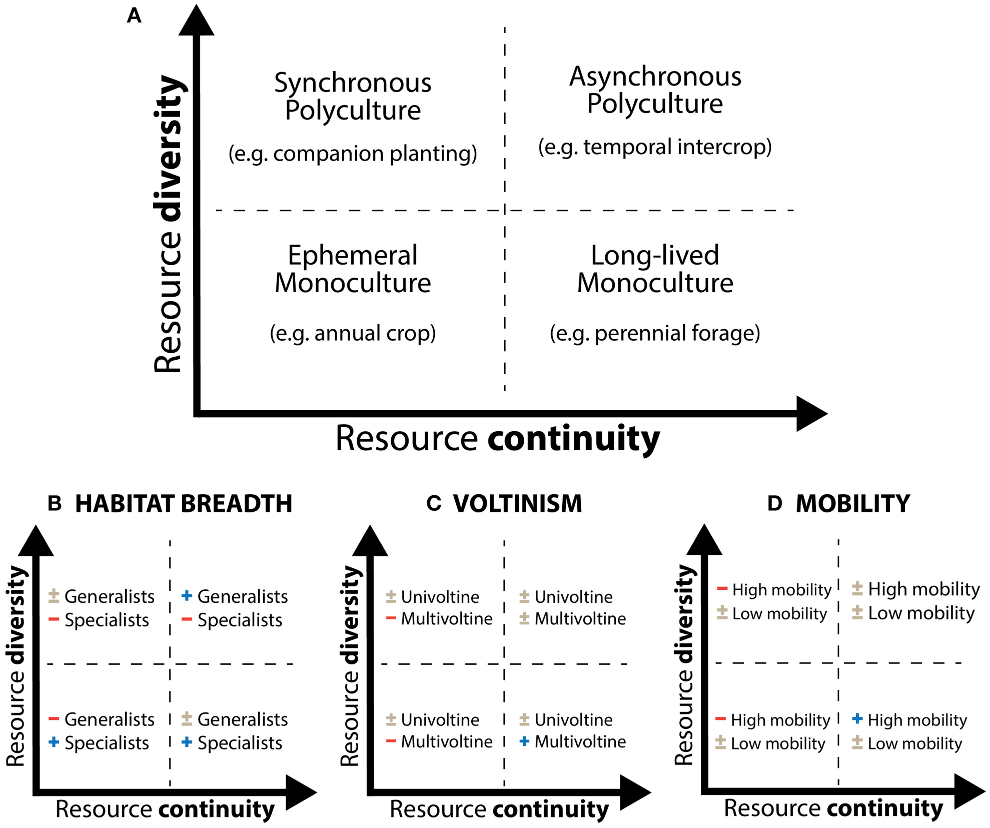

**FIGURE 3 |** Framework for analyzing resource patterns in agroecosystems incorporating both diversity and continuity dimensions. **(A)** Depicts four broad agroecosystem types in each quadrant. **(B–D)** Speculate how different arthropod life history traits (habitat/diet breadth, voltinism, and mobility) may interact with resource conditions. Symbols correspond to expectations of positive (+), negative (–), or mixed effects (±) on species with a given life history trait.

(in the case of enemies) at multiple time points (for each generation), and thus stand to suffer more from resource gaps (**Figure 3C**, left quadrants). Enhancing trophic resource continuity may therefore be more likely to improve pest control outcomes when natural enemies are multivoltine. Univoltine natural enemies, on the other hand, would not be as sensitive to variability in trophic continuity or diversity (since they are presumably adapted to coincide with their prey), but enhancing structural resource continuity may benefit univoltine enemies if they are limited by appropriate substrate for their non-feeding (e.g., overwintering) phase. The consequences of resource diversity *per se* would be a function of diet breadth (i.e., **Figure 3B**), rather than voltinism.

As previously mentioned, the distance which a species is able to travel to disperse or forage in large part determines the spatial scale at which resource distribution patterns affect population dynamics. Species' mobility may also matter for the ability of resource manipulation to enhance pest control outcomes by influencing their fidelity to a given area. If highly mobile species (e.g., wind-dispersers, strong fliers, or crawlers) experience resource gaps locally they may leave in search of resources elsewhere (e.g., the harlequin lady beetle; Osawa, 2000; Forbes and Gratton, 2011). If the species in question are pests this dynamic would be desirable, but if they are enemies it could result in reduced top-down control of subsequent pests. In contrast, low-mobility species (e.g., small ground dwellers) may be unable to escape local resource scarcity and die from starvation, or persist long enough to respond to a resource influx (i.e., new crop growth or pest outbreak) when it arrives. Accordingly, engineering resource gaps may be desirable when pests are highly mobile but enemies are not (**Figure 3D**, left quadrants). As with voltinism, the consequences of resource diversity will depend on whether arthropods can take advantage of few or many resource types in the agroecosystem.

By explicitly assessing the temporal resource dimensions for both natural enemies and their pests, in addition to diversity *per se*, the conceptual framework presented here could serve as a valuable starting point for testing novel agroecosystem designs for pest management within a field, farm, or landscape.

## Research Outlook and Conclusion

The temporal dynamics of food and shelter resources for arthropods can have important consequences for natural enemy conservation and pest control services in agroecosystems. By shifting focus away from habitat features themselves and toward the underlying mechanisms that drive insect-mediated processes and functions, the temporal continuity framework described here can generate more accurate predictions and targeted management interventions for CBC. Within fields, habitat management with temporal complementation in mind could maintain the pest control benefits of diversification while minimizing negative effects of direct plant competition that result in yield losses (Letourneau et al., 2011), since the benefits of diversity are spaced over time. At the landscape scale, it could point to natural enemy conservation strategies that do not necessitate taking land out of production—i.e., by growing phenologically complementary crops rather than just restoring long-lived semi-natural habitats (Schellhorn et al., 2015).

It is important that researchers and practitioners maintain a strong systems approach to CBC that accounts for arthropod dynamics at appropriate spatial extents and temporal resolutions. What happens in crop fields at peak growing season is certainly important, but for pest control service providers it is not the only place or time that matters (Vasseur et al., 2013). Landscape-scale studies rightfully acknowledge the effects that landscape context may have, but it is insufficient to assume what resources the habitat patches surrounding a focal crop field actually provide based on coarse land cover classifications alone (Cohen and Crowder, 2017). Directly measuring these resources, their use, and the movement of natural enemies over time typically provides a clearer picture of the roles that spatial and temporal heterogeneity play in conservation and ecosystem service delivery. Furthermore, more studies that measure resource patterns before planting, after harvest, and during overwintering periods could deepen our understanding of resource gaps and be crucial for achieving natural enemy conservation objectives. Studies focusing on the temporal dimensions of pest and enemy resources are particularly lacking in the tropics and sub-tropics (at least in papers published in English). This is unfortunate, as tropical agroecosystems may be especially poised to take advantage of temporal resource manipulation due to the long (and in some cases continuous) growing season in these regions. Expanding the geographic scope of temporally-focused CBC research would be invaluable for clarifying the idiosyncratic mechanisms that drive arthropod community dynamics in specific local contexts as well as patterns that repeat across the globe.

To facilitate the wider adoption of a pest management paradigm that emphasizes preventing outbreaks rather than treating them after they have occurred, farmers need reliable management techniques that in many cases depend on sufficient natural enemy populations to keep herbivores in check. Ensuring the availability of the limiting resources that these enemies need to persist on farms and in agricultural landscapes requires attention to their continuity over time. By studying and manipulating this resource continuity, CBC research may be able to advance agricultural practices that sustain both people and the diverse organisms on which we depend.

## AUTHOR CONTRIBUTIONS

BI and CG conceived of the review topic and contributed significantly to subsequent drafts. BI researched and wrote the first draft. Both authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2020.00127/full#supplementary-material

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# Social Context Influence on Urban Gardener Perceptions of Pests and Management Practices

**Heidi Liere[1]*, Monika Egerer[2,3], Carly Sanchez[3], Peter Bichier[3] and Stacy M. Philpott[3]**

*[1] Department of Environmental Studies, Seattle University, Seattle, WA, United States, [2] Department of Ecology, Ecosystem Sciences/Plant Ecology, Technische Universität Berlin, Berlin, Germany, [3] Department of Environmental Studies, University of California, Santa Cruz, CA, United States*

**Edited by:**
*Kris A. G. Wyckhuys,*
*Chinese Academy of Agricultural Sciences (CAAS), China*

**Reviewed by:**
*Susanne Padel,*
*Thuenen Institute, Germany*
*María Carmen Castrillón Valderrutén,*
*University of Valle, Colombia*

***Correspondence:**
*Heidi Liere*
*liereheidi@seattleu.edu*

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Community gardens are important urban green spaces with a variety of social and ecological benefits, one of which is access to healthy food. Similar to rural agriculture, the quantity and quality of the food produced can be compromised by pest damage. In fact, many urban gardeners report crop damages caused by vertebrate and invertebrate pests. Yet, because the food produced in community gardens is mostly for self-consumption and thus not under market quality standards, the damage thresholds and the point when gardeners perceive a pest problem and how they decide to manage it, may greatly vary from gardener to gardener. Here, we investigated how socio-demographic factors and experience affect whether gardeners report having a pest problem and which pest management practices they use. We surveyed 187 gardeners from 18 different urban community gardens in three counties in the California central coast, USA. We also collected information about gardener socio-demographic factors (age, gender, ethnicity), as well as education, and years of experience in agriculture. The majority of gardeners reported having pests in their plots but their ethnicity, the amount of time they spend in the gardens, and whether they work in agricultural-related employment or not influenced the likelihood of reporting pests. We found that the majority of gardeners use curative, non-synthetic practices for managing pests, but that some use preventive practices and some don't do anything to control pests. The likelihood of using practices that are curative depended on gardeners' ethnicity, the amount of time they spend in the gardeners, and their gender. Our results suggest that the agricultural knowledge of urban community gardeners and the practices they use varies greatly and that, in order to be successful, extension programs may need to take this diversity into account when promoting the agroecological paradigm in urban agricultural (UA) systems.

**Keywords: urban agriculture, pest control, conservation biological control, urban community gardens, agroecology**

## INTRODUCTION

In response to the growing urban population and increased demand for local fresh fruits and vegetables, urban community gardens have expanded dramatically (Reynolds, 2017), especially in low-income and underserved communities (Alig et al., 2004). For the past 50 years, urban agriculture (hereafter UA) has increased by 3.6% annually in developing countries and in the US, and by more than 30% in the past 30 years (Siegner et al., 2018). During the growing season, gardens supply a substantial proportion of gardener fruits and vegetables needs (Gregory et al., 2016). For low-income and food-insecure gardeners, the harvest from community gardens is often their main source of produce in the growing season (Gregory et al., 2016). In addition to food, community gardens provide numerous benefits and can improve the physical and mental well-being of urban residents (Brown and Jameton, 2000), especially for gardeners living in low-income communities with little or no access to other green-spaces for social and physical interactions (Saldivar-Tanaka and Krasny, 2004; Glowa et al., 2019). In addition, UA can be a source of job creation and provide education opportunities (Reynolds, 2017), as well as improve community-building and environmental stewardship (McVey et al., 2018). Furthermore, urban green-spaces, including urban community gardens, can serve as refuges for biodiversity and decrease the negative effects of urbanization (Goddard et al., 2010; Lin et al., 2017).

Similarly to rural farmers, urban farmers and gardeners are met with a variety of challenges related to pests, pollination, soil quality, and water availability (Gregory et al., 2016) and have to continuously adjust their management practices. In rural settings, where often farmers come from families with a long history of farming, agricultural knowledge is passed from generation to generation and farmers build upon it constantly based on their own experiments and experience (Morales and Perfecto, 2000; Curry et al., 2015). In addition, farmers often rely on support from a variety of external sources of information, including extension programs and farmer networks, to build upon their own knowledge (Stallman and James, 2015; Noy and Jabbour, 2020). In contrast, the agricultural background and knowledge of urban gardeners varies greatly (Kim et al., 2014; Oberholtzer et al., 2014; Gregory et al., 2016) and so do their management practices. Pest and disease management, for example, is of major importance in some urban systems and almost ignored in others (Prain, 2006). In a recent survey that asked 315 urban farmers across 15 US cities about their challenges and training needs, the majority of them expressed significant challenges in managing pests (>90% of surveyed urban farmers), and reported critical needs for technical assistance (Oberholtzer et al., 2014). Compared to rural agriculture, there is still relatively sparse technical support for urban agriculture (Cohen and Reynolds, 2015). However, there are a growing number of policies that allow and support urban food production (Reynolds, 2017). The USDA (United States Department of Agriculture), e.g., now funds training to support UA commercial farming (USDA, 2016). Nevertheless, we lack the scientific expertise to inform non-commercial urban gardeners about how their production and management practices impact pest control. Given that challenges in managing pests is a common concern among urban gardeners (Oberholtzer et al., 2014; Gregory et al., 2016), it is vital to have all tools available to promote agroecological pest management practices in urban agriculture.

Agroecological principles, where external inputs are replaced by natural processes, have been applied to improve small scale agriculture for years (Altieri, 1995) and the same principles can be applied to urban gardens and farms (Gregory et al., 2016; Altieri and Nicholls, 2018). In particular, agroecological practices for preventing pests (i.e., avoiding that herbivore populations reach damage thresholds in the first place), can be implemented in urban agroecosystems by managing farms or gardens and surrounding landscapes to conserve biological control agents and minimize herbivore damage (Morales et al., 2018). There is a growing number of studies in urban gardens that investigate the local and landscape factors that affect insect predators and parasitoids (pest control agents or natural enemies) (Gardiner et al., 2014; Egerer et al., 2017, 2018a; Philpott and Bichier, 2017; Lowenstein and Minor, 2018; Morales et al., 2018), providing valuable information that could be disseminated to urban gardeners (Arnold et al., 2019). Because of its high levels of socio-economic and ecological complexity, where top-down approaches have been shown to have little to no impact (Van Veenhuizen et al., 2001; Prain, 2006), the promotion of agroecological methods for pest control in UA should incorporate participatory methods (Morales and Perfecto, 2000). An early step toward this goal is to understand urban gardeners' agricultural knowledge (Prain, 2006) in relation to pests and pest management.

In rural agriculture, farmers' perception of crop risk and subsequent crop management decisions depends of a variety of factors including personal (e.g., socioeconomic, experience, social network connections) and external factors (e.g., political conditions, geographic setting), as well as access to extension services (Meijer et al., 2015). Farmers' decisions on pesticide use, for example, depend on perceived health and economic risks as well as trade-offs between crop protection and other objectives (Hashemi et al., 2014). An important factor that most likely drives pest perceptions and pest control practices is the ultimate goal of growing crops. In particular, whether a crop is grown for commercial purposes or self-consumption likely determines the threshold of pest damage that is tolerated by the farmer or gardener. For example, subsistence farmers in Guatemala were less likely to consider insects as pests (and try to control them) and more likely to "share" their crops with insects than farmers that grew cash crops (since companies reject "damaged" produce) (Morales and Perfecto, 2000). In fact, traditional corn farmers only classify insects as pests if they cause economic damage to their crop (Morales and Perfecto, 2000; Girard, 2015). Thus, understanding whether a farmer reports pests in their farm can shed light not only into actual plant damage but to the farmer's perception of pests, their tolerance for having insects on their crops, and an acceptance of some level of damage.

Furthermore, because perceptions vary across socio-cultural contexts, it is important to consider how social factors influence perceptions and management in urban agriculture. Farmers' socio-demographic backgrounds and environment also influence their knowledge and perceptions, and these, in turn, influence their farming practices, including pest management (Wyckhuys and O'Neil, 2007; Curry et al., 2015). In UA, gender and inter-generational relations and sustainability considerations are part of the decision-making processes in management practices (Prain, 2006). Understanding this could, and should, help inform agroecological practices extension and adoption (Girard, 2015; Gregory et al., 2016). For example, a study in rural China found that women farmers use less pesticides than men and more often apply protective measures or behaviors when using pesticides (Wang et al., 2017). The authors thus suggest that gender-sensitive educational programs should be implemented. Integrated Pest Management adoption behaviors in rice-cropping systems in Iran were influenced by farmers' gender and experience level (Veisi, 2012). Thus, the author recommends consideration of these variables as determinant factors in "targeted policy approaches." Among surveyed vegetable rural farmers in Botswana, the farmer age significantly influenced their knowledge of pests, while the proportion of farmers using cultural practices to prevent pests differed among study regions, leading the authors to recommend region-specific education strategies (Obopile et al., 2008).

In urban community or allotment gardens, plots of land are rented by individuals for non-commercial gardening (McVey et al., 2018). Consequently, multiple people from a variety of socio-economic and experience backgrounds grow food, medicinal, and ornamental plants in a common space (Cohen et al., 2012; Egerer et al., 2019) and do so mostly for self-consumption (Egerer et al., 2018d), and non-commercial reasons (McVey et al., 2018). Gardeners have different perceptions on garden properties and risks to crops that influence their management practices (Kim et al., 2014). Thus, these agricultural spaces of high social diversity represent an ideal system in which to investigate how social factors and experience influence perceptions of pests and pest management practices (irrespective of commercial quality standards).

Here we studied how socio-demographic factors and experience of urban community gardeners affect their perception of pest presence and their pest management strategies. We ask two main questions: (1) Does the likelihood of reporting pests depend on gardeners' experience and socioeconomic background? and (2) Does the likelihood of using curative practices (as opposed to preventive practices or doing nothing) vary with gardener's experience and socio-demographic factors?

# MATERIALS AND METHODS

## Study System

We conducted this study in 18 urban community gardens distributed across three counties in the California Central Coast, USA: Monterey (36.2400° N, 121.3100° W), Santa Clara (37.3600° N, 121.9700° W), and Santa Cruz (37.0300° N, 122.0100° W). This is a region of recent urbanization and industrial agriculture production, in addition to high levels of human diversity. The Central Coast region is increasing in density of built infrastructure to accommodate population growth, and there is a wide spectrum of socio-demographics (ethnicity, education, income) in the region. The region of these gardens varies in socio-economic and socio-demographic composition due to the history of urbanization, industrial agriculture, and corresponding demographic change. Santa Cruz and Monterey Counties – considered the salad bowl of the USA – are leaders in the production of strawberries and leafy greens. Many migrants from Mexico and Latin America left their own rural farming livelihoods to seek work in this region (e.g., through the Bracero Act, or later because of the North American Free Trade Agreement, or NAFTA). Yet, many of the workers that pick these fruits and vegetables live in food insecure neighborhoods (Brown and Getz, 2011). This has made community gardening, and the access to arable land, an appealing opportunity to increase food security, nutrition, and justice in the region (e.g., Mesa Verde Gardens, Watsonville, CA; http://www.mesaverdegardens.org/). Furthermore, because many of these gardeners come from rural traditions and backgrounds, urban agriculture provides a space to practice traditional agricultural knowledge and a range of agroecological practices (Glowa et al., 2019). Santa Clara County is also a diverse socio-demographic region. This region's agricultural history as the "Valley of Heart's Delight" brought populations of Italians, Croatians, Chinese, Japanese, Filipino and Mexican/Central American immigrants to work in the orchard landscape (Pellow and Park, 2002). Furthermore, this region has experienced refugee resettlement from Vietnam, Cambodia, and Bosnia, among others. Now, the region is experiencing another demographic shift as it has transformed into Silicon Valley in the recent decades, bringing skilled technology workers from across the world. The community gardening program in San Jose, the largest city in the Bay Area, supports over a thousand urban gardeners that use urban agriculture to grow a range of ethnic foods, to practice rural traditions, and to grow community (San Jose Parks, Recreation & Neighborhood Services 2017). Thus, the community gardens in this study provide a system to assess how changes in social characteristics affect garden management, pest perceptions, and sustainable pest control practices. The gardens range in size (405–8,134 $m^2$), years in cultivation (2–39 years), and number of gardeners served (5–105 plots/garden that serve individuals or families). All are managed in an allotment style where households cultivate individual plots within the garden and are relatively well-supported by local organizations or by the city government. All of the gardens have policies to use "organic" practices, prohibiting the use of synthetic pesticides.

## Survey Questionnaires

We used paper survey questionnaires in each of the gardens to collect information on gardener experience and socio-demographic information (i.e., *our effect variables*; **Table 1**). To collect information on gardener experience in agriculture, we asked gardeners who taught them how to garden or farm (multiple choice; family member, friend, self-taught, workshop/class, other gardeners, other), how many years they have been gardening (open-ended), and how many hours per week they spend in the garden (open-ended). We also asked them about their main source of employment because many gardeners in this region work in agriculture-related

**TABLE 1 |** Independent variables derived from surveys, sample sizes, and classification and grouping used for data analysis.

| Survey question | Name of variable | Levels | Type of variable |
|---|---|---|---|
| Who taught you how to garden or farm? | Teacher | Class/workshop (*n* = 4), family (*n* = 111), friend (*n* = 10), other gardeners (*n* = 6), self (*n* = 48), other (*n* = 2), no answer (*n* = 6) | Experience |
| How many hours per week do you spend at this garden? | Hours gardening | In hours: < 5 (*n* = 96), between 5 and 10 (*n* = 54), more than 10 (*n* = 24), no answer (*n* = 13) | |
| How long have you been gardening? | Years gardening | In years: < 10 (*n* = 91), between 10 and 30 (*n* = 49), more than 30 (*n* = 46), no answer (*n* = 1) | |
| What's your occupation? | Employment | Agriculture related (*n* = 30); not related to agriculture (*n* = 109); not working (*n* = 45), no answer (*n* = 3)⦹ | |
| What's your ethnicity? | Ethnicity | Asian Pacific islander (*n* = 37); Black/African American (*n* = 4); Hispanic/latino (*n* = 54); White (*n* = 80); Middle East (*n* = 3); other (*n* = 6); no answer (*n* = 3)* | Socio-demographic |
| What is your highest level of completed education? | Education | No schooling (*n* = 7), Primary (19), Secondary (*n* = 24), Post secondary (*n* = 136), no answer (*n* = 1)⦶ | |
| What is your gender? | Gender | Male (*n* = 87), female (*n* = 97), no answer (*n* = 3) | |

⦹ *Ag related employment includes all who marked "Agriculture" as one of their employment options. Not related to ag. included: Construction, Sales, Domestic Service, education, Legal Services, Health Services, Office Administration, Technological Services, Restaurant/Food Service, as well as "other" not related to agriculture.*

**Asian/Pacific islander includes those that marked Asian/Pacific Islander and those that in the "other" category included: Indian, White Asian. Hispanic/Lanino includes those that marked this category and those who in "other" included White Hispanic, Hispanic Native, and White Hispanic.*

⦶ *Primary education includes: Elementary school; Secondary education includes: Middle school, Some high school, High school graduate; Postsecondary education includes: Trade/technical/vocational training, Some college, Associate degree, Bachelor's degree, Master's degree, Professional degree, Doctorate degree.*

jobs (including horticulture). This may influence gardening practices and therefore relates to gardening experience. Thus, while we provided 12 options for employment (in addition to an "other" category), we reviewed all responses and created a binary employment variable of either (1) employment in agriculture or (2) non-agriculture employment. To collect information about gardener socio-demographics, we asked a series of questions on highest education level (multiple choice; from no formal schooling, Elementary School, Middle School, High School, Vocation/Associates Degree, Bachelor's Degree, Master's Degree, Professional Degree, Doctorate), gender (multiple choice; male, female), and ethnicity (multiple-choice options of racial categories used in the US Census) (**Table 1**).

Using the surveys, we also collected information on perceptions of pest problems as well as pest control practices (curative and preventative) (i.e., our *response variables*). To measure gardener perceptions of pest problems, we asked gardeners whether they perceive problems with pests or diseases in their gardens (multiple choice; yes, no, don't know). To measure gardener's pest control practices, we asked gardeners which of the following methods they use to protect their crops from pests or diseases: hand remove pests; use organic purchased spray; use homemade sprays; use pesticides; release ladybugs. Gardeners were allowed to choose multiple methods, and we additionally included an open-ended "other" option to allow gardeners to elaborate on their practices.

We surveyed between 6 and 14 gardeners per garden, which represented between 9.5 and 65% of the gardener population in a garden. The surveys were given in English (*n* = 142), Spanish (*n* = 38), Korean (*n* = 1), and Bosnian (*n* = 1), and were either read out loud by the researcher in person (*n* = 150) or via phone (*n* = 2), filled out by the gardener themselves (*n* = 27), or read out loud to the gardener by another gardener (*n* = 3). The surveys were distributed over the course of 4 months during the growing season, from June to the beginning of October 2017.

## Data Analysis

We used binomial logistic regression to determine whether gardener socio-demographic background and agricultural experience (effect variables) influence their perceptions of pest problems and pest management practices (response variables). **Tables 1**, **2** provide information on the effect and response variables and their levels used in the analyses. The non-correlated effect variables included the gardener's socio-demographic characteristics (ethnicity, education, and gender), and four effect variables relating to agricultural experience (teacher [who taught you to garden/farm?], hours spent gardening, years of gardening experience, and employment [job related to agriculture or not]).

For the response variables, perceptions of pest problems were reduced to a binary variable (yes, no), because only 5 respondents answered "I don't know" (we removed these cases). For the pest control practices, we reviewed all responses (including open-ended "other" responses) and based on the answers, grouped the reported practices into six categories: hand removal, purchased spray or repellant, homemade spray, trapping, release or habitat manipulation for natural enemies, physical exclosures, and plant, soil, and water management (**Table 2**). Each practice was then further categorized as either "Curative" or "Preventive" (**Table 2**). Because gardeners reported up to four pest control practices, we calculated the proportion of curative, preventive, and "do nothing" practices per gardener. For example, if a gardener only provided one answer that was preventive, they would get 100% preventive, as would a gardener with four preventive practices. If a gardener reported two practices, one preventive

**TABLE 2 |** Pest control methods described by gardeners and the corresponding categories and groups where they were placed.

| Group | Pest method group | Pest method details | # of respondents |
|---|---|---|---|
| Curative | Hand remove pests | Hand remove pests | 66 |
| | | Picking off the slugs or squishing them | 1 |
| | | Use water to remove aphids | 1 |
| | Homemade sprays | Homemade sprays | 37 |
| | | Eliminate snails with salt | 1 |
| | | Lime (calcium carbonate) and water with salt | 1 |
| | | Soap or soapy water spray | 4 |
| | | Garlic for voles | 1 |
| | Trapping | Mechanical traps for gophers and squirrels | 6 |
| | | Sticky traps | 1 |
| | Organic, purchased sprays/repellents | 3 in 1 | 1 |
| | | Neem oil | 3 |
| | | Baking soda | 1 |
| | | Sluggo | 4 |
| | | Copper strip | 1 |
| | | Granuales for voles | 1 |
| | | Diotomacious earth | 1 |
| Preventive | Physical barrier | Enclose roots with mesh cages to avoid gopher and root insect damage | 11 |
| | | Eclose plants in cages/fencing to avoid squirrel and possum damage | 9 |
| | Plant, Soil, water management | Cut leaves and pull out plants with damage | 5 |
| | | Create an ecosystem where all microorganisms can live | 1 |
| | | Moving the drip irrigation hose away from certain plants/roots so that it is less wet, and that helps avoid the "fleas"; that also helps avoid root diseases | 1 |
| | | Plant disease-resistant crops | 1 |
| | | Planting green onions as a repellent | 1 |
| | | Raise the plants higher up (so that the animals cannot get on them) | 1 |
| | | Relocate plants, roll up newspaper and rolled plants | 1 |
| | | Water more consistently | 1 |
| | | Pick neighbors infested crops | 1 |
| | Natural enemies | Cats (they eat the gophers) | 1 |
| | | Leave orb spiders | 1 |
| | | Release ladybugs | 1 |
| | | Put water out for lizards (they eat pests) | 1 |

and one curative, they would receive 50% for each category, as would a gardener with four answers, two preventive and two curative.

To determine whether the likelihood of reporting pests or use of curative vs. preventive practices vary with gardener socio-demographic characteristics or agricultural experience, we used binomial logistic regressions (response variable is either yes/no; or proportion of practices that were curative). We created two global models with either (1) pest perception (yes/no), or (2) proportion of practices that were curative as the response variables, and ethnicity, education, gender, teacher, hours gardening, years gardening, and employment as effect variables. For the latter, we only used data for the gardeners that reported pests in their plots. We checked the variable inflation factor with the "vif" function in the "car" package version 3.0-2 (Fox and Weisberg, 2011). For all global models, all VIF scores were below 2.4 (**Supplementary Tables 1**, **2**). We then used the "dredge" function in the "MuMIn" package version 1.42.1 (Barton, 2012) to run all iterations of predictor variables, and ran model selection with the AIC scores to select the best models. If any models were within 2 AIC scores of the best model, we use the "model.avg" function to average these top models. All statistical analysis was conducted in RStudio version 1.1.456 (R Development Core Team, 2018).

## RESULTS

We had a total of 187 respondents. **Table 1** summarizes the total number of respondents for each of the gardening experience and socio-demographic effect variables. After removing 7 "I don't know" or "no answers" to the "do you have pests?" question, and

**TABLE 3 |** Results of GLMM model selection for models examining relationships between gardener socio-demographic factors and gardening experience with the likelihood of reporting pests in their plots.

| Model | Intercept | Education | Employment | Ethnicity | Hours gardening | df | logLik | AICc | Delta |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.49 | | | + | | 6 | −80.95 | 174.5 | 0 |
| 2 | 0.75 | | | + | + | 8 | −79.02 | 175 | 0.55 |
| 3 | 0.57 | + | + | + | | 11 | −75.78 | 175.4 | 0.92 |
| 4 | −0.30 | + | | + | | 9 | −78.11 | 175.5 | 0.97 |
| 5 | 0.18 | + | | + | + | 11 | −76.06 | 176 | 1.48 |
| 6 | 1.40 | | + | + | | 8 | −79.52 | 176 | 1.54 |

*All models within two AIC points of the top model are shown and were included in the averaged model. A plus (+) indicates that a variable was present in that model.*

**TABLE 4 |** GLMM model results for averaged best model (**Table 2**) pairwise comparisons examining differences in the odds of reporting pests based on gardeners' sociodemographic factors and experience gardening.

| **Ethnicity (6)** | **Hispanic** | **Asian Pacific islander** | **Black/African American** | **Middle eastern** |
|---|---|---|---|---|
| White | −0.90 ($z = 1.67$, $p = 0.09$) | −1.20 ($z = 2.27$, $p = 0.02$) | 14.89 ($z = 0.01$, $p = 0.99$) | −18.33 ($z = 0.01$, $p = 0.99$) |
| Hispanic | | −0.30 ($z = 0.51$; $p = 0.60$) | 15.80 ($z = 0.011$, $p = 0.99$) | 2.30 ($z = 51$, $p = 0.60$) |
| Asian Pacific islander | | | 16.09 ($z = 0.01$, $p = 0.99$) | −17.43 ($z = 0.01$, $p = 0.99$) |
| Black/African American | | | | −33.23 ($z = 0.12$, $p = 0.99$) |

| **Education (3)** | **Primary** | **Secondary** | **Post-Secondary** |
|---|---|---|---|
| No school | 1.15 ($z = 1.15$, $p = 0.25$) | −0.24 ($z = 1.75$; $p = 0.81$) | 1.01 ($z = 1.04$, $p = 0.30$) |
| Primary | | −1.39 ($z = 1.70$, 0.08) | −0.14 ($z = 1.18$, $p = 0.86$) |
| Secondary | | | 1.25 ($z = 2.13$, $p = 0.03$) |

| **Hours Gardening (2)** | **5–10** | **10+** |
|---|---|---|
| < 5 | −0.38 ($z = 0.84$, $p = 0.40$) | −1.09 ($z = 1.96$, $p = 0.05$) |
| 5–10 | | −0.71 ($z = 1.2$, $p = 0.230$) |

| **Employment (2)** | **Job not ag. related** | **Not working** |
|---|---|---|
| Ag. related job | −1.24 ($z = 1.75$; $p = 0.07$) | −0.83 ($z = 1.05$; $p = 0.29$) |
| Job not ag. related | | 0.40 ($z = 0.75$, $p = 0.45$) |

*Numbers show model coefficient and z and p-values for pairwise comparisons of different levels for each variable. In parenthesis next to the variable, are the number of models (which went into the averaged model) in which the variable was present (out of 6 models).*

any rows with "no answers" for the independent variables, 154 surveys were used for the final analysis.

1) Does the likelihood of reporting pests depend on gardeners' experience, and socioeconomic background?

Out of the final 154 surveys analyzed, 113 of the responding gardeners reported or perceived pests in their gardens compared to 41 gardeners that reported no pests in their gardens. The likelihood of reporting pests depended on gardeners' experience, and socioeconomic background. *Ethnicity* was the only variable present in all the six top models (within 2 AIC of best) that went into the averaged model (**Table 3**). White people were more likely to say that they have pests in their plots compared to Hispanics and Asian/Pacific islanders (**Table 4**, **Figure 1**).

*Education* appears in 3 of the 6 top models (within 2 AIC of best) that went into the averaged model (**Table 3**). Gardeners with Secondary education (middle school and high school) were less likely to say that they have pests in their plots than gardeners with Primary education and those with Post-secondary education (**Table 4**). Both *hours gardening* and *employment* (both related to experience in agriculture or gardening) appeared in two of the 6 top models (**Table 3**). Gardeners employed in an agricultural-related job were more likely to say they have pests in their plots compared to those with jobs that are not agricultural-related (**Table 4**, **Figure 1**). Gardeners who spend 10 h or more in gardens were less likely to say they have pests in their plots compared to gardeners who spend < 5 h in the gardens (**Table 4**, **Figure 1**).

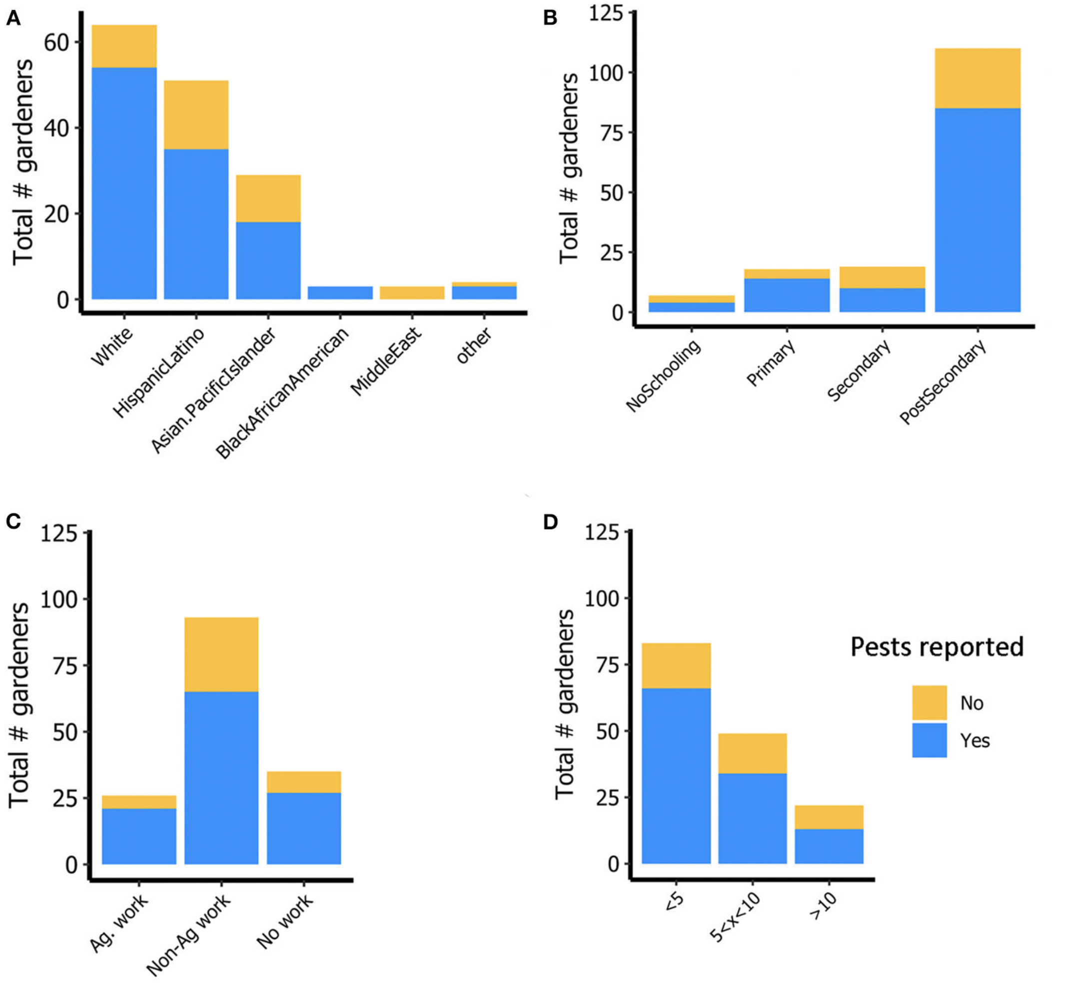

**FIGURE 1 |** Relative frequencies of gardeners reporting pests and no pests in their plots in community urban gardens in California. Panels represent the four variables present in the averaged best GLMM model explaining the likelihood that a gardener reported pests in their plot: **(A)** gardener ethnicity, **(B)** education, **(C)** employment, and **(D)** hours per week spent in the garden. See **Table 1** for explanation of variables.

2) Does the likelihood of using curative practices (as opposed to preventive practices or doing nothing) vary with gardener's experience and socio-demographic factors?

No gardener reported using pesticides but they reported a variety of preventive and curative practices (**Table 2**). Of all the gardeners, only eight directly stated that they do not do anything to control pests (e.g., "there's nothing I can do," "I have to accept my fate"). However, an additional 52 respondents, including gardeners that reported pests in their plots, did not report any pest control practices (**Figure 2**). The majority of gardeners that reported having no pests in their plots did not provide any answer for the pest control question ($n = 33$) but some did (**Figure 2**). Most of the gardeners that did report pests, reported using at least one pest control practice (**Figure 2**). For the gardeners that did report pests, *hours gardening* explained the proportion of practices that were curative in the top models that were included in the averaged model (**Table 5**). Gardeners who spend more than 10 h in gardens, reported using a higher proportion of curative practices (**Table 6**, **Figure 3**). In addition, *ethnicity* was included in 2 of the four top models that were included in the averaged model (**Table 5**). Asian-pacific islanders reported using a lower proportion of curative practices than Hispanics (all others are not significantly different) (**Table 6**, **Figure 3**). Lastly, *gender* also explained the proportion of curative practices used in two of the top four models (**Table 5**); however, the pairwise comparisons were not statistically significant (**Table 6**).

## DISCUSSION

In urban agriculture, gardeners and farmers face a range of challenges in maintaining their crops. One such challenge is to protect plants from insect pests and diseases that may have unique ecological interactions in urban environments (Faeth et al., 2005; Eriksen-Hamel and Danso, 2010; Egerer et al., 2020). In response, gardeners may employ a range of methods and practices to reduce crop damage or loss and to promote crop production. Yet the practices that gardeners choose, and whether they even perceive "pests" in their gardens, is likely related to their social background, experience, and agricultural knowledge (among many other factors). Here, we show that the majority of surveyed gardeners report that they have pests in their plots but that this significantly relates to the gardener's ethnic background. Furthermore, gardeners are using many different practices to combat pests, but the proportion of those practices that are curative (vs. preventive) is most related to the amount of time gardeners spend in their garden. In the following, we discuss how our findings inform the relationships between socio-demographics, education and experience, and pest management tactics by small-scale, non-commercial urban gardeners. Furthermore, we discuss how urban gardeners (and small-scale urban agriculture broadly) may further advance a prevention paradigm for sustainable pest management.

## Perceptions of Pest Problems

Our study confirms that urban gardeners are challenged by pests in their garden plots: 73% of gardeners report pests in their plots. Gardeners' perception of the severity of pest damage may correlate with actual herbivore infestation levels (Wyckhuys and O'Neil, 2007). A study conducted in the same gardens and year that our surveys were done, found a great abundance and diversity of herbivores in Brassica plants (a common crop at almost all study gardens). Herbivore abundance, however, depended on Brassica density in gardens and the amount of agriculture in the landscape (Philpott et al., 2020). Pest damage in our study sites varies greatly (Egerer et al., 2020) and brassica plants can have large aphid infestations (Egerer et al., 2018b). However, we do not have direct pest damage data for the year of the surveys to corroborate a direct correlation between gardeners' perception of pest damage and actual pest damage. Future studies should pair gardener questionnaires with herbivore population assessments and herbivory damage estimations.

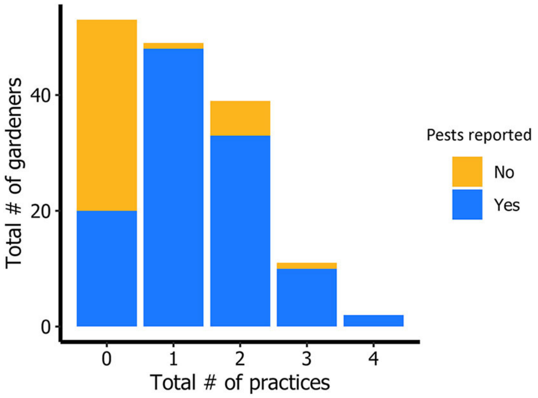

**FIGURE 2 |** Histogram of the number of pest control practices (curative and preventive) used by urban community gardeners who reported having pests in their plots (blue) and gardeners who did not report pests in their plots (yellow) (*n* = 154).

Whether gardeners report pests in their plots does not always reflect the actual pest infestations or plant damage and largely relates to gardeners' perceptions of what pests are and the problems they cause. In a study about pest control knowledge in Guatemala, Morales and Perfecto (2000) found that subsistence farmers were more likely to say that they "share" the crops with insects and thus less likely to report pests than commercial farmers. Similar to other studies in urban community gardens, gardeners in our study system use the produce that they harvest mostly for their own consumption, or for sharing with family and friends (Kim et al., 2014; Egerer et al., 2018c). Thus, their produce does not need to meet the same quality standards required for commercial growers. As such, gardener perceptions of pest problems might be related to (a) the gardener's attentiveness or observation levels, (b) preconceived notions of what represents a pest, or (c) their own tolerance for herbivory damage to their crops.

Whether a gardener reports pests or employs pest control practices may depend on whether they notice the herbivores in the first place (Obopile et al., 2008). Gardeners that spend more time in the gardens may have more time to scout their plants, and thus are more likely to detect herbivores and report pests. This would be especially true for difficult to observe herbivores like thrips and mites (Van Mele et al., 2002). In our study, gardeners who spend more than 10 h in gardens were actually less likely to say that they have pests in their plots than gardeners who spend 5 h or less. But we also found that gardeners who spend more than 10 h in the gardens use a higher proportion of curative practices to reduce pests. On the one hand, lower pest reporting for those who spend more than 10 h per week in the gardens may be because gardeners are not only tending plants but may be performing a multitude of garden tasks, or may spend time at

**TABLE 5 |** Average best models for the proportion of curative practices used by gardeners who reported pests in their plots (*n* = 113).

| Model | Intercept | Ethnicity | Gender | Hours gardening | df | logLik | AICc | Delta |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.3261 | | | + | 3 | −74.168 | 154.6 | 0 |
| 2 | 0.2504 | + | | + | 7 | −70.238 | 155.5 | 0.99 |
| 3 | 0.4451 | + | + | + | 8 | −69.494 | 156.4 | 1.82 |
| 4 | 0.3955 | | + | + | 4 | −74.061 | 156.5 | 1.94 |

*Results show GLMM model selection for models examining relationships between gardener socio-demographic factors and gardening experience with the likelihood of pest control practices that were curative. All models within two AIC points of the top model are shown and were included in average models. A plus (+) indicates a variable was present in that model.*

**TABLE 6 |** GLMM model results for averaged best models (**Table 4**) pairwise comparisons examining differences in the odds of pest control practices that were curative based on gardeners' sociodemographic factors and experience gardening.

**Hours Gardening (4)**

| | **5-10** | **10+** |
|---|---|---|
| < 5 | 0.1349 ($z = 0.302$, $p = 0.763$) | 1.6418 ($z = 1.789$, $p = 0.07$) |
| 5-10 | | 1.5070 (1.58, $p = 0.11$) |

**Ethnicity (2)**

| | **Hispanic** | **Asian Pacific islander** | **Black/African American** | **Other** |
|---|---|---|---|---|
| White | 0.66 ($z = 1.32$, $p = 0.18$) | −0.50 ($z = 0.89$, $p = 0.30$) | 15.94 ($z = 0.012$, $p = 0.99$) | −1.20 ($z = 0.89$, $p = 0.3742$) |
| Hispanic | | −1.1657 ($z = 1.792$, $p = 0.07$) | 15.2840 ($z = 0.012$, $p = 0.99$) | −1.8569 ($z = 1.34$, $p = 0.24$) |
| Asian Pacific islander | | | 16.4497 ($z = 0.012$, $p = 0.993$) | −0.6912 ($z = 0.494$, $p = 0.976$) |
| Black/African American | | | | −17.1409 (z=0.013, p=0.993) |

**Gender (2)**

| | **Male** |
|---|---|
| Female | −0.1126 ($z = 0.366$, $p = 0.4515$) |

*Numbers show model coefficient and z and p-values for pairwise comparisons of different levels for each factor. In parenthesis next to the variable, are the number of models (which went into the averaged model) in which the variable was present (out of 4 models).*

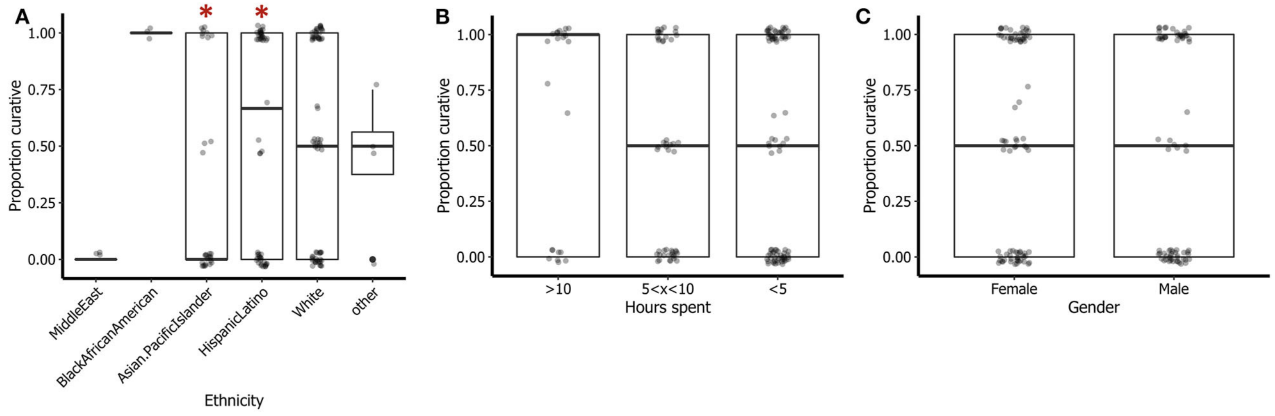

**FIGURE 3 |** The proportion of pest control practices that were curative used by urban community gardeners in California. The panels show the three variables that were present in the averaged best GLMM model explaining the proportion of practices that were curative: **(A)** ethnicity, **(B)** number of hours per week spent in the garden, and **(C)** gardeners' gender. See **Table 1** for explanation of variables. *Pairwise comparison significant at the $p = 0.07$ level.

the garden for non-gardening activities such as socializing with family or friends (e.g., Egerer et al., 2018c). More socializing can lead to more opportunities for knowledge and practices sharing between gardeners (McVey et al., 2018). On the other hand, gardeners that spend more than 10 h per week in their gardens may be able to control pests more effectively, due to more use of curative practices, and thus, less likely to report having pests in the first place. Additionally, more time in the gardens may also allow more detailed observations of ecological interactions that lead to the realization that not all animals present on the plants are herbivores and that not all herbivores do major damage.

Farmers and gardeners have preconceived notions of what represents a "pest" and the meaning of "pest" can have variable interpretations (Kogan and Jepson, 2007). For example, "pest" could be interpreted as any animal seen on plants or as only those doing significant herbivore damage (Morales and Perfecto, 2000). Our results suggest that these preconceived notions may depend on gardeners' ethnicity, education, and whether they work in agriculture-related jobs.

Another factor influencing whether a gardener reports pests or not may be how much damage to the crops the gardener is willing to accept before deeming the produce inedible. Reporting "pests" may thus relate to how much of the harvest is unacceptable to eat and this can vary greatly among growers as well as among consumers (of which gardeners are both). For example, social and demographic variables influence consumer attitudes and preferences toward sensory characteristics of organic produce (Yiridoe et al., 2005) and there is great variation in consumer willingness to accept insect damage in the produce they purchase (Goldman and Clancy, 1991). Accordingly, we found that the likelihood of reporting pests was influenced by gardeners' ethnicity. Small scale rural farmers employ their own economic and damage thresholds and not those assigned by scientists (Stonehouse, 1995; Wyckhuys and O'Neil, 2007; Obopile et al., 2008; Curry et al., 2015). Similarly, urban community may gardeners decide, based on their own personal preferences and attitudes toward consuming "imperfect" produce, when herbivores become "pests" (i.e., when damage levels render the produce inedible). In our study, this could suggest that gardeners who identified as Hispanic/Latino and Asian/Pacific Islander have a higher tolerance for herbivory damage to their crops than gardeners who identify as White.

## Curative vs. Preventive Practices

Synthetic pesticides have a suite of negative ecological (biodiversity loss) and social (health) impacts. In fact, one important motivation for growing fruits and vegetables in urban gardens is to avoid consuming synthetic pesticides present in conventional store-bought produce (Wakefield et al., 2007; Pourias et al., 2016). In addition, most gardens in our study prohibit the use of chemical pesticides. Thus, it is not surprising that no gardener in our study reported using synthetic pesticides, corroborating other studies in urban community gardens (Kim et al., 2014). Few gardeners reported zero pest control methods or that they do nothing to control pests. In contrast, the majority of gardeners reported a variety of pest management practices. These included curative practices like hand picking or crushing pests, cages and traps, and the use of homemade or purchased organic sprays as well as preventive practices such as enhancing habitat for natural enemies, using pest and disease resistant varieties, using plants as repellents, and crop rotation. This all shows the wide diversity of practices that urban gardeners use to manage their plots.

The majority of gardeners that reported having no pests failed to provide answers about how they control pests, which could mean that they actually do not do anything to prevent or control pests, but also that since they reported no pests, that they did not feel like they needed to respond or were not prompted to provide further answers about pests. Alternatively, these gardeners may be using gardening practices that prevent herbivore populations from becoming pests in the first place. It is thus possible that some gardeners may inadvertently be preventing pest damage but do not consider their used practices to be "pest control."

Of the listed attributes for control methods preferred for rural farmers in California, methods that were quick and inexpensive were highly preferred among farmers (Baldwin et al., 2014). Accordingly, the majority of gardeners in our study reported using curative practices to manage pests in their plots. Curative practices like using purchased or home-made sprays are quick and, in the case of home-made sprays, inexpensive options to manage pests. Furthermore, these practices align well with input-substitution organic agriculture, where the focus is to substitute chemical pesticides and fertilizers with organic alternatives (Rosset and Altieri, 1997).

Socio-demographic factors, like gender (Hovorka, 2005) and education (Nyirenda et al., 2011), can affect the type of pest control practices used in rural agriculture. For example, in vegetable farms in Malawi and Zambia, female respondents and respondents with more education were both more likely to report using preventive pest control practices like including plants with pest repellent properties (Nyirenda et al., 2011). In our study, although gender was present in the best averaged model, there was no statistically significant difference in the likelihood of using of curative vs. preventive practices between males and females. Furthermore, in our study, education was not related to pest control practices. The lack of agriculture-related materials in the curriculum in urban schools compared to rural ones may explain this difference (Hess and Trexler, 2011; Kovar and Ball, 2013). Instead, in our study, hours gardening was positively related to the likelihood of using curative practices. As stated above, more time spent in the gardens may increase social interactions between gardeners (McVey et al., 2018) and thus increase knowledge sharing about pests and pest control practices. This may explain the increased likelihood of using curative practices among gardeners who spend more than 10 h in the gardens.

Which practices are used, curative vs. preventive, may also relate to what specific pests gardeners are most challenged by, and on what particular crop plants. Here, because we only asked about pest management practices, but not specific pests, we can only infer the pest from the response to practices. Thus, future studies to further investigate how curative vs. preventive practice implementation relates to particular pests and particular crops to better inform pest management suggestions.

## Facilitating the Agroecological Paradigm in Urban Agriculture

In accordance with this research topic, we discuss how small-scale urban gardeners can participate in and advance the field of agroecological pest management which would entail shifting from a curative to a more preventative pest management paradigm. Gardens are interesting spaces in cities where gardeners adopt and experiment with agricultural practices due to the combination of environmental challenges, social organization, and garden to city level policies (Lin and Egerer, 2020). Many community gardens prohibit the use of synthetic pesticides and, in response, gardeners come up with different and unique ways to manage herbivory in their plots, and such creativity and experimentation may fuel knowledge generation in cost-effective and environmentally-sound management tactics.

It is important to recognize that not all UA practices increase sustainability (Mougeot, 2000; Weidner et al., 2019) and that some can have negative environmental impacts, especially in cities with no regulations regarding synthetic fertilizer and pesticide use (Lee et al., 2010). In the efficiency-substitution-redesign (ESR) framework, for instance, the transformation to a more sustainable agriculture is recognized as a process with three stages: *efficiency*, where the consumption and waste of inputs is reduced; *substitution*, where environmentally destructive inputs are substituted by more benign ones (organic fertilizers and pesticides, etc.); and *redesign*, where the root of causes of the ecological problems are identified and prevented (Hill and MacRae, 1996). In the case of pest control, an ecologically sound agricultural system, which is often attained with increased biodiversity and complexity, leads to autonomous pest control where no external inputs are needed (Vandermeer et al., 2010). Here, the goal should be to promote more biodiversity-enhancing practices that prevent herbivore populations from reaching damaging levels in the first place, so that curative practices are less needed. For sustainable UA, this implies that even in cities with strong regulations against synthetic inputs, like the ones where our study was conducted, practices that prevent herbivores from becoming pests in the first place should be promoted. And this should be done with a participatory approach (Weidner et al., 2019) that starts with understanding current knowledge about potential pests and pest management practices used by UA practitioners.

In our study, we found that even if the majority of gardeners use curative practices, many also use preventative practices. These include practices used by traditional rural farmers worldwide including crop resistance, weed management, harvest residue management, natural enemies management, mechanical control, repellents, and traps (Morales, 2002). For example, one gardener reported providing water and habitat for lizards in their plot to support this natural enemy. Another gardener reported creating an ecosystem where all microorganisms can live. Gardeners also reported improving plant health and resistance to reduce pests (moving the drip irrigation hose away from certain plants / roots so that it is less wet, and that helps avoid the "fleas"). Gardeners also reported using repellent plants (planting green onions as a repellent) and selecting disease-resistant crops, as well as mechanical control (such as clipping infested plants or part of plants) and crop rotation (moving plants), and traps or barriers (mostly for gophers, birds, and ground squirrels). These responses lend new insights into the ways that urban gardeners perceive and manage the biodiversity within their plots for pest control services. Other practices reported by rural traditional farmers like soil management, timing of planting and harvesting, and intercropping (Morales, 2002) were not directly reported by our surveyed gardeners as part of their pest control strategies. However, many gardeners are very likely using these practices (personal observations) even if not fully aware that these are helping to prevent herbivore population build up. This all shows that agricultural knowledge and managing practices of some urban gardeners is comparable to those of traditional rural farmers, and suggests that, similarly to farmer-to-farmer exchanges, more gardener-to-gardener activities and interactions may be very beneficial in the promotion of agroecological practices.

In addition to farmer-to-farmer exchanges, participatory interaction with agricultural outreach professionals (e.g., "Cooperative Extension" in the US) and scientists is also necessary for the promotion of agroecological practices. In rural communities in Honduras, for example, farmers who had attended pest control workshops delivered by a diversity of national and international institutions knew more about arthropod natural enemies and about pesticide alternatives than farmers who hadn't (Wyckhuys and O'Neil, 2007). Very few gardeners in our study reported to have learned to garden from classes or workshops. This may point to the lack of such activities or that those that are offered are not successfully advertised or are not accessible to the different needs (time and language constraints, e.g.).

Some gardeners in our study were familiar with the idea of enhancing habitat to promote natural enemies. This suggests that preventative pest control practices like conservation biological control, which is the conservation and augmentation of natural enemies that are already in the area or nearby areas (Barbosa, 1998), could be promoted and disseminated in community garden activities. This would help urban agriculture to follow a true agroecological transformation instead of staying in the input-substitution stage which emphasizes on alternatives to agrochemical inputs (Hill and MacRae, 1996; Rosset and Altieri, 1997). By considering the wide diversity of knowledge and needs of the urban gardeners, these activities would have to be readjusted to create a truly participatory learning process (Girard, 2015). Extension programs will need to adjust to local realities and, importantly, rely on trusted and deep-rooted members of the community to pass on the information (Noy and Jabbour, 2020). This may prove particularly challenging in urban community gardens where gardeners from such a diverse socio-economic and ethnic backgrounds work side-by-side in the same garden.

## CONCLUSION

Given the many failures of the current food system, the increasing interest in UA is likely to continue. Yet, despite the importance of UA generally, and community gardens specifically, for food security and access, there is still minimal research on pest prevention and sustainable pest management strategies for urban practitioners, especially for non-commercial ones. Our study contributes to this knowledge gap by showing how urban gardeners perceive pests and the range of strategies that they use to prevent and combat perceived pests. Our results also support studies in rural agricultural systems, which demonstrate the importance of integrating social context. In our case, identified ethnic/racial background, gardening experience, and time spent in gardens, were significant drivers of urban gardeners' decisions around pest management methods.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## ETHICS STATEMENT

The studies involving human participants were reviewed and approved by University of California Santa Cruz IRB Protocol # 2569. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

## AUTHOR CONTRIBUTIONS

HL, ME, and SP conceived the ideas and designed the methodology. ME, SP, PB, and CS collected the field data. HL analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2020.547877/full#supplementary-material

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# *Mestizo* Farmers' Knowledge of Entomofauna Is Reflected in Their Management Practices: A Case Study in the Andean-Amazon Foothills of Peru

*Lucila Marcela Beltrán-Tolosa*[1,2*], *Gisella S. Cruz-Garcia*[1,3], *Reynaldo Solis*[4] *and Marcela Quintero*[1]

[1] International Center for Tropical Agriculture, Cali, Colombia, [2] Universidad Nacional de Colombia, Palmira, Colombia, [3] Oxfam Novib, The Hague, Netherlands, [4] Instituto de Investigaciones de la Amazonía Peruana (IIAP), Iquitos, Peru

Local knowledge of entomofauna can influence environmental actions, particularly crop management practices, which can be sustainable or unsustainable. A farmer's decision-making is associated with their knowledge of beneficial insects and pests. This study aimed to assess local knowledge of entomofauna in relation to associated management practices, within a context of socio-cultural and environmental change. The research was carried out in Santa Lucía, a small *mestizo* village located in the deforestation frontier of the Peruvian Amazon. *Mestizos* are migrants, or descendants of migrants, from non-Amazonian regions of Peru. First, freelistings were conducted with a group of 19 female and 25 male farmers to evaluate their theoretical knowledge of insects, and to select the most salient insects associated with cassava, maize, and plantain. Second, two focus groups (which separated women and men) evaluated the practical knowledge of management practices for the most salient insects in the context of climate change. The most salient insects were collected and identified to the minimum possible taxonomic level. The results showed that farmers have a negative perception of entomofauna associated with cassava, maize, and plantain, as they considered insects to be harmful to their staple crops. Most farmers are not aware of the importance of beneficial insects such as pollinators and natural enemies. The findings of the study further showed that *mestizo* farmers did not have any management practices to preserve beneficial entomofauna, half of the insects they regarded as pests did not present any associated management practices, and the other half applied both sustainable (preventive and curative) and unsustainable practices (e.g., use of pesticides). The paper further discusses the dynamics of *mestizo* local knowledge on entomofauna in a changing environment and concludes that local capacities should be built to enrich knowledge about the recognition, biology, and ecological role of entomofauna (e.g., pollination, natural predation), and associated management practices (e.g., agroecological preventive practices that decrease pest incidence and protect pollinators, instead of curative practices) as an adaptation strategy to climate change.

**Keywords: local knowledge, agroecological practices, beneficial insects, pests, climate change**

**Edited by:**
*Helda Morales,*
*The South Border College (ECOSUR), Mexico*

**Reviewed by:**
*Jeffery W. Bentley,*
*Cornell University, United States*
*Elda Miriam Aldasoro Maya,*
*National Council of Science and Technology (CONACYT), Mexico*

***Correspondence:**
*Lucila Marcela Beltrán-Tolosa*
*lumbeltranto@unal.edu.co*

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# INTRODUCTION

Local knowledge (LK) is defined as "A cumulative body of knowledge, practice, and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment" (Berkes, 1999). LK is linked to the necessity of interacting, using, and managing local ecosystems and has a holistic approach that includes beliefs, a system of knowledge or theory (theoretical knowledge), and a group of practices (practical knowledge). Farming communities build images from nature based on their beliefs and establish interpretations of their environment by observing elements, facts, and patterns. They tend to recognize and name elements that are not only easily observed, but also culturally important for both utility or harm (Bentley and Rodríguez, 2001). Then, based on their cognition and interpretation they decide on and carry out practices to manage the environment. LK is acquired through trial and error in processes of learning and experimentation (Price, 2001). It is accumulated, transmitted, and modified through generations, and mediated by gender (Toledo et al., 1992; Toledo, 2002; Barrera-Bassols and Toledo, 2005; Sunderland et al., 2014).

LK influences environmental actions (Price, 2001), particularly management practices, which could be environmentally friendly (e.g., agroecological practices) or, unsustainable. Agroecological practices contribute to sustainable crop production by promoting farm diversification and the use and conservation of natural resources (Altieri, 2002; Wetzel et al., 2013). These practices increase the adaptive capacity of agroecosystems, making farmers less vulnerable to climate extreme events (Altieri et al., 2015). For example, these practices promote pest management through natural enemies, biopesticides, or management practices that protect beneficial biota, such as soil organisms and pollinators, contributing to soil fertility, and crop production. Unsustainable conventional practices promote the excessive use of chemical pesticides to control pests, which not only decrease the population of beneficial organisms but also contaminate the environment, negatively affecting rural households whose livelihoods depend on multiple ecosystem services. For example, recent studies have demonstrated that one of the main causes of the decline of beneficial entomofauna is the use of synthetic pesticides (Sánchez-Bayo and Wyckhuys, 2019). In addition, climate change is also contributing to this decline. For example, the changes in temperature and precipitation patterns caused by climate change might cause shifts in flowering seasons that affect the continuous availability of pollen throughout the foraging season of bees (van der Sluijs and Vaage, 2016). Moreover, floods, caused by climate change, are likely to be risky to bee species that nest or hibernate underground (Goulson et al., 2015). The negative effects of synthetic pesticides on pollinator populations might be exacerbated by climate change, decreasing crop production, and affecting human food security (van der Sluijs and Vaage, 2016).

Farmers who understand the ecological function of beneficial insects are less likely to have unsustainable management practices associated with entomofauna (Price, 2001; Wyckhuys and O'Neil, 2007). For example, based on the knowledge that ants and social wasps are natural enemies of pests, farmers in Honduras invented sugar-watery sprays to attract these insects (Wyckhuys and O'Neil, 2007). Maya farmers in Patzún, Guatemala, are familiar with insects associated with *milpa* (intercrop of corn, beans, and other edible plants). While they recognize all insects identified as pests by scientists, they do not consider them to be pests, arguing that all animals have a function in nature. Thus, they do not use any curative methods to manage insects, but their agricultural management methods (site selection, terrain preparation, and timing of planting) act as preventive methods that manage pests, resulting in a low incidence of pests in their *milpas* (Morales and Perfecto, 2000). Price (2001), and Price and Gurung (2006) mentioned that it is important to enhance the environmental knowledge of farmers to improve pest management behavior and sustainable management practices.

Conversely, a lack of knowledge about the ecological importance of insects makes farmers more likely to use unsustainable practices to manage pests (Wyckhuys and O'Neil, 2007; Midega et al., 2012; Wyckhuys et al., 2019). For example, López De La Cruz et al. (2018) found that limited knowledge about natural enemies of *milpa* pests and their life cycles in Maya farmers from Chiapas, Mexico, could impede farmers from employing biological control of insect pests. Munyuli (2011) also reported that 90% of farmers in a banana-coffee system of the Lake Victoria Arc in central Uganda were not aware of the role played by pollinators in the plantations, which was reflected in the excessive use of pesticides. Kasina et al. (2009) have documented that even beekeepers are likely to adopt pesticides to repel aggressive bees due to poor knowledge of their pollination service. Likewise, Gurung (2003) has explained that negative local beliefs associated with certain insects that have valuable roles in the agroecosystem (e.g., praying mantises pull out people's eyes and earwigs enter people's ears), might encourage the use of pesticides in Nepal. Thus, ecological literacy among farmers is key in determining the type of management practices that they use to manage insects (Wyckhuys et al., 2019).

Rural communities in the Andean-Amazon foothills (AAF) of Peru, which is one of the richest biodiversity eco-regions on Earth (Dinerstein et al., 2017), mainly depends on smallholder agriculture for their subsistence. The major staple crops in the AAF are cassava, maize, and plantain. These crops play a key role in the food security of the region, where they are not only central to the diet of local people but also constitute a source of income, particularly for poor farmers (Huamán Espino and Valladares, 2006; Ortiz et al., 2013; Molina Recio et al., 2016). However, climate change could cause an increase in temperatures in the AAF (Beltrán-Tolosa et al., 2020), which could affect the metabolic rate of pest insects, increasing their consumption of food and their population growth rates (Deutsch et al., 2018). As a result, crop damage would intensify, decreasing the production of key staple crops and exacerbating food insecurity in the AAF. In addition, the region is going through rapid processes of socio-cultural and environmental change, which are reflected in the expansion of the agricultural frontier, increased cash crop production, and deforestation (Finer et al., 2018). In this context, the use of agroecological adaptation strategies to manage entomofauna is necessary to strengthen local efforts to face climate change.

Understanding LK of both beneficial insects and pests, and their associated management practices, might provide insights for the design of agroecological management strategies of entomofauna aimed at decreasing the impact of climate change on crop production. This would ultimately contribute to improved food security and environmental conservation. This is certainly necessary for the AAF, where major processes of migration have been occurring in recent decades, alongside an increase of unsustainable agricultural practices (Murad and Pearse, 2018) and the vulnerability of farms to climate change. The hypothesis underlying this study is that smallholder farmers distinguish pests over beneficial insects associated with cassava, maize, and plantain (theoretical knowledge), and this is reflected in their practical knowledge (i.e., the absence of sustainable practices to protect beneficial entomofauna and reduce the incidence of pests). The research is based on a case study conducted in Santa Lucía, a small largely *mestizo* village in Yurimaguas, located in the AAF of Peru. *Mestizos* are migrants, or descendent from migrants, from non-Amazonian regions of Peru, and usually of mixed Indigenous and European heritage. *Mestizos* in Yurimaguas arrived since the 1960s from other provinces of the Peruvian Amazon and in the last 10 years from the highlands of the country. This study aims to assess LK about entomofauna associated with major staple crops in relation to their associated management practices, in the context of socio-cultural and environmental change.

LK was assessed from an ethnobiological approach. Ethnobiology studies how an ethnic, linguistic, or cultural group of people classify and organize their knowledge about the environment (Price, 2001). In this way, the study of LK was based on an *emic* approach, which refers to the understanding of local people's categorizations and classifications of the cultural domain or subject of interest (i.e., insects) that is based on the way they perceive the world using their language (in contrast to the *etic* approach, which is related to the researcher's categorization and classification of the object of study) (Martin, 2004). The study also has a gendered approach, given that gender affects LK, management, use, and access to environmental resources (Westermann et al., 2005; Dovie et al., 2008; Sunderland et al., 2014).

## STUDY SITE

The research was conducted in the village of Santa Lucía, which is located at 180 m.asl. and 22 km from the main city of Yurimaguas, situated along the Paranapura River, in the Yurimaguas district, Alto Amazonas province, Loreto region, Peru. Santa Lucía is in the forest-agriculture interface, possessing forested areas alongside agricultural fields. Previous studies have identified a loss of 34,012 ha of forest in Yurimaguas from 2004 to March 2017 with an annual loss rate of 2,557 ha/year since 2016 (Terra-i, 2017). The main causes of deforestation are the introduction of annual and perennial crops such as palm oil, rice, and papaya (Terra-i, 2017; Finer et al., 2018) The annual average rainfall in Yurimaguas fluctuates from 2,200 mm, and the average annual temperature oscillates between 22 and 26°C. The rainy season takes place from December to March when the river water level rises, generating floods that affect local subsistence activities. It has been projected that the temperature will increase 2.2°C by 2050 and 4.2°C by 2080, and that precipitation will increase 89 mm by 2050 and 350 mm by 2080 in the business as usual scenario (RCP 8.5), compared to the average temperature and precipitation from 1981 to 2010 (Beltrán-Tolosa et al., 2020). Farmers from Santa Lucía have already reported changes in climate patterns during a previous participatory rural appraisal conducted in the community (Beltrán-Tolosa et al., 2016). For instance, they argued that rainfall and temperatures have increased in the last 5 years, detrimentally affecting crop yields and increasing pests.

Santa Lucía has ∼64 families (460 inhabitants), and 90% of them are *mestizos*. This study was conducted with *mestizos*. Before the 1960s Santa Lucía was a territory occupied by the indigenous *Shawi* people. After the 1960s, a first wave of migrants from different regions of Loreto settled in this territory, founding the village of Santa Lucía in March 1962. In 2009, there was a second wave of migration after the construction of a road, which connects Yurimaguas with Tarapoto. The population of Santa Lucía is mainly employed in subsistence farming growing cassava, maize, beans, and plantain for self-consumption and income generation, and the production of rice and cacao for income generation [Autoridad Nacional del Agua (ANA) del Peru, 2018]. They also depend on fishing and hunting to complement their diet.

The results of a household survey conducted in 2016 by the "Sustainable Amazonian Landscapes" project, which included a representative sample of 417 households in 35 settlements of Yurimaguas (including 20 households from Santa Lucía), indicated that the population is composed of 54% men and 46% women. The mean household size was four persons, with 93% of the households being male-headed. The women heading the remaining 7% of households were mainly divorcees or widows. Two percentage of men and 3% of women older than 15 years were illiterate. Families cultivated an average area of 15 ha and reported a low number of agroecological practices for crop management (a mean of 1.5 out of 10 practices evaluated) (see note at the end of the paragraph). Some (22% households, only three from Santa Lucía) participated in training on the implementation of silvopastoral and agroforestal systems, and agroecological practices, including soil management during 2015–2016 (Quintero et al., 2019). Most of the local inhabitants from Santa Lucía do not have access to sanitation services, electricity, and running water; their houses are built from wood with floors made of sand, and the main road is not paved (Beltrán-Tolosa et al., 2016).

Note: The agroecological practices evaluated were: crop rotation, intercropping, no slash and burn, cover crops, organic fertilizers, natural weed control, natural pesticides, no tillage, fallow lands, and lime application. The practices carried out were natural pesticides and no tillage.

# METHODS

## Methods of Data Collection

Data collection took place in October 2017 in the *mestizo* village Santa Lucía, as part of the 4-year "Sustainable Amazonian Landscapes" project. Through the ongoing research project, one of the authors (RS) from the Instituto de Investigaciones de la Amazonía Peruana (IIAP) built a rapport with the local population, which facilitated approaching them for the assessment of LK. Village authorities were informed and consulted for approval before conducting the study. All persons who participated in the study did so freely and with prior informed consent.

To assess theoretical LK, first, the cultural domain, defined as the "*set of items that are all of the same type*" (Borgatti, 1998), was evaluated for the type "insect." For that, a group of 19 female and 25 male farmers were selected randomly from the village and asked to write on a piece of paper what they understand by the term "insect." Second, written freelistings, where informants are asked to elicit the different items that are part of a cultural domain, were conducted to assess the components of the cultural domain "insect" in relation to the main crops in the village and to identify which insects are the most cognitive salient ones (according to the cognitive salience index or CSI, explained in the data analysis sub-section). The freelistings were the first step in the ethnobiological analysis and were applied to uncover a cultural domain (Gatewood, 1984; Borgatti, 1998), and insect naming was the main indicator of theoretical LK (Gurung, 2003; Price and Gurung, 2006). In this exercise, informants were asked to write down all insects associated with cassava, maize, and plantain, with 10 min to write down the insects associated with each crop. It was explained to informants that they could include in their lists beneficial insects and/or pests. The insect names that people provided were recorded in the order they were given.

Practical LK was assessed through focus group discussions. Two separate focus groups (each composed of five women and five men) were carried out to capture the relations of the elicited insects and their respective crops, the management practices associated with beneficial insects and pests, and the perceived effects of climate change on the entomofauna. Participants were selected from the farmers who participated in the freelisting exercise based on their knowledge and willingness to participate in the focus group discussions. Focus groups took place 3 days after the free-listings (during these 3 days free-listings were analyzed and the lists of all elicited insects were prepared, as explained in the sub-section on data analysis). In the focus group discussions, participants were first shown the list of the most cognitively salient insects (highest CSI) per crop and asked if they agreed with or would like to add to the list. Second, informants were asked to discuss the following for each insect associated with each crop: (1) the relationship with the crop (i.e., if it is a beneficial insect or pest) and (2) the type of associated management practices (i.e., practices aiming at enhancing, tolerating or controlling the insect population). Third, to understand how farmers perceived the effects of climate change on entomofauna (which could partly explain the management practices they apply), they were asked if they think the climate has changed in the last 5 years and how, highlighting the indicators of climate change that caused more severe effects in agriculture; followed by the explanation of the effect of each indicator on each insect associated with cassava, maize, and plantain.

The taxonomical identification of the most cognitively salient insects was conducted after collection visits to cassava, maize, and plantain plantations in Santa Lucía. The visits were guided by a local informant (a focus group participant recognized as knowledgeable on entomofauna by villagers) who helped to search for the specimens. Insects were collected and preserved in ethanol 95% and identified to the minimum taxonomic possible level (following Borror and De Long, 1988), with the collaboration of the IIAP. The collected insects were deposited in the Laboratory of Phytopathology of the IIAP, located in San Martín, Peru.

## Methods of Data Analysis

*Emic* definitions of insects were analyzed by frequency of mention. Data from free listings were analyzed by combining both frequencies of mention and mean position of an insect across lists as part of the CSI index (Sutrop, 2001), separately for men's and women's lists per crop. The CSI was calculated as follows:

$\mathrm{CSI} = \mathrm{F} / (\mathrm{N}\ \mathrm{mP})$

F = Frequency of mention (number of lists in which the insect is named)

N = Total number of participants (number of lists)

$\mathrm{mP} = (\sum \mathrm{Rj}) / \mathrm{F}$ (Mean position of the term across participants' list)

Rj = Range of the term in an individual list.

The CSI assumed that the items (i.e., insects) more frequently mentioned and named first across informant lists are more salient or prominent than those named at the end. Scores can range from 0 to 1, where 1 is the most salient insect, and 0 is the least salient insect. Most salient insects were defined as those with a CSI of 0.05 or higher. In addition, the mean length of lists was calculated for each crop (separately for men and for women), and a Mann-Whitney *U*-test for non-parametric data was used to test the statistical significance of the differences between men's and women's list lengths per crop, using the software R (R Studio Team, 2015).

Finally, the results of the focus groups were transcribed and presented in tables, separately for men and women.

## Methodological Limitations

The methodology used has several limitations. First, the study did not include the local classifications of entomofauna, given that local people might classify insects under criteria other than associating them to specific crops; such assessment could have provided additional insights for the interpretation of the study results. Asking people for insects related to certain crops might have circumscribed people's comprehension of entomofauna, which is a wider universe than one of the insects associated with crops. Second, the way the question was asked in the freelisting exercise (i.e., which insects are associated to specific crops) could have caused participants to not consider other species beyond the

**TABLE 1 |** Frequency of farmers' emic conceptualizations of entomofauna.

| Group of definitions | Local insect definition | English translation | Frequency of mention (number of people) | |
|---|---|---|---|---|
| | | | **Women** | **Men** |
| Harmful for plants and people, insects in general | *"Animales que atacan las plantas y pican personas"* | Animals that attack plants and sting people | 1 | 2 |
| | *"Son malos para los sembríos y para el campesino"* | They are prejudicial for crops and farmers | 1 | |
| | *"Son animales que vuelan y pican"* | Animals that fly and sting | 1 | |
| | *"Pican a la gente y transmiten enfermedades"* | They sting people and transmit diseases | 1 | 3 |
| | *"Hacen que la gente se enferme y pierda la comida"* | They make people ill and make people lose food | | 1 |
| | *"Animales que hacen daño"* | Animals that hurt | 1 | |
| Harmful for plants, insects in general | *"Es un animal que ataca y que puede matar a las plantas"* | Animal that attack plans and can kill them | 1 | |
| | *"Son plagas"* | They are pests | 4 | 5 |
| | *"Son parásitosde las plantas"* | They are parasites of plants | 1 | 2 |
| | *"Malogran los sembríos"* | They damage crops | 5 | 4 |
| Harmful for plants, related to a specific insect | *"Mariposa que pone los huevos y que afecta las plantas"* | Butterfly that lay eggs and affects plants | | 1 |
| | *"Chinches que comen hojas de las plantas"* | Leaf footed bugs that eat leaves of plants | | 1 |
| | *"Gusanos que malogran las plantas"* | Worms that cause plant damage | 1 | 4 |
| | *"Mariposa que pone huevos"* | "Butterfly that lay worms" | | 1 |
| | *"El papaso pone los gusanos en el plátano y lo malogra"* | The adult of a butterfly lay worms on plantain and damage it | 1 | |
| Not a negative perception | *"Hay insectos buenos y malos para las plantas"* | Insects are both beneficial and harmful | | 1 |
| | *"Son animales que tienen muchas patas"* | Animals with many legs | 1 | |

*Data obtained from 44 people (19 women and 25 men).*

pests, and results might have been different if the question would have been framed differently (e.g., which are the insects present in the fields where specific crops are cultivated). Third, given that data was collected in written form, the length of the lists might be affected by men's and women's writing skills (although support was provided during the exercise). Four, only practical LK was documented, but not actual management practices. Finally, factors such as age, household composition, and income, which could also explain variation in LK were not part of the scope of this study. Despite these limitations, the study yields valuable insights into the understanding of the relations between the theoretical and practical LK of entomofauna in the context of socio-cultural and climate change.

# RESULTS

## Theoretical LK of Entomofauna Associated With Staple Crops

### Emic Definition of Insects

Both men and women in Santa Lucía showed a negative perception of entomofauna associated with cassava, maize, and plantain. They considered insects to be harmful. Most definitions were related to their harm to plants and people, or their harm to plants only (i.e., related to insects in general or specific insects). For example, some general definitions for insects were "*insects are pests*," "*insects are worms that cause plant damage*," and "*insects damage crops*," except for two people who mentioned that "*insects are animals with many legs*" and "*insects are both beneficial and harmful*" (**Table 1**).

### Cognitive Salience of Insects

The results of cognitive salience indexes are in **Table 2**. Four insects, all pests, were mentioned for cassava. The most mentioned insects were "curuinsi" leafcutter ant (*Atta* spp.) by 73% of women and 64% of men, and "gusano blanco" stemborer (*Chilomima* spp.) by 84% of women and 60% of men. Five insect pests and one beneficial insect were mentioned for maize. The most mentioned pest was "gusano cogollero" armyworm (*Spodoptera frugiperda)* by 73% of women and 84% of men, and the beneficial one was "abejas" bees (*Apis* spp.) elicited by 42% of women and 28% of men. One pest and one beneficial insect were mentioned for plantain. The insect pest was "suri de plátano" giant moth borer (*Castnia licus*), and the beneficial insect was "hormiga" (ant) mentioned by 20% of men and 16% of women. Pests for the three crops were compared with the literature, which indicates that these insects have also been described as pests following an *etic* approach (**Table 3**).

The least salient insects (i.e., elicited by less than five persons) were "avispa" (wasp), araña (spider), and "lombriz" (earthworm) for cassava, "mosca blanca" (white fly), "mosca" (fly), and "comején" (termites) for maize; and "araña" (spider), "comején" (termites), and "alacrán" (scorpion) for plantain.

The insect list length was not significantly different between men and women for cassava (median = 3, interquartile range = 2 for women; median = 3, interquartile range = 1 for men;

**TABLE 2** | Most salient insects associated with cassava, maize, and plantain listed by *mestizo* women and men, indicating the percentage of women and men that mentioned each insect and their corresponding Sutrop's cognitive salience index (CSI).

| **Crop** | **Insect** | | **Women** | | **Men** | |
|---|---|---|---|---|---|---|
| | **Common name** | **Taxonomy** | **CSI** | **percentage (*n* = 19)** | **CSI** | **percentage (*n* = 25)** |
| Cassava | Curuinsi (leaf cutter ants) | Order: Hymenopetra<br>Family: Formicidae<br>*Atta* spp. | 0.69 | 73 | 0.47 | 64 |
| | Gusano blanco (stemborer) | Order: Lepidoptera<br>Family: Pyralidae<br>*Chilomima* spp. | 0.40 | 84 | 0.32 | 60 |
| | Gusano cornegacho | Order: Lepidoptera<br>Family: Sphingidae<br>*Manduca* spp. | 0.15 | 31 | 0.05 | 8 |
| | Grillo (grasshopper) | Order: Orthoptera<br>Family: Acrididae | 0.05 | 16 | 0.16 | 36 |
| Maize | Gusano cogollero (fall armyworm) | Order: Lepidoptera<br>Family: Noctuidae<br>*Spodoptera frugiperda* | 0.57 | 73 | 0.65 | 84 |
| | Chinche (leaf footed bugs) | Order: Hemiptera<br>Family: Coreidae | 0.05 | 5 | 0.21 | 48 |
| | Abeja (bee) | Order: Hymenopetra<br>Family: Apidae<br>*Apis* spp. | 0.24 | 42 | 0.12 | 28 |
| | Gorgojo (weevil) | Order: Coleoptera<br>Family: Bostrichidae | 0.14 | 21 | 0.02 | 12 |
| | Grillo (grasshopper) | Order: Orthoptera<br>Family: Acrididae | 0.08 | 21 | 0.12 | 36 |
| | Curuinsi (leaf cutter ants) | Order: Hymenopetra<br>Family: Formicidae<br>*Atta* spp. | 0.06 | 21 | 0.12 | 36 |
| Plantain | Suri de plátano (giant moth borer) | Order: Lepidoptera<br>Family: Castnidae<br>*Castnia licus* | 0.57 | 73 | 0.66 | 92 |
| | Hormiga (ant) | Order: Hymenoptera<br>Family: Formicidae | 0.08 | 16 | 0.04 | 20 |

*Data were obtained from 44 people (19 women and 25 men).*

W = 214, $p = 0.5692$), and plantain (median = 3, interquartile range = 1 for women; median = 2, interquartile range = 2 for men; W = 174, $p = 0.11$). However, for maize, men provided significantly longer lists (median = 2, interquartile range = 2 for women; median = 3, interquartile range = 2 for men; W = 336.5, $p < 0.05^*$).

## Practical LK: Management Strategies Associated With the Entomofauna

For women, 50% of insects did not have any associated management practices, 30% had sustainable practices (mainly curative such as the manual elimination of worms), and 20% unsustainable practices (such as spraying pesticides). For men, 40% of insects did not have any associated management practice, 40% had sustainable practices (both curative and preventive), and 20% had unsustainable practices.

Some curative strategies practiced by men are manual elimination of worms and eggs. The preventive strategies mentioned by men are terrain preparation (putting ashes around the plant to prevent moths from laying their eggs), site selection (planting in clay soil instead of sandy soil) and cultivating insecticidal plants around crop fields. For example, planting "rosasisa," also known as African marigold (*Tagetes erecta* L), around cassava and maize fields is a practice to manage *Atta* spp. "Rosasisa" acts as an insecticidal plant when the ant feeds on it instead of crops. However, during focus groups, men mentioned that if they could afford to buy agrochemicals to manage *Atta* spp., they would apply them instead of "rosasisa," because growing "rosasisa" requires extra time and work.

Women considered a curative strategy as the main management strategy to manage "gusano blanco" stemborer (*Chilomima* spp.) in cassava, which is the manual elimination of the worms. In contrast, men mentioned a preventive strategy that consists of planting cassava in clay soil instead of sandy soil, as stemborers increase in sandy areas. A similar result was found for managing "suri de plátano" giant month borer (*Castnia licus*) in plantain, i.e., women mentioned a curative strategy of manual elimination of eggs, larvae, and damaged stems; while men mentioned a preventive strategy that consists of putting ashes

**TABLE 3 |** Etic description of the most salient insects identified by women and men based on the literature.

| Crop | Common name | Taxonomy | Description | References |
|---|---|---|---|---|
| Cassava | Curuinsi (leaf cutter ants) | Order: Hymenopetra<br>Family: Formicidae<br>*Atta* spp. | It is a generalist species that cut leaves of different crops, but it can produce total losses of the crop if is not controlled | Vanegas, 2018 |
| | Gusano blanco (stemborer) | Order: Lepidoptera<br>Family: Pyralidae<br>*Chilomima* spp. | It is considered one of the most important pests for cassava. Females put the eggs near to the bud and the caterpillar eats from de cortex to the stem, thus perforations fracture the stem producing low yields of roots | Ospina and Ceballos, 2002; Perozo et al., 2007 |
| | Gusano cornegacho | Order: Lepidoptera<br>Family: Sphingidae<br>*Manduca* spp. | It is a pest that affects in less proportion cassava than other pests such as *Chilomima* spp., but it can defoliated a complete plant if is not controlled | Nicaragua et al., 2004 |
| | Grillo (grasshopper) | Order: Orthoptera<br>Family: Acrididae | They are generalist species that attack not only cassava, but different crops. They cut plants after hatching, also cause damage on the base of the plant leaving it susceptible to overturning | Ospina and Ceballos, 2002 |
| Maize | Gusano cogollero (fall armyworm) | Order: Lepidoptera<br>Family: Noctuidae<br>*Spodoptera frugiperda* | This species prefers maize, but can cause significant damage to 80 species of crops. Female moth put the eggs on the leaves, after hatching the caterpillars feed on leaves and move to the protective region on the whorl, resulting in ragged holes in the leaves. If feeding is on young parts, the growing point is killed resulting in no new leaves or cob developing. But, if the plant have developed cobs, the larvae will feed on the kernels | Food and Agriculture Organization of the United Nations (FAO), 2018 |
| Plantain | Suri de plátano (giant moth borer) | Order: Lepidoptera<br>Family: Castnidae<br>*Castnia licus* | This species attack plantain, coconut and sugar cane. The moth lay the eggs on dry leaves of plantain and when the caterpillar hatches it tunnels into the stem and destroy it affecting plant development and fruit production | Vela Panduro and Marca, 2007 |
| | Hormiga (ant) | Order: Hymenoptera<br>Family: Formicidae | It feeds on the eggs of *C. licus* helping to control it naturally | Skinner, 1930 |

around the plant to prevent moths from laying their eggs on the plant (**Tables 4**, **5**).

Women considered bees to be pests because they believed that they fed on maize flowers, causing maize kernels to not develop properly. In contrast, some men mistakenly considered bees to be important insects for maize pollination, although maize is pollinated by wind. In either case, they did not know of any practices to conserve them. "Hormigas" were considered beneficial by men and women, since they fed on the eggs of "suri de plátano" (*Castnia licus*), helping to decrease the number of emerging moths. Both male and female farmers did not report using any practices to preserve beneficial insects (**Tables 4**, **5**).

## Perceived Effects of Climate Change on Entomofauna

People in Santa Lucía identified the following indicators of climate change in order of severity (i.e., starting with indicators that most negatively affect agriculture): (1) increase in rainfall, (2) increase in temperature, and (3) heavy winds. Farmers mentioned that the first two indicators have negatively affected crop production and increased pests (**Tables 4**, **5**). The last indicator affected crop production because it overturned the plants but did not affect pests. Men and women agreed on the effects of the indicators of climate change on most insects identified as prominent for each crop, except for the effects on "gusano cogollero" armyworm (*Spodoptera frugiperda),* and "abejas" *Apis* spp. (**Tables 3**, **4**). Armyworm increases were associated with high temperature for women and with rains for men. Bees would be affected by high temperatures according to men, but not women.

# DISCUSSION

The hypothesis "smallholder farmers mainly distinguish pests over beneficial insects associated with cassava, maize, and plantain (theoretical LK), and this is reflected in their practical LK (i.e., the absence of sustainable practices to protect beneficial insects and reduce the incidence of pests)" was only partly fulfilled based on the results of the study conducted in Santa Lucía village. Regarding the first part of the hypothesis, most of the most salient insects are pests. For instance, while eight out of 11 of the most salient insects were classified as pests by all informants, only two out of 11 were regarded as beneficial by $<34\%$ of informants. Of these, 16% of women and 20% of men recognized ants as beneficial to manage "suri de plátano" (*C. licus*) in plantain, and 28% of men explained that bees are important maize pollinators (while maize is pollinated by wind), and 42% of women classified bees as pests. The negative connotation of insects starts from their *emic* definition of the cultural domain "insect," where both men and women considered insects harmful for crops. Our results are aligned with Bentley and Rodríguez (2001), who argued that farmers mostly recognize insects that are culturally important such as disease organisms or pests of crops.

Regarding the second part of the hypothesis, the lack of knowledge of most informants about beneficial insects was

**TABLE 4 |** Practical knowledge of common management strategies associated with entomofauna among women.

| **Crop** | **Insect** | | **Crop effect** | **Management strategy** | **Climate effects** |
|---|---|---|---|---|---|
| | **Common name** | **Taxonomy** | | | |
| Cassava | Curuinsi (leaf cutter ants) | Order: Hymenopetra<br>Family: Formicidae<br>*Atta* spp. | Breaks the stem and eats the leaves | Pesticides if they can afford them | Not affected by climate |
| | Gusano blanco (stemborer) | Order: Lepidoptera<br>Family: Pyralidae<br>*Chilomima* spp. | Eats the stem and leaves | Manual elimination, birds eat them | Increases with high temperatures |
| | Gusano cornegacho | Order: Lepidoptera<br>Family: Sphingidae<br>*Manduca* spp. | Breaks the leafs when the plant is juvenile | Manual elimination | Increase with rains |
| | Grillo (grasshopper) | Order: Orthoptera<br>Family: Acrididae | Feeds in the whorl when the plant is juvenile | No action taken | Increase with rains |
| | Gusano cogollero (fall armyworm) | Order: Lepidoptera<br>Family: Noctuidae<br>*Spodoptera frugiperda* | Feeds in the whorl | No action taken | Increases with high temperatures |
| | Chinche (leaf footed bugs) | Order: Hemiptera<br>Family: Coreidae | Burns the leaves | No action taken | Increases with rains |
| | Abeja (bee) | Order: Hymenopetra<br>Family: Apidae<br>*Apis* spp. | Steals pollen which makes corn kernels not to grow | No action taken | Not affected by climate |
| Maize | Gorgojo (weevil) | Order: Coleoptera<br>Family: Bostrichidae | Eats the grain | Pesticides (Phosfin tablets located between bags of maize inside a container) | Increases with high temperatures |
| | Grillo (grasshopper) | Order: Orthoptera<br>Family: Acrididae | Breaks the stem | No action taken | Not affected by climate |
| | Curuinsi (leaf cutter ants) | Order: Hymenopetra<br>Family: Formicidae<br>*Atta* spp. | Eats grain and leaves | Pesticides if they can afford them | Not affected by climate |
| Plantain | Suri de plátano (giant moth borer) | Order: Lepidoptera<br>Family: Castnidae<br>*Castnia licus* | The butterfly put eggs in the stem, the larvae enters into the stem and kill the plant | Manual elimination of eggs, larvae and damage stems | Not affected by climate |
| | Hormiga (ant) | Order: Hymenoptera<br>Family: Formicidae | They kill "suri de plátano" | Do not kill it | Not affected by climate |

**TABLE 5 |** Practical knowledge of common management strategies associated with entomofauna among men.

| Crop | Insect | | Crop effect | Management strategy | Climate effects |
|---|---|---|---|---|---|
| | **Common name** | **Taxonomy** | | | |
| Cassava | Curuinsi (leaf cutter ants) | Order: Hymenopetra<br>Family: Formicidae<br>*Atta* spp. | Eats the leaves, the root hardens and is not palatable to eat | Planting Rosasisa (*Tagetes erecta L.*) that kill the ant or using poison<br>Pesticides if they can afford them | Not affected by climate |
| | Gusano blanco (stemborer) | Order: Lepidoptera<br>Family: Pyralidae<br>*Chilomima* spp. | Breaks the stem | Avoid planting in sandy soil because the worm increases, planting should be in clay soil | Increases with high temperatures |
| | Gusano cornegacho | Order: Lepidoptera<br>Family: Sphingidae<br>*Manduca* spp. | Eats the leaves | Manual elimination | Increase with rains |
| | Grillo (grasshopper) | Order: Orthoptera<br>Family: Acrididae | Eats the branches | No action taken | Increase with rains |
| | Gusano cogollero (fall armyworm) | Order: Lepidoptera<br>Family: Noctuidae<br>*Spodoptera frugiperda* | Feeds in the whorl of corn, perforates the leaves | Wait for heavy rains to flood the stem and kill it<br>Manual elimination | It appears after dry periods and increase with rains |
| | Chinche (leaf footed bugs) | Order: Hemiptera<br>Family: Coreidae | Dries the Leaf and delay corn production | No action taken | Increase with heavy rains and dryness |
| | Abeja (bee) | Order: Hymenopetra<br>Family: Apidae<br>*Apis* spp. | Bees contribute to produce maize | No action taken | Decrease with high temperatures |
| Maize | Gorgojo (weevil) | Order: Coleoptera<br>Family: Bostrichidae | Eats the grain | Wash the cob<br>Pesticides (Phosfin tablets located between bags of maize inside a container) | Increase in hot periods |
| | Grillo (grasshopper) | Order: Orthoptera<br>Family: Acrididae | Breaks the trunk when it is emerging and kills the plant | No action taken | Increase with rains |
| | Curuinsi (leaf cutter ants) | Order: Hymenopetra<br>Family: Formicidae<br>*Atta* spp. | Eat the leaves | Planting Rosasisa (*Tagetes erecta* L.) that kill the ant or using poison<br>Pesticides if they can afford them | Not affected by climate |
| Plantain | Suri de plátano (giant moth borer) | Order: Lepidoptera<br>Family: Castnidae *Castnia licus* | Eats the whorl and affect fruit production | Kill manually the eggs of the moth and put ash surrounding the plant to prevent the butterfly to put the eggs | Not affected by climate |
| | Hormiga (ant) | Order: Hymenoptera<br>Family: Formicidae | Eats "Suri de plátano" | Do not kill it | Decrease with heavy rains |

reflected by the lack of management practices to preserve or promote them. While most management practices reported were mainly to control pests, half of the insects lacked any type of management practice. The other half of insects were managed by sustainable (curative and preventive) or unsustainable (e.g., use of pesticides) management practices. In addition, farmers explained during focus groups that they would use more pesticides if they could afford to buy them. Our results agree with previous studies that reported that a lack of ecological literacy among farmers has consequences for the farming management practices that they use. For example, it was reported that many potato farmers in the Kabale, Kisoro, Mbale, Kapchorwa, Mubende, and Kyegegwa districts in Uganda lacked knowledge about the natural enemies of potato pests, which resulted in them using pesticides for pest control (Okonya and Kroschel, 2016). Similar results were found in Maranda, Asego, Uranga, Lambwe, and Madiany districts in Kenya where a lack of knowledge about the natural enemies of cotton pests was reflected in the indiscriminate use of pesticides (Midega et al., 2012). LK on agroecological practices for pest management must be improved to prevent the widespread use of unsustainable management practices (such as the excessive use of harmful pesticides) which could have a detrimental effect on local ecosystems, and ultimately on local food security, health, and biodiversity conservation.

One of the explanations for the lack of recognition of beneficial insects is that *mestizo* smallholder farmers in Santa Lucía recently settled in the village: i.e., they migrated in the 1980s from other provinces of Loreto and in the last 10 years from the highlands of Peru. They came from regions with different environmental characteristics, culture, and farming activities, and started new productive activities in the Amazon region. In contrast with inter-generational processes of knowledge transmission, which are typical of indigenous peoples who have long-term history and knowledge of the environment where they live, *mestizos*' knowledge of the crops, their agronomy, and the local entomofauna have been acquired by recent trial and error (e.g., while experimenting with crops that might have been new to them), and/or transmitted from other *mestizos* or indigenous peoples from surrounding villages. There have been similar findings from another region of the Peruvian Amazon where *mestizo* children were found to have lost or failed to acquire knowledge about food plants due to socio-cultural change in the region (Cruz-Garcia et al., 2018). In contrast, studies conducted with indigenous peoples have reported a thorough knowledge of beneficial insects such as pollinators or natural enemies. For instance, knowledge of bee pollinator systems is found in many cultures: 17 species of stingless bees were identified by people in Yucatan (Mexico), 23 by Hoti people in Venezuela, 25 among Tatuno, Siriano, and Bara people of the Vaupes and Apaporis rivers of Colombia, and 43 by Nukak indigenous from the Colombian Amazon (Hill et al., 2019). The deep knowledge of these indigenous cultures about pollinators was accompanied by bee conservation practices such as the conservation of nesting trees, construction of beehives, protection of flowering resources and forests, and farming diversification represented in agroforestry and home gardening, among others (Hill et al., 2019).

Although most of the insects elicited in Santa Lucía were pests, the number of pests that were identified by local people was lower in comparison to *etic* knowledge, i.e., with pests reported in the literature for the three crops. On one hand, some publications on crop pests are general and not specific to the Amazon region, therefore they may report pests that are not common to the types of agroecosystems present in Santa Lucía. On the other hand, this might be explained by the fact that Santa Lucía still has subsistence agriculture, characterized by including a diverse mixture of plants for own consumption, instead of intensified monocropping. The diversity in the agricultural fields prevents pest proliferation because a field with a variety of plants does not offer a large block of food for insects (as a monoculture does), so pests will not get the nutrients necessary to proliferate (Davis University of California, 2016; Wetzel et al., 2016). In this study, while only two insects associated with cassava, "curuinsi" (*Atta* spp.) and "gusano blanco" (*Chilomima* spp.), were the most cognitively important among participants in Santa Lucía, there are several additional groups of insects that have been recognized as pests for this crop in the literature, including mites, thrips, hornworms, white flies, ants, termites, grasshoppers, gall midges, lace bugs, stem borers, white grubs, fruit flies, shoot flies, scale insects, mealy bugs, and cutworms (Belloti and van Schoonhoven, 1978). Whereas, most men and women in Santa Lucía highlighted "gusano cogollero" (*S. frugiperda*) as the most important insect associated with maize, there are several pests reported for maize in the literature, including thrips, moths, grasshoppers, and beetles (CESAVEG, 2018). Particularly, "gusano cogollero" (*S. frugiperda*), "gusano soldado" (*Mocis* spp.), "barrenador de la caña de azúcar" (*Diatraea saccharalis*), "gusano choclero" (*Helicoverpa zea*), and "pulgón del maíz" (*Rhopalosiphum maidis*), all of which have been reported as maize pests in the region of San Martín, which is located near Yurimaguas, where the study took place (Meléndez, 2013). Most men and women listed "suri de plátano" (*C. licus*) as the most salient insect for plantain, while it is known that there are other pests including beetles and moths (ICA, 2012). In particular, "suri de plátano" (*C. licus*) and "gorgojo negro" (*Cosmopolites sordidus*) have been reported as major pests in the province of Datem del Marañon, Loreto region (Cuñachi, 2014).

Results have shown that farmers in Santa Lucía use sustainable practices to manage entomofauna such as using insecticidal plants and the manual removal of pests. For example, the use of the insecticidal plant "rosasisa" was mentioned by men to manage *Atta* spp. on cassava and maize. When the plant is cultivated in agricultural fields next to crops, ants transport leaf cuts of "rosasisa" (*T. erecta*) to the nest for feeding purposes, but the plant has biochemical lethal components for the ant, thus acting as an insecticide. Participants reported that this technique was learned from indigenous people. The use of *T. erecta* as an insecticide has also been reported among indigenous Maya people in Patzun, Guatemala (Morales and Perfecto, 2000). In addition, Parugrug and Roxas (2008) have reported the repellent action of this plan against the maize weevil, *Sitophilus zeamais*. Likewise, Verma et al. (2009) reported the termiticidal properties of *T. erecta*. Another example of sustainable management practices is the manual removal of "gusano blanco" (*Chilomima* spp.) from cassava plants, reported by women. This is aligned to studies that indicate that the management of this insect is curative, as the use of pesticides is impractical as the insect feeds inside the stems where pesticides cannot reach it (Belloti and van Schoonhoven, 1978; Almonacid et al., 2016). In addition, some men and women have reported that "suri de plátano" (*C. licus*) is controlled naturally by ants. Certainly, other studies have revealed that ants destroy a considerable proportion of the eggs laid by this moth helping to control their populations (Skinner, 1930). Farmers in Santa Lucía have explained that moths lay eggs covered by phlegm on the plant and ants have been observed feeding on the eggs. The recognition of the eggs by local villagers might have been learned from their observations, from other farmers, or obtained from technical training (although the amount of training was minimal). However, according to the survey mentioned in the study site, only 3 of 20 households in Santa Lucía received training capacity on agricultural practices in 2015–2016.

The results showed that the main indicators of climate change that affect pests are the increase in rainfall and temperature. Similarly, previous participatory rural appraisals conducted in the village (Beltrán-Tolosa et al., 2016) showed that farmers perceived an increase of pests associated with cassava, maize, and plantain in the last 5 years and they ascribed it to the same indicators of climate change. When comparing the findings of this study to *etic* knowledge, the literature has predicted that insect pest species will respond differently to increased temperatures, depending on their geographical distribution and the target crop (Deutsch et al., 2018). For example, stem borers such as "gusano blanco" (*Chilomima* spp.) associated with cassava seem to be influenced mainly by temperature, and to a lesser extent by precipitation and relative humidity (Emana et al., 2002; Mutamiswa et al., 2017), which agrees with the observations of local farmers in Santa Lucía. It has also been reported that "gusano cogollero" (*S. frugiperda*) migrates in response to increases in temperature (Westbrook et al., 2016), which is aligned with the observations of local men and women. Regarding beneficial insects, Schweiger et al. (2010) predicted the decrease in the populations of bees with higher temperatures, as it impacts the abundance, distribution, and phenology of bees and their host plants, which is aligned to men's observations in Santa Lucía. Farmer's resilience to climate change should be improved as it has been predicted that climate change may contribute to an increase in the incidence of crop pests (Deutsch et al., 2018) and decrease in pollinators such as bees, local capacities on the identification, biology, and ecological role of beneficial and pest insects, as well as on sustainable or agroecological management practices.

It is recommended that future studies could delve deeper into understanding local classifications and categorizations of entomofauna supported by qualitative ethnographic work, as well as local processes of knowledge transmission, and documenting actual management practices (and relating them to LK). Future studies might also explore the effect of other factors such as age, household composition, and income, on the variation of LK and practices. Finally, to provide additional insights into the LK of entomofauna under processes of socio-cultural change, future research could also be conducted with indigenous populations from the region.

## CONCLUSIONS

Results showed that in Santa Lucía, a small village at the AAF in Peru, *mestizo* farmers (men and women) had a negative perception of entomofauna associated with cassava, maize, and plantain because they considered most insects to be harmful to crops. Only a few of them highlighted the existence of beneficial insects such as pollinators and natural enemies. Consequently, the management practices that farmers use are focused on controlling pests, and not on preserving beneficial insects. This is certainly related to the socio-cultural dynamics of *mestizos* in the forest-agricultural frontier, and that Santa Lucía is a *mestizo* village, inhabited by migrants who arrived in two migration waves (1960 and 2009) to start new productive activities in an environment new to them. Their crop management knowledge has been acquired by trial and error experiments or has been transmitted from other *mestizos* or indigenous peoples, and their surroundings.

Although farmers mentioned preventive and curative sustainable management practices for about one third of insects, half of them did not present any associated management practices and the rest only showed unsustainable practices (such as the use of pesticides). Farmers in Santa Lucía explained that they do not apply pesticides commonly because they cannot afford to buy them and were not aware of their negative effects on the biota and environment. The lack of knowledge about beneficial entomofauna and sustainable management practices for pest control might also result in the use of unsustainable practices that may have detrimental effects on the environment and, ultimately, local food security, health, and biodiversity. Therefore, local capacities should be built to enrich theoretical knowledge on the recognition, biology, and ecological role of entomofauna (e.g., pollination, natural predation), and associated management practices (e.g., agroecological practices to manage pests and protect pollinators). The implementation of agroecological practices, alongside the rescue and promotion of existing preventive practices to manage entomofauna such as insecticidal plants (e.g., *T. erecta*), will strengthen the adaptive capacity of the agroecosystem and decrease farmers' vulnerably to climate change.

## DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

## ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The patients/participants provided their written informed consent to participate in this study.

## AUTHOR CONTRIBUTIONS

LB-T and GC-G conceived the manuscript idea. LB-T developed the theory, collected the data, and wrote the manuscript with support from GC-G. RS collected the data and provided critical feedback to the manuscript. GC-G supervised the study, the findings of this work, and verified the analytical methods. MQ helped supervise the project, discussed the results, and contributed to the final manuscript. All authors contributed to the article and approved the submitted version.

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# The Promise of a Multi-Disciplinary, Mixed-Methods Approach to Inform Insect Pest Management: Evidence From Wyoming Alfalfa

*Randa Jabbour*[1*†] *and Shiri Noy*[2†]

[1] Department of Plant Sciences, University of Wyoming, Laramie, WY, United States, [2] Department of Anthropology and Sociology, Denison University, Granville, OH, United States

Pest management strategies involve a complex set of considerations, circumstances, and decision-making. Existing research suggests that farmers are reflexive and reflective in their management choices yet continue to employ curative rather than preventative strategies, and opt for chemical over biological solutions. In this piece, we detail work from a two-year, multidisciplinary, mixed-methods study of insect pest management strategies in alfalfa in Wyoming, integrating data from four focus groups, a statewide survey, and biological sampling of production fields. We outline how these different sources of data together contribute to a more complete understanding of the challenges and strategies employed by farmers, and specifically on biological pest control. We applied this approach across alfalfa hay and seed crop systems. Relatively few farmers acknowledged biological control in focus groups or surveys, yet biological exploration yielded abundant parasitism of common pest alfalfa weevil. On the other hand, parasitism of seed alfalfa pest *Lygus* was far less common and patchy across fields. It is only in integrating quantitative and qualitative, biological and social data that we are able to generate a more complete portrait of the challenges and opportunities of working with farmers to embrace a preventative paradigm. In doing so, we offer insights on possible barriers to the adoption of preventative insect management strategies and provide a case study of integrating social science and biophysical techniques to better understand opportunities to expand biological pest control in cropping systems.

**Keywords: alfalfa weevil, parasitoid, biological control, *Lygus*, farmer decision-making, mixed-methods, *Hypera postica*, *Medicago sativa***

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*David Gonthier,*
*University Press of Kentucky,*
*United States*

**Reviewed by:**
*Deirdre Anne Prischmann-Voldseth,*
*North Dakota State University,*
*United States*
*Neelendra K. Joshi,*
*University of Arkansas, United States*

***Correspondence:**
*Randa Jabbour*
*rjabbour@uwyo.edu*

*† These authors have contributed equally to this work*

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## INTRODUCTION

Farmer decision-making has long been an area of interest to scientists to increase efficiency and provide useful scientific insight to assist growers. Recent research has paid growing attention to the need to integrate social and biological understandings of insect pests (Lamp et al., 1991; Summers, 1998). Such work has the benefit of being attentive to grower needs and practices, so that interventions may be designed in a way that incorporates realistic considerations and so that information is responsive to producer needs and interests. Further, insect pest management can be more sustainable by moving away from an overreliance on chemical treatments toward more preventative forms of insect pest management. Such preventative practices can include, but are not limited to, conservation or augmentative biological control (Landis et al., 2000) and systems-level diversification of an agroecosystem, for instance via increased crop or habitat diversity across spatial and temporal scales or integration of crop and livestock systems (Kremen and Miles, 2012). These preventative approaches are in contrast with preventative prophylactic pesticide applications common in many conventional cropping systems (i.e., calendar sprays, seed treatments). Promotion of such practices to encourage reduced pesticide use must empower farmers in farmer-centered communication and outreach strategies (i.e., Matteson, 2000). However, pest management research rarely integrates both quantitative and qualitative social data analysis techniques, commonly termed a "mixed-methods approach" (Cresswell and Plano Clark, 2011) with biophysical measures of actual pest pressures in the field.

Integrated pest management (IPM) is likely the most widely recognized framework for employing multiple pest management strategies to reduce reliance on chemical control (Peterson et al., 2018). Classically, it is defined as a systems-approach to pest management with the aim of reducing pests below defined threshold levels "by using methods that are effective, economically sound, and ecologically compatible" (Pedigo, 1989). However, recent attention by pest management scientists has largely turned to reflect on whether IPM is actually being employed as originally intended with think pieces such as "Whatever Happened to IPM?" (Peterson et al., 2018) and discussion of new IPM paradigms for the "modern age" (Dara, 2019). Pest management is in its essence a human enterprise, and Gott and Coyle (2019) pose that engaged and effective communication is critical to adoption of IPM. For example, farmer awareness of insect natural enemies in one case depended on prior education and management experience (Wyckhuys and O'Neil, 2007).

## BACKGROUND

Alfalfa *Medicago sativa* L. is an important crop in the Western United States and much of the globe. Insect pests are a costly challenge to producing both quality alfalfa hay and seed crops, with alfalfa weevil *Hypera postica* (Gyllenhal) (*Coleoptera*: *Curculionidae*) and *Lygus spp.* (*Hemiptera*: *Miridae*), respectively, identified as particularly problematic pests in these distinct management systems. Alfalfa seed production differs from hay production in several biologically relevant ways. Seed production fields have lower alfalfa plant density per area than hay production fields. Producers harvest the seeds thus allowing alfalfa to mature beyond the vegetative plant stage typical in forage fields. Seed producers have the additional challenge of balancing chemical management with pollinator conservation, both of which are crucial for production of a high-yielding seed crop. *Lygus* plant bugs include a few closely related species whose nymphs and adults primarily feed on terminals, buds, flowers, and developing seeds, hence their particularly pernicious role in seed production (Blodgett, 2006). Growers of both hay and seed crops primarily rely on chemical control of alfalfa insect pests, although the type and timing of management disturbances differ greatly across these systems.

Both adult and larval alfalfa weevil feed on alfalfa, but the majority of defoliation is accomplished by late-instar larvae in the early season, usually in the first cutting (Pellissier et al., 2017). Hay alfalfa is typically harvested three to four times per growing season, while alfalfa seed is harvested only once. Hay growers apply insecticides to reduce weevil populations if needed, possibly based on existing economic thresholds for larval abundance. Seed growers generally rely heavily on chemical control for pests, applying neonicotinoids or pyrethroids for pest control three to five times per season (**Figure 1**). Right before bloom, seed growers may do a "pre-bee clean up" chemical application before release of alfalfa leafcutter bees *Megachile rotundata* F. (Hymenoptera: Megachilidae). In August, many seed growers will then use an herbicide as a desiccant to defoliate their field and get ready for seed harvest. Insecticides are not only costly to growers, but repeated applications could lead to resistance in target pests, leading some Extension educators to recommend chemical rotation (e.g., Long and Getts, 2018). These products are also highly toxic to non-target organisms like pollinators and natural enemies (Evans et al., 1993). Products approved for certified organic production, such as spinosads, may be less toxic to bees but are both more expensive than conventional products and less effective (Godfrey et al., 2005). Certified organic production of alfalfa in Wyoming is rare, which further limits adoption of biopesticide substitutions.

Though several parasitoid releases have occurred over the past century for biological control of the alfalfa weevil in particular, persistence, and activity of those parasitoids has been patchy and limited in this region (Brewer et al., 1997; Rand, 2013). Suggestions for promoting natural enemies within alfalfa fields are limited to strip harvesting, which is agronomically inefficient, and reduced pesticide use, which carries the risk of direct losses in the first cutting and carryover losses in the subsequent cuttings due to reduced plant vigor (Latheef et al., 1988). Recent evidence showed that provisioning of floral resources near alfalfa plots enhanced parasitoid abundance and richness, although biocontrol of alfalfa weevil specifically was unchanged (Pellissier and Jabbour, 2018).

Our focus group analysis suggests that growers are interested in preventative strategies, and that they are concerned about chemical treatment in a variety of ways: cost, questions of interests and bias on the part of chemical companies, as well as the effects on beneficial insects, including pollinators and natural enemies (Noy and Jabbour, 2020). However, chemical and other curative approaches provide much needed flexibility, which is prized among farmers handling complex and sometimes competing considerations of when to perform management events such as planting and harvest. We argue that it is important to consider different sources of data (quantitative and qualitative, sociological and biophysical) and incorporate grower perspectives with intention if the goal is to pursue agricultural redesign that is preventative, "nature-friendly," and does not threaten biodiversity. Such work must include producer perspectives, insight from agricultural professionals and advisors,

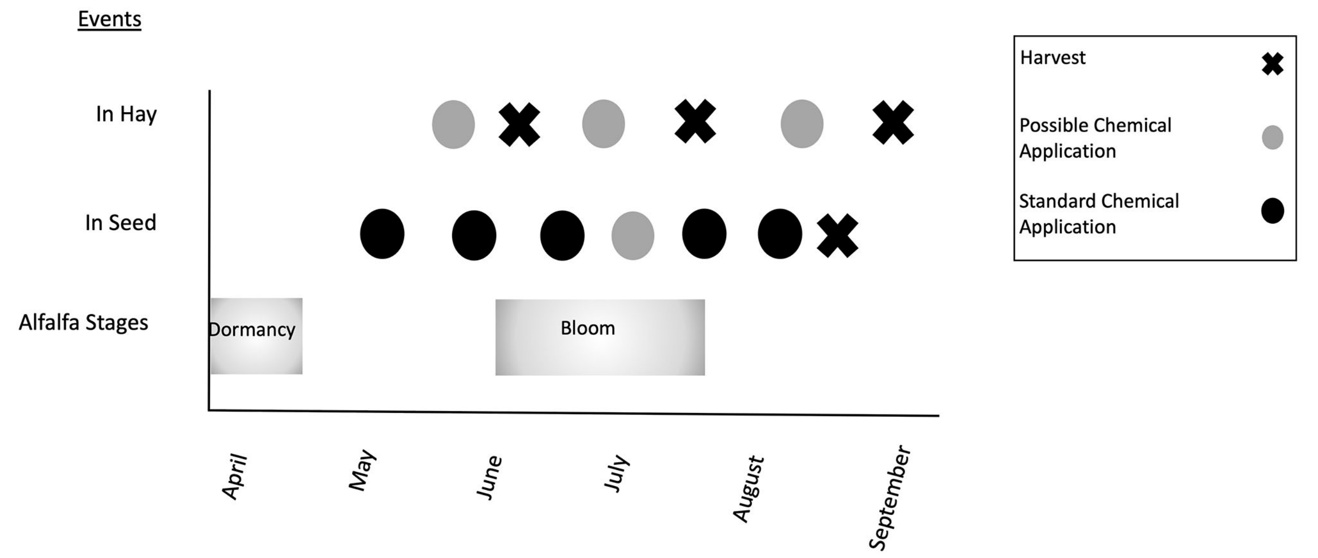

**FIGURE 1 |** Comparison of typical management practices in alfalfa hay and seed crops.

and field-based biophysical data to present a full picture of the current pest challenges and the effects, both positive and negative, of shifts to preventative, agroecological methods. These methods have the potential to be more efficient, cost-effective, and environmentally sound but must triangulate biological information with grower perspectives in order to craft an approach that will be useful and embraced by the primary stakeholders: growers.

## MATERIALS AND METHODS

Our analysis draws from a multidisciplinary, mixed-methods study of insect pest management in Wyoming alfalfa production with data collected over approximately 2 years. "Mixed-methods research" is a methodological approach in the social sciences which refers to the integration of quantitative and qualitative data within a research project and draws on interpretation from both data sources (Cresswell and Plano Clark, 2011). Our study involved the collection of both biological and social data, including qualitative and quantitative data. The project was motivated by our interest in gaining an understanding of the prevalence of and motivation across management strategies of insect pests among Wyoming alfalfa farmers. Therefore, we sought to collect data on farmer perspectives as well as insect management strategies and practices. We conducted four focus groups, surveyed over 600 alfalfa farmers, and collected biological data about insect pests and biocontrol from both commercial production fields and research farms. In other publications (Pellissier, 2016; Jabbour and Noy, 2017; Noy and Jabbour, 2017, 2020; Pellissier and Jabbour, 2018) we have conducted detailed analysis drawing from single data sources only. Here, we integrate all three data sources and describe how these data build and inform one another to enhance our understanding of insect pest management of Wyoming alfalfa.

We draw on three sources of data: first, focus groups in four counties to understand farmer challenges and decision-making; second, surveys of Wyoming alfalfa farmers to gather information about growers' perceptions of pests and farm characteristics; and third, samples from production fields capturing the prevalence of pests and naturally-occurring biological pest control. For our social data, elaborated below, we chose to conduct focus groups because this method is especially good at illuminating participant perspectives, giving priority to their language and concepts and their framework for understanding the world (Kitzinger, 1994). Focus groups are generative and collaborative, and therefore they are less centered on individuals but instead on information-sharing where participants provide an audience for one another. Researchers are able to observe discussion and shared meanings. Survey data on the other hand allow more generalizable insight. However, this breadth comes at the expense of depth. Questionnaires then allow the collation of individual responses and discernment of patterns. Ideally, samples are representative of the populations from which they are drawn which allows a baseline understanding of trends. The overall project—including the survey and focus groups—was reviewed and approved by the University of Wyoming Institutional Review Board on November 14, 2013. Finally, we collected samples from production fields to provide biological evidence of the prevalence of biological pest control. We summarize the overall project design, a concurrent mixed-methods design including social and biological data, in **Figure 2**.

### Focus Group Data

Our focus groups served two purposes: first, to generate important interactional information on insect pests and management strategies in their own right, and second, to validate the survey instrument which would be administered

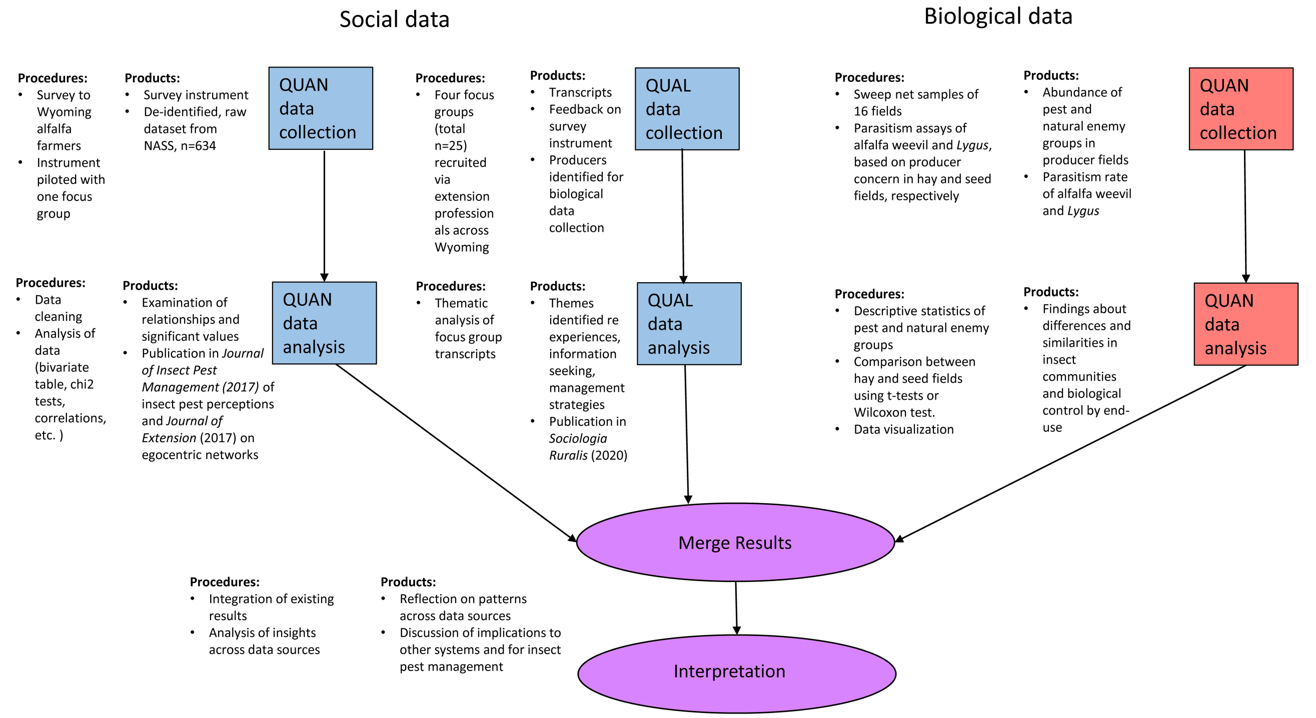

**FIGURE 2 |** Overview of mixed-methods research design and outcomes for overall project on alfalfa insect pest management in Wyoming.

to the population of alfalfa growers in the state. As such, we strategically selected four Wyoming counties with variation in markets and production circumstances, including diversity in end-use market (e.g., hay vs. seed).

We conducted focus groups in Spring 2014 and Fall 2015 in four counties in Wyoming (**Table 1**). Informed consent was obtained from all individual participants included in the study and we have assigned pseudonyms to both the counties and the individual growers to protect grower privacy. We chose to conduct these focus groups in counties across the state to include diversity in field size, markets, and agronomic conditions. We relied on a county-based Extension educator to help recruit producers, seeking diversity along farm characteristics and experience among participants. A short survey administered before the focus group gathered information about the growers and their operations (**Table 1**). In the focus groups, we asked questions about grower experiences, insects pests, information seeking, and management strategies. Each focus group was audiorecorded, transcribed, and the data analyzed thematically.

## Survey Data

We designed and administered a survey (**Supplementary Material**) via the United States Department of Agriculture-National Agricultural Statistics Service (USDA-NASS) which had a master list of alfalfa producers in Wyoming. We designed the survey instrument to examine the priorities and perceptions of Wyoming alfalfa producers with a focus on insect pests, particularly to establish a baseline for this group as no systematic information had been collected prior to our study despite the importance of this crop in the state. The survey included questions about respondents' socio-demographic characteristics; farm size, production, and output; alfalfa insect pests and pest management; and questions about respondents' social networks. We sought feedback from four Extension professionals when crafting our survey instrument. We then piloted the survey with a focus group consisting of six alfalfa producers (East County in **Table 1**).

We received data from 634 surveys completed by farmers. USDA-NASS mailed the survey to a total of 3,141 farmers (of 3,246 in their confidential total roster because the U.S. Postal Service was unable to locate 105) in Wyoming in March 2015. Eighty-three surveys were returned uncompleted because farmers reported they did not grow alfalfa, were not farming, refused to respond, and/or asked to be removed from the survey list. Via USDA-NASS, we sent one postcard reminder, 2 weeks after the initial survey was mailed to attempt to maximize the response rate (Dillman et al., 2014). Of eligible respondents, we had a 20.7% completion rate. Raw data from returned surveys were entered by USDA-NASS staff and de-identified data were provided to us for analysis.

## Biological Data

During summer 2015, biological data from alfalfa production fields was collected with a focus on estimation of rates of biological pest control. In our region, no biological assessment of biocontrol rates of alfalfa weevil had been completed in alfalfa since 1996 (Brewer et al., 1997) and none had ever occurred, that we know of, to document prevalence of native *Lygus* parasitoids.

**TABLE 1 |** Descriptive statistics for focus group respondents.

| County | East | South | North | Middle |
|---|---|---|---|---|
| Date of focus group | January 2014 | February 2014 | February 2015 | March 2015 |
| Number of participants | 6 | 9 | 7 | 3 |
| Average acres for total dryland crop production | 23.33 | 50 | 0 | 0 |
| Average acres for dryland alfalfa | 6.67 | 12.5 | 0 | 0 |
| Average acres total irrigated crop production | 883.33 | 396.88 | 1022.11 | 234.33 |
| Average acres irrigated alfalfa | 537.5 | 318.75 | 274.22 | 126.67 |
| Average acres total rangeland | 12.5 | 4115.38 | 415.67 | 143.33 |
| Alfalfa produced for | Primarily hay | Primarily hay, some feed | Half seed, half on feed, and hay | Hay and on farm feed |

Collection of these in-field biological data in concert with the focus groups and surveys allowed us as researchers to evaluate which preventative measures were both most feasible and most likely to have impact upon investment of future research by scientists and future time, effort, and finances of producers.

We collected biological data from a three-county area in Wyoming where both alfalfa hay and seed production occur. Fields were identified with the help of Extension educators and crop advisors in these counties, including a subset of fields of the participants in one of our previous focus groups who indicated willingness. Fields were at least 4 km apart from one another. We collected insects from eight seed fields and eight hay fields twice in summer 2015: in early June (June 1–5, 2015) and in mid-July (July 14–17, 2015). These sampling periods were selected based on growing degree day models and discussion with area crop scouts. Early June was the best time to measure parasitism of alfalfa weevil larvae and mid-July was the best time to measure parasitism of *Lygus* nymphs.

Insects were sampled using sweep nets (Al Ayedh et al., 1996; Rand, 2013). In each field, we collected six 50-sweep samples, at least 20 m from the field edge, with each sample 10 m apart. Samples were sealed in gallon size plastic bags, with a paper towel added to collect extra moisture, and stored in a cooler with ice until return to the lab. Herbivore insects in the following categories were identified and counted: alfalfa weevil adults and larvae, *Lygus* nymphs and adults, and aphids (*Hemiptera*: *Aphididae*). Natural enemies in the following categories were identified and counted: lady beetle larvae and adults (*Coleoptera*: *Coccinellidae*), damsel bugs (*Hemiptera*: *Nabidae*), green lacewings (*Neuroptera*: *Chrysopidae*), and spiders (*Araneae*). In the lab, a subset of alfalfa weevils (in June sampling) or *Lygus* (in July sampling) were counted and removed across all six subsamples per field to complete parasitism assays as described below.

Parasitism rates of alfalfa weevil larvae were estimated through a rearing assay. We collected 100 third and fourth-instar alfalfa weevil larvae from each field, or as many as we could if abundances were low, to measure parasitism rates by *Bathyplectes* parasitoid wasps (Al Ayedh et al., 1996). These parasitoids have distinctive cocoons that can be easily identified, with a single cocoon per larva. Weevil larvae were placed in paper bags with two stems of freshly harvested alfalfa, replaced with fresh alfalfa every 2 days until weevils reached the adult stage. At this time, samples were examined and the number of parasitoid cocoons and adult weevils were tallied to calculate the parasitism rate [percent parasitism = parasitoid cocoons/(parasitoid cocoons + adult weevils)]. Larvae that died before reaching adulthood or parasitoid cocoon stage were not included in the estimate.

Parasitism rates of *Lygus* nymphs were estimated based on dissection. We collected 100 *Lygus* nymphs from each field, or as many as we could if abundances were low, placed them immediately in 80% ethanol, and dissected at a later date to quantify parasitism rate by native *Peristenus* parasitoids (Day et al., 1999).

Arthropod community data was log-transformed and examined using multivariate analysis with "vegan" package in R (Oksanen et al., 2019). Differences in arthropod community composition were visualized through principal components analysis. The effect of sampling round (1 = June, 2 = July), end use (hay, seed), and the interaction between sample round and end use on arthropod communities was tested using a PERMANOVA. Parasitism rates of alfalfa weevil were compared between hay and seed fields using a *t*-test with the base package of R (R Core Team, 2020). Due to non-normality of *Lygus* parasitism data, we used a non-parametric Wilcoxon test.

## RESULTS

### Focus Group Data

The focus groups yielded rich data on grower perspectives, challenges, and solutions. Elsewhere, we have discussed findings from these focus groups as they pertain to farmer views on expertise and sources of information (Noy and Jabbour, 2020). We found that growers reported using chemical treatment for insect pests to maximize crop yields and importantly, flexibility, rather than to save on time, or labor. However, they used spraying and other pest management strategies in coordination, seeking advice from trusted experienced contacts, including Extension personnel. Our analysis revealed that neighbors function both as sources of information and as variables to consider. For example, spray timing was influenced by what neighbors were doing, sometimes in order to utilize the same plane (and save costs) for aerial spraying (Lawrence, Middle County) and also due to insect mobility, as one respondent explained: if your neighbor sprays but you do not, the insects often migrate to your field (Ned, South County).

Here, we focus on growers' discussion of insect pest management in the focus groups, and in particular, mentions related to biological control. The issue of biological pest control came up several times during the focus groups, in North and East counties. North County included farmers who grew alfalfa for seed in addition to hay and on-farm feed, the only focus group for which this was the case (**Table 1**).

Both Grant and Richard agreed that *Lygus* species are the biggest "killer for seed" (Richard, North County) and was particularly problematic because it "builds up resistance so quick" (Grant, North County). In this discussion, they noted that *Lygus* builds up resistance to some pesticides, while other pesticides are not preferred because they kill pollinators. Further, Grant noted that damsel bugs in the family Nabidae are also important to protect because they are predators of aphids, *Lygus* and other soft-body insects. Richard chimed in with mention of "ladybugs." Grant further emphasized that "with the correct management, we can limit the use of insecticides and let the beneficials do the controlling of pests, but we can't always count on that." He goes on to discuss pest populations "exploding" as a result of both insecticide resistance and non-target effects on natural enemies.

Therefore, producers report being constrained in what they can spray. Cole, in East County, noted the importance of being sensitive to neighbors, reporting that four neighbors had honey bees, and he needed to give them warning before spraying pesticide to allow for them to take precautions. Another solution was to spray at night when the bees were less active or spray earlier in the season to avoid "hurting the beneficials" (Cole, East County).

In East County, growers noted that contemporary pesticides are less effective than previous ones, as evidenced in the following exchange:

> Tim: When we had herbicides that were highly persistent, and insecticides, you could spray the border of your field and that, that insecticide would still be killing grasshoppers 30 days later, we don't have access to any of those insecticides that are that persistent anymore but it hasn't been that long ago, probably 15 years ago, and I forget what we were spraying for the insecticide at the time but you could spray them, spray the borders of those fields and the outside, outside the field, and you could hold those grasshoppers for the entire season with one spraying but—
> Matt: Doesn't the University, has the extension office in the University have a program, you know if you get to your grasshoppers early enough and they're still in the nymph stage you can spray'em, what is that? That they'll do a cost share on—
> Art: Biological control so they don't molt
> Matt: Right, do you, you have to get them
> Interviewer: Is it a fungus or something different?
> Art: Stops their instar and they can't molt
> Matt: Their exoskeleton is just they get stuck in there and then they die
> Art: You can't do it over the second instar
> Matt: Right. Yeah, you have to be, I mean [cross talk] it has to be a certain stage [cross talk] when you see grasshopper a small one you have to be very diligent at your timing or, or that, that insecticide won't work.
> Gabe: But they'll only cost share on grassland, they won't do it on farm ground
> Matt: I've cost shared, I've done it on my borders
> Gabe: Really? Cause I talked to'em and—
> Matt: Cause that's on your borders, on the outside that's where a lot of times the grasshoppers are anyways, and they'll cost share on your borders.

The above exchange provides several important insights: first, cost is clearly a concern given discussion of cost-sharing. The cost-share program described is not referring to a biological control product *per se*, but rather a recommended pesticide at the time of the focus group that is an insect-growth regulator with a more specific target than some of the generic pesticides previously used. Thus, they may be associating this "softer chemistry" with biological control due to the reduced non-target effects. Second, growers are aware of the decreased toxicity of the newer options, even if they may miss the "good old days" of using more potent pesticides.

## Survey Data

While the focus group data allowed us to generate interactive data and refine our survey instrument, we aimed to get a broader view of the challenges experienced by alfalfa farmers across the state, motivating a mixed-methods approach. Surveys necessarily sacrifice depth in the interest of breadth, but in combination with focus groups yields a comprehensive approach. Elsewhere we have discussed some sections of the survey (Jabbour and Noy, 2017; Noy and Jabbour, 2017). Here, we present additional information about why alfalfa weevil and *Lygus* were labeled as most problematic (**Table 2**), elaborating on our published work (Jabbour and Noy, 2017). Understanding the perceived impact of pests is important for those seeking to promote biological control methods that are most appropriate. Overall, Wyoming farmers considered alfalfa weevil (65% of respondents), grasshoppers (18% of respondents), and aphids (7% of respondents) as their most problematic insect pests. Although alfalfa seed production is an important industry in Wyoming, there are far fewer producers who grow alfalfa seed than alfalfa hay. Only 2% of survey respondents (12 individuals) produced seed.

In previous analyses of these data we found that while 5.5% of respondents reported trying biological control strategies for alfalfa weevil, only 7.7% of those that had tried it found it to be the most effective management strategy (Jabbour and Noy, 2017). For grasshoppers, the second most problematic pest, only 2.3% of respondents had tried biological control while for aphids this number was 10.9%. Alfalfa weevil was identified as the most problematic pest by 65% of respondents and was one of the pests we focused on in biological data collection. Although the survey responses from seed producers were minimal, any seed producers that identified a most problematic pest selected *Lygus*. This observation, paired with the focus group discussions referenced above, highlight that predominant insect concerns in alfalfa seed production center on this insect. Here, we provide additional information from the survey on why farmers considered these

**TABLE 2 |** Commonly mentioned themes by Wyoming alfalfa producers to explain problematic nature of insect pests in hay (alfalfa weevil) and seed (*Lygus*) production.

| | Alfalfa weevil | *Lygus* |
|---|---|---|
| Agronomic & economic | • Decreased yield and quality<br>• Timing (always there)<br>• Chemical control costly | • Extensive damage to blooms and seed<br>• Limited effective insecticide chemistries available |
| Biological & weather | • Pest biology<br>• Link with weather<br>• Landscape perspective | • Insecticide control of this pest can also harm pollinators<br>• Multiple generations |

**TABLE 3 |** Growers who have tried biological control by farm acreage.

| Alfalfa acreage | Number of respondents | Percent of respondents | Number of respondents who have tried biological control | Percentage of total respondents who have tried biological control |
|---|---|---|---|---|
| 1–50 | 321 | 50.6 | 12 | 3.7 |
| 51–100 | 103 | 16.3 | 11 | 10.7 |
| 101–200 | 103 | 16.3 | 11 | 10.7 |
| 201–500 | 72 | 11.4 | 9 | 12.5 |
| 501–100 | 30 | 4.7 | 3 | 10 |
| 1,000+ | 5 | 0.8 | 1 | 20 |
| Total | 634 | 100 | 47 | 7.4 |

two pests particularly challenging. These details may provide information about possible openings for preventative and biological control research and interventions, underscoring the importance of integrating biological and social data.

## Challenges of Alfalfa Weevil

Respondents listed a variety of agronomic challenges when explaining why they thought alfalfa weevil was the most problematic insect. These challenges included decreased alfalfa yield and quality and challenges related to timing, either within the season or across years. Chemical control was repeatedly indicated as necessary although costly. The biology of alfalfa weevil was referenced by those who either thought that it was the only insect that caused problems in alfalfa or a particularly abundant pest. Respondents described alfalfa weevil as the "only real damaging pest" or the "only insect we encounter." Two respondents stated that alfalfa weevil was most problematic because of the behavior of their neighbors, with one stating "I am surrounded by large producers that may choose not to chemically control these insects." Another reported, "my neighbors don't spray. Last year, my neighbor's fields were full of weevil which moved to my field. We cut the hay and found thousands." They are inferring that insect movement between fields of different landowners is important.

## Challenges of Lygus

Although far fewer survey respondents identified *Lygus* as their most problematic pest, they consistently pointed to similar reasons for identifying it as such. The main agronomic challenge was the considerable damage to bloom and seed stages of alfalfa. Chemical control was again repeatedly discussed centered on efficacy including mention of "lost chemistries" to regulation and suspicions of insecticide resistance development in *Lygus*. The challenge of using chemical control while protecting pollinators was cited including mention of the limited number of effective "bee-safe" insecticides available and the need to time applications around leafcutter bee activity (i.e., night applications).

## Management Strategies and Biological Control of Alfalfa Insect Pests

We found that for alfalfa weevil, grasshoppers, and aphids, insecticide and early harvest were the most common practices that producers reported having tried (Jabbour and Noy, 2017). For alfalfa weevil, respondents reported using insecticide (55.2% of responses), early harvest (35.3%), and biological control most often (4.3%). These response rates shift when respondents indicated which management practices are most effective against alfalfa weevil, with most respondents indicating insecticides are most effective (79.9%), with biological control lagging in popularity (7.7%), followed by early harvest (4.8%). For both grasshoppers and aphids, insecticide was identified as the most effective tool and the one used most often.

Our results indicate that 7.4% of respondents (47 of 634) had ever tried biological control (for any insect pest). These results suggest that many growers have not tried biological control strategies and rely heavily on insecticides and chemical control. Our focus group data suggests that they value chemical control because of the flexibility it allows, and its effectiveness. There seems to be an interest in biological control, though limited exposure to it, and our data suggests that focusing on flexibility and effectiveness may be useful strategies to highlight when appealing to growers.

Here, we focus on biological control in particular to better understand which growers are best acquainted with this practice. Although inferences should be undertaken carefully because of small sample size, we generally find that as alfalfa acreage increases, the percent of respondents are more likely to have tried biological control (**Table 3**). However, because around half of our respondents have smaller farms this may be a particularly important group to target with information about biological control. Our focus group results suggest that perhaps this group is less likely to focus on biological control because of dependence on neighbors (e.g., sharing aerial insecticide spraying) or otherwise being constrained by neighbors' behavior. Therefore, such efforts should proceed cooperatively and communally.

Of the 47 respondents who indicated trying biological control, 38 identified a pest that was most problematic. 60.5% ($n = 23$) of those 38 indicated that alfalfa weevil was most problematic, 10.5% ($n = 4$) indicated aphids, while only 5.3% ($n = 2$) indicated grasshoppers. Again, these small numbers should be viewed with caution in terms of generalizability but suggest that there is room

**TABLE 4** | Alfalfa end use of famers who have tried biological control, $n = 47$.

| End use | Sample size | Percent (of 47) |
|---|---|---|
| For on-farm hay | 38 | 80.85 |
| For off-farm hay | 21 | 44.68 |
| For off-farm seed | 3 | 6.38 |
| For on-farm hay and off-farm hay | 15 | 31.91 |
| For on-farm hay and off-farm seed | 1 | 2.13 |
| For off-farm hay and off-farm seed | 2 | 4.26 |

*Our survey gave respondents the first three options: on-farm feed, hay, and seed. Respondents could select any combination of the three. The latter three categories were calculated based on those responses.*

to consider biological control, especially among alfalfa farmers struggling with aphids, and grasshoppers as they are a small proportion of those who have tried biological control.

We also examined reports of trying biological control according to end-use of the crop, including all combinations of the responses for on-farm hay, and seed and hay marketed off-farm (**Table 4**). On-farm hay was included as a distinct survey option, because we hypothesized that those who market their hay to others may have different priorities than those who grow hay to feed their own on-farm animals. Those that had tried biological control were mostly growing alfalfa for on-farm hay while under half were growing it for off-farm hay markets and very few were growing it for seed. This again suggests that future research should examine this disparity and in particular not only why so few alfalfa farmers have tried biological control but whether and how end-use has affected their practice. Only 1% of survey respondents were certified organic.

Altogether, our survey results suggest that there may be demand for pest management strategies beyond traditional pesticide use. However, there may be a variety of reasons that farmers have not or will not try biological control. Chemical solutions are popular for a variety of reasons: flexibility of timing, effectiveness, etc. but there are also concerns with resistance, cost, needing to factor in neighbors' behavior, etc. Further, our data suggest that only a small minority of Wyoming alfalfa farmers have tried biological insect pest management strategies. This, again, suggests the time is ripe for introducing such practices. However, in order to be successful efforts will need to be sensitive to the existing context, network, and the challenges posed by different insect pests and investigate the barriers across end-use.

### Egocentric Network Data

Another component of the survey (**Supplementary Material**) elicited egocentric network data: we asked growers to identify "the five people you have most often discussed farming with within the last 12 months" and then asked whether they received and/or gave advice about alfalfa farming and/or farming in general, information about these "alters" (people named) in terms of whether they were friends and how they knew this person (e.g., neighbor, extension professional etc.). As we discussed elsewhere (Noy and Jabbour, 2017), growers on average listed 1.76 alters (people they turned to from advice). We further found that advice networks were characterized by friendship and that the most common category of alters were neighbors. This suggests that advice networks are localized and not only professional, but often personal (Noy and Jabbour, 2017). We note that this suggests an opportunity for experts including Extension professionals and Weed and Pest personnel to provide advice and information, but that they will likely need to build personal relationships before becoming trusted advisors. This was confirmed by our focus group findings (Noy and Jabbour, 2020). This may be particularly important for disseminating information that is viewed as trustworthy about biological control and targeting central "nodes" in the network, people who are broadly trusted and densely connected to try biological control may facilitate its use across networks of growers—which was bolstered by discussions of trust and expertise in the focus groups as well.

## Biological Data

Parallel to the collection of social data, we conducted a series of biological studies in alfalfa. Other published work includes an experiment testing the effect of the conservation biological control approach of habitat management, providing different types of floral resources adjacent to alfalfa (Pellissier and Jabbour, 2018). We also explored landscape and local effects of non-crop habitat on weevil densities in production fields in southeastern Wyoming, where only hay alfalfa is grown, not seed (Pellissier, 2016). Here, we share biological findings from a different growing region in Wyoming that includes both alfalfa hay and seed production across the landscape.

Arthropod community composition differed significantly between sample rounds (1 = June, 2 = July), end-use of hay or seed, and the interaction between sample round and end use ($p < 0.001$ for all predictors). The first two principal components, visualized in **Figure 3**, explained 50.8% variance in arthropod community composition. The highest loadings on the first principal component (>0.4) were lady beetle adults, lady beetle larvae, and green lacewings. Along this component, communities in seed fields in July had the highest abundances of these natural enemies, as well as *Lygus* adults, distinctive from seed fields in June. Communities in hay fields, both in June and July, were clustered midway along the first principal component. The second principal component had highest loadings (>0.4) from alfalfa weevil adults and larvae, with hay samples clearly clustered according to sample date: more alfalfa weevils in June samples than July.

In our parasitism assays, we found evidence of biological control by parasitoids of both alfalfa weevil and *Lygus* in both hay and seed fields, although the parasitism rate varied widely between individual production fields (**Figures 4**, **5**). We sampled eight seed fields and eight hay fields, but only found alfalfa weevil larvae in four seed fields and seven hay fields. Parasitism of alfalfa weevil ranged from 0 to 47.5% across all fields assayed (percentage calculated from total of 22–92 weevils per field, mean of 67). Generally, parasitism of alfalfa weevil was higher in hay fields than seed fields, although this difference was not statistically significant ($t = 1.34$, $p = 0.22$). The smaller sample size in seed fields may reflect the earlier and more aggressive chemical management norms in seed production

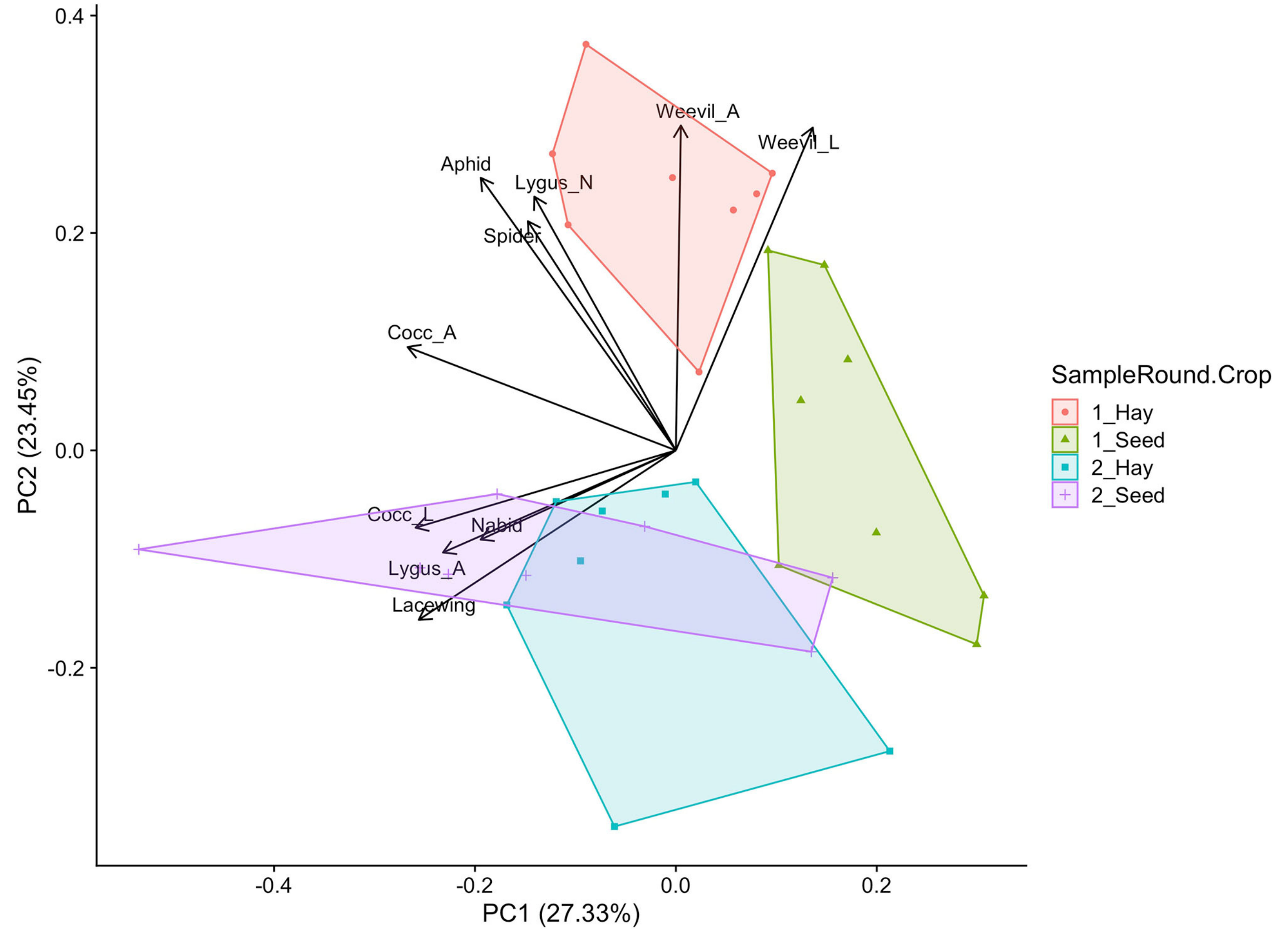

**FIGURE 3 |** Principal component analysis bi-plot of principal component (PC) 1 and 2. Color and shape distinguish samples according to crop type (hay or seed) and sample round (1 = June, 2 = July). Arrows indicate loadings of arthropod groups representing alfalfa weevil adults (Weevil_A) and larvae (Weevil_L), *Lygus* adults (Lygus_A) and nymphs (Lygus_N), lady beetle adults (Cocc_A), and larvae (Cocc_L) and other groups indicated by common name.

(**Figure 1**). As demonstrated by others (Al Ayedh et al., 1996; Rand, 2013), it is not rare for scientists to find evidence of alfalfa weevil parasitoids in the Western United States. This common biological occurrence contrasts with the producer perspective: parasitoid natural enemies were not mentioned in any of our focus groups or mail survey data. Producers were more likely to mention more visually apparent predators such as lady beetles when discussing biological control. This suggests that there may be important opportunities for education on these forms of biological control which may be best uncovered by research that takes a more holistic, system-based, stakeholder-centered approach—combining biological data with social data.

Parasitism of *Lygus* offers a different story (**Figure 5**). Again, we sampled 16 fields but only found *Lygus* nymphs in six hay and seven seed fields. We dissected anywhere from 5 to 100 nymphs per field, mean of 41 nymphs. Rates of parasitism were generally low or non-existent, and did not significantly differ between production types ($W = 14.5$, $p = 0.39$), with the exception of one seed field in which 85% of *Lygus* dissected were parasitized (29 out of 35 dissected). Some but not all of the fields sampled were managed by focus group participants. This field with evidence of high biocontrol activity was actually farmed by one of the growers from North County who spoke at length about biological control agents such as Nabidae in his field.

## DISCUSSION

In this article we have sought to bring together insights from disparate biological and mixed-methods social data, combining qualitative, and quantitative data in the latter. Our project is an ambitious multidisciplinary one, and we take an approach we believe is both increasingly necessary and valuable in insect pest management, and agroecology more broadly. We must seek to understand farmer decision making and complexity from several angles if we are to meet the stated goal of making insect pest management more efficient, accessible, and less damaging to ecosystems. Multidisciplinary collaborations between biophysical scientists

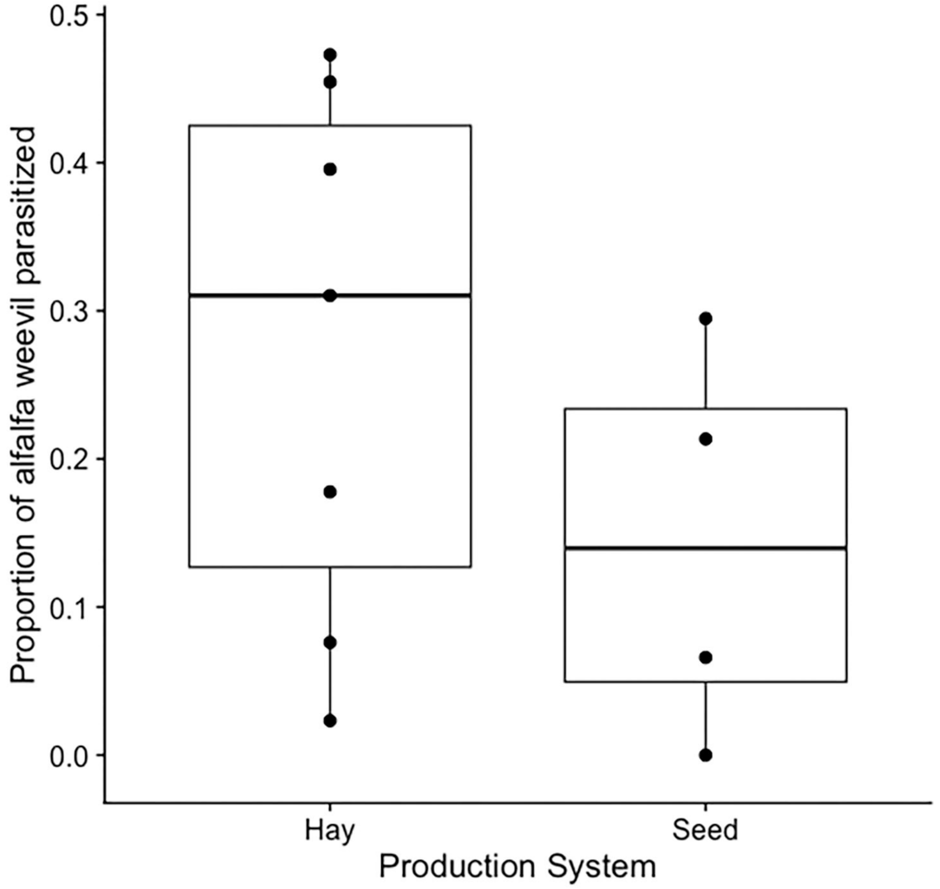

**FIGURE 4 |** Proportion of late-instar alfalfa weevil larvae parasitized by wasp *Bathyplectes curculionis* in June samples.

and social scientists are critical to best tackle research on environmental problems while building on foundations established in each discipline, using appropriate methodology and interpreting results rigorously (Martin, 2020). We propose that mixed-methods research, a social scientific approach which integrates contextual and relational understandings together with biological and entomological expertise is a valuable one. Underlying mixed-methods research—drawing from quantitative and qualitative data—within the social sciences is the contention that these data (in our study: survey and focus groups, respectively) provide a better understanding of the research issue than either approach alone (Cresswell and Plano Clark, 2011). For instance, quantitative approaches alone result in few consistent predictors of farmer adoption of conservation practices, but integration of qualitative approaches allow better understanding of this decision-making process (Ranjan et al., 2019). Using multiple methods that incorporate quantitative and qualitative data has also been touted as a recent and important innovation in evaluation of Extension programming (Edwards et al., 2019).

Our social data along with our biological data provide complementarity in our understanding of the challenges and successes Wyoming alfalfa farmers experience in insect pest management as well as opportunities for information dissemination, education, and strategies that farmers may be interested in but are underutilized for a variety of reasons. Although we have published some aspects of the study in isolation, we have brought new information from the surveys and focus groups about biological control to this article, as well novel biological data, to outline the project in its entirety and place the data and results in conversation with each other. We have demonstrated that efforts to promote biological insect pest management strategies must account for differences in insect communities across different end-use systems (biological data), that farmers do not seemingly assign much importance to parasitoid activity but are aware of predators (focus group and survey data), and that biological control has not been extensively deliberately employed but is naturally occurring in many production fields (survey, focus group, and biological data). We show that farmers rely on social networks, not only professional but also personal (family and friends) to make decisions (survey and focus group data), prizing chemical approaches for the flexibility they provide (focus group data).

Relying on survey data alone would have obscured the ways in which farmers make decisions, and not just who they turn to for advice, but why. The survey provided an important

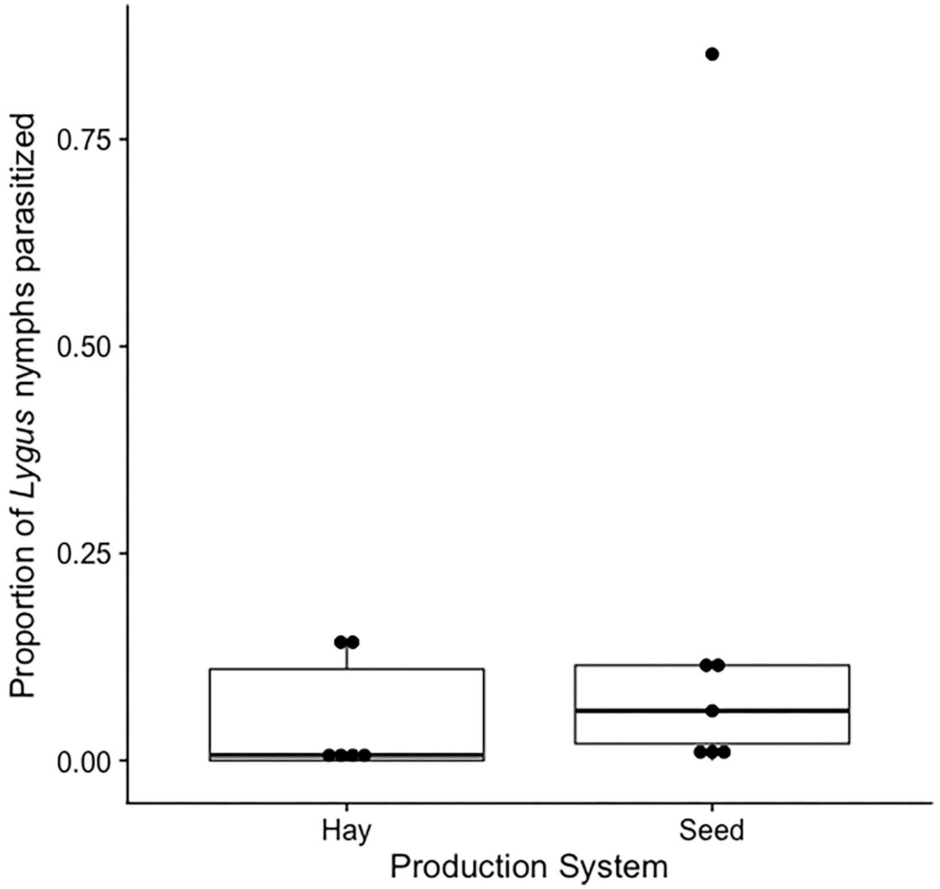

**FIGURE 5 |** Proportion of *Lygus* late-instar nymphs parasitized by wasps in July samples.

baseline for who has tried biological control but does not provide grower perspectives on *why* they rely on chemical treatments so avidly. Similarly, relying only on focus group data does not allow us the broad understanding of which pests farmers found most problematic, and a broader, state-wide understanding of egocentric networks as well as how prevalent chemical and biological control are across the state and across end use. Finally, the biological data allowed us to deepen our understanding of pests and parasitoids across alfalfa end use (hay vs. seed) and triangulate information with grower perspectives.

In particular, we uncover an important opportunity for education about parasitoid conservation. The opportunity for education about cryptic biological control echoes the findings from a multidisciplinary collaboration in Washington. Apple producers had varying perceptions of the function of nocturnally-active earwigs, with some perceiving them as pests, and biological studies demonstrated their role as important aphid predators (Orpet et al., 2019). In our informal discussion with alfalfa producers, they have often asked about lady beetles, inquiring about the success of purchasing many lady beetles and releasing them in their fields. Commercially purchased and released lady beetles often disperse away from release sites quickly [as described in Cranshaw (2014)]. Generalist predators, including *Coccinellidae*, have not been found to impact alfalfa weevil populations, although they do suppress aphids in alfalfa (Rand, 2017) and can be active against *Lygus* as discussed in our focus groups.

Using survey, focus group, and biological data allows us to elaborate and clarify results across data sources. For example, although our quantitative, survey data suggests that only 7.4% (47/634) of survey respondents have tried biological control, our qualitative, focus group data provides context for this low percentage: suggesting that chemical control allows for more flexibility—especially in timing, coordination with neighbors, and is a tried-and-true strategy. Biological data documents the occurrence of biological control of important pests in production fields, but this activity is highly variable across fields and thus allows us to triangulate various farmer accounts of distinct experiences.

Even with our multi-disciplinary, mixed-methods approach, it is important to acknowledge that our starting focus on insect pest management is still simplified, and perhaps even reductionist, compared to the approach farmers must take in their work. Farmers solve problems across disciplinary boundaries. They engage in systems thinking, although producers who already have adopted conservation strategies are more likely to be systems thinkers than those who have not (Church et al., 2020). Similarly, Orpet et al. (2020) describe subjective perceptions of biological control strategies by producers that highlight a challenge in moving toward systems-level changes, regardless of whether producers are conventional or organic. For example, organic producers are more likely to adopt biopesticides rather than planting intercropped sweet alyssum as a conservation biological practice. When we completed our focus groups, prior to any open discussion or questioning, each participant completed a short written survey. We first asked them to discuss challenges to producing alfalfa, and nearly all of them mentioned non-insect pests and challenges with water and drought. The importance of these non-pest management challenges echoes the suggestion that we must not only demonstrate effectiveness of biological control, but also embrace practicality and the ability to address multiple management needs through suggested practices (Orpet et al., 2020).

Multiple management needs may interface with other non-insect pest management and conservation goals. Non-insect pests discussed were mostly vertebrates (we list names as expressed by participants): gophers, deer, birds, mice, racoons, skunks, and in one focus group, grizzly bears. This discussion highlighted the importance of these other animals to producers, also an issue at the interface of pest management and conservation. Birds, for example, have been documented as pests of crops (Kross et al., 2020) but also have been shown to contribute ecosystem services including, specifically, insect pest management in alfalfa (Kross et al., 2016). Alfalfa and other perennial forage crops are often highlighted as ideal cropping systems to advance conservation efforts in otherwise intensive landscapes (i.e., Strum, 2018). Through our framing of the problem and our respective areas of disciplinary expertise, data collected via the survey, focus groups, and entomological sampling addressed the specific focus of insect pest management. The opportunity remains to more broadly link management for biological control with other conservation-oriented goals (Sidhu and Joshi, 2016). In addition, IPM is not innately pollinator-friendly, and recent attention focuses on how to explicitly integrate both pest and pollinator management into a new "IPPM" (Egan et al., 2020).

Our work focused on the perspectives of producers themselves. Although they mention the importance of agricultural professionals such as crop advisors and Extension in both the network portion of the survey and the focus group discussions, we did not separately engage with those professionals to identify their perspectives. Comparison of priorities and perceptions across groups of different stakeholders in the agricultural industry can highlight commonalities and gaps between producers and the professionals who work with them (Jabbour et al., 2014; Wilmer et al., 2019; Boeraeve et al., 2020). Work to bridge these gaps can take the form of sociological research to define perceptions (i.e., Eanes et al., 2019; Boeraeve et al., 2020) or result from participatory, community-engaged research (i.e., Kerr et al., 2018; Wilmer et al., 2019).

This work demonstrates the value of designing research that both honors producer priorities (e.g., a focus on pests of concern) while pursuing scientist interests (e.g., quantification of parasitism). In our study, quantitative data has allowed us to examine trends and broad patterns while our qualitative data has allowed us to understand farmer perspectives and contextualize and interpret these findings. Such a mixed-methods approach, that blends social and biological data, has recently been shown to be fruitful in examples of biological control of apple pests in the United States (Orpet et al., 2019, 2020) and to evaluate social sustainability of biocontrol for dengue in Vietnam (Tran et al., 2015). It has also proven effective in other agroecological studies beyond insect pest management, for example Boeraeve et al. (2020) use survey, field data, and open-ended questions to understand landscape and ecosystem services in transitioning landscapes in Belgium while another recent study by Kerr et al. (2018) utilized focus groups, interviews, observations, surveys, and participatory agroecology experiments to examine perceptions and effects of climate change in Malawi. As we have discussed and demonstrated above, understanding insect pest management, and promoting preventative and biological control mechanisms is enhanced by collecting qualitative and quantitative, as well as social and biological, data. In order to design, develop, and understand biological insect pest management we must endeavor to advance not only the biological information, but also understand farmers' needs and motivations if we are to promote such strategies successfully and in ways that benefit growers.

## DATA AVAILABILITY STATEMENT

The biological data will be made available by the corresponding author upon request.

## ETHICS STATEMENT

The studies involving human participants were reviewed and approved by University of Wyoming Institutional Review Board. The patients/participants provided their written informed consent to participate in this study.

## AUTHOR CONTRIBUTIONS

SN and RJ both conceptualized the manuscript, designed the research, collected and analyzed data, wrote, and edited the manuscript. Both authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2020.548545/full#supplementary-material

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REVIEW
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# Beyond the Headlines: The Influence of Insurance Pest Management on an Unseen, Silent Entomological Majority

*Christian H. Krupke*[1]* *and John F. Tooker*[2]

[1] *Department of Entomology, College of Agriculture, Purdue University, West Lafayette, IN, United States,* [2] *Department of Entomology, College of Agricultural Sciences, The Pennsylvania State University, University Park, PA, United States*

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***Correspondence:**
*Christian H. Krupke*
*ckrupke@purdue.edu*

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For most of the last two decades, insect pest management in key grain and oilseed crops has relied heavily on an insurance-based approach. This approach mandates a suite of management tactics prior to planting and in the absence of pest data. Because there is little flexibility for using these tactics individually, most producers have adopted this full suite of practices despite mounting evidence that some components do not provide consistent benefits. In North America in particular, this preventive approach to insect pest management has led to steep increases in use of neonicotinoid insecticides and subsequent increases in neonicotinoids in soil and water within crop fields and beyond. These increases have been accompanied by a host of non-target effects that have been most clearly studied in pollinators and insect natural enemies. Less attention has been given to the effects of this practice upon the many thousands of aquatic insect species that are often cryptic and offer negligible, or undefined, clear benefits to humans and their commerce. A survey of the literature reveals that the non-target effects of neonicotinoids upon these aquatic species are often as serious as for terrestrial species, and more difficult to address. By focusing upon charismatic insect species that provide clearly defined services, we are likely dramatically under-estimating the effects of neonicotinoids upon the wider environment. Given the mounting evidence base demonstrating that the pest management and crop yield benefits of this approach are negligible, we advocate for a return to largely-abandoned IPM principles as a readily accessible alternative path.

**Keywords: aquatic insects, corn, maize, neonicotinoid, non-target effects, seed treatment**

## INTRODUCTION

Insect pest management using chemical insecticides predates the industrial revolution, with uses of lead arsenate and Paris Green (Pedigo and Rice, 2014) being early examples of invaluable, if unsophisticated and heavy-handed, approaches to keep insect pests at bay. While our arsenal of pest management chemistries has been refined over time, the vast majority of our chemical insecticides are still non-specific, with broad activity on a wide range of target and non-target organisms. Some classes of insecticides have emerged that are more selective (e.g., insect-growth regulators, Bt toxins), but the expectation of "selective insecticides" that was articulated in one of the original descriptions of IPM (Stern et al., 1959) largely remains elusive in modern pest management. Given our current insecticide options, it remains a challenge to strike the delicate balance between safeguarding food production and human health while avoiding deleterious effects upon the wider environment—these are commonly grouped under the inclusive term "non-target effects." The goal of this paper is to consider whether current agricultural use of neonicotinoids, the most popular class of insecticides in the world, is achieving this balance. For this assessment, we focus primarily on U.S. agriculture where most of the principal crops are routinely grown from neonicotinoid-treated seed. We review neonicotinoid use patterns, their potential for effective pest management and subsequent yield benefits. We then discuss the potential for non-target effects. Because neonicotinoids are highly water soluble, aquatic environments have proven to be an environmental sink for these compounds (**Figure 1**); we discuss some of the observed non-target impacts of neonicotinoids upon aquatic communities, and whether these negative effects matter in a broader context. Finally, we outline remedial steps for how the situation can be improved in the short and longer term.

## NEONICOTINOID USE PATTERNS AND POTENTIAL FOR TARGETED PEST MANAGEMENT

Surveying the current insecticide landscape in the United States reveals that a single class of compounds, the neonicotinoids, clearly stands above the others in terms of both the prevalence of use on the landscape and in terms of their potential toxicity to insects (DiBartolomeis et al., 2019; Douglas et al., 2020). Compared to older classes of insecticides, neonicotinoids were originally touted as being more selective because of their systemic nature (i.e., it was thought that only insects feeding on the crop would be exposed) and their apparently lower toxicity to mammals and other vertebrates (Han et al., 2018), although recent data indicate that the latter should be re-evaluated (Berheim et al., 2019; Eng et al., 2019; Wu et al., 2020).

The U.S. is the top user of neonicotinoids, by a wide margin, and the majority of use is as coatings on seeds of annual crops, principally corn, soybeans, cotton, and wheat (Douglas et al., 2015; DiBartolomeis et al., 2019). Although recent estimates of use rates on these crops are not publicly available (the United States Geological Survey discontinued estimates in 2015), we know these compounds are used on virtually every hectare of corn planted in the United States, and that the amount of active ingredient applied to corn seeds doubled between 2011 and 2014 (Tooker et al., 2017). There are also high rates of use on seeds of soybeans, cotton and many other crop species (Douglas et al., 2015, 2020). It is important to note that these trends have been documented even as transgenic hybrids—Bt corn and cotton—have increasingly dominated the market, successfully reducing outbreaks of key pests of these crops (Dively et al., 2018) and even decreasing regional pest populations (Hutchison et al., 2010; Bohnenblust et al., 2014). Notably, however, the adoption rates of both Bt crops and neonicotinoid seed coatings have not corresponded with any new or increased pest threat. In fact, current insecticide use rates far exceed the <50% of corn acres and <10% of soybean acres that were typically treated with an insecticide from the 1950s to the 1990s (Osteen and Fernandez-Cornejo, 2013), when patterns of insecticide use were dictated primarily by the same key pests that are now largely controlled by transgenic hybrids. There are no longitudinal datasets to cite on pest trends over that time, but recent reviews reflect that most of the target pests listed for neonicotinoid seed treatments in registration and marketing materials were never common, are not more common now, and usually do not cause significant yield loss when they are present (Bredeson and Lundgren, 2015; Hesler et al., 2018; Sappington et al., 2018; Labrie et al., 2020; Smith et al., 2020). In other words, rather than "replacing" older insecticide classes with neonicotinoids, the seed-treatment approach fostered by neonicotinoids has created an entirely new and exceptionally convenient way to deliver insecticides without regard for documentation or monitoring of actual pest infestations on the most widely grown commodities in the U.S.

Before understanding how neonicotinoids may affect non-target organisms, it is useful to review how and why they were rapidly and thoroughly adopted in virtually every cropping system where insect pest management is required. Neonicotinoids are extremely water soluble, meaning that once in aqueous solution, they will readily move "upward" within xylem tissues from roots into newer aboveground plant tissues. Initially, this systemic characteristic was hailed as a breakthrough, and a "perfect" approach to pest management (Elbert et al., 2008; Jeschke et al., 2011). In theory, applying a water-soluble insecticide on or near a plant or seed, offers both immediate protection of the most vulnerable stages of the plant's life cycle and lasting insurance, as it is taken up into plant tissues and can protect plants from future pest attacks. This mode of action meant that, despite the very high and broad toxicity of neonicotinoids to most insects, the initial marketing was credibly able to claim that any organisms that are not pests—for example, insects and other arthropods merely resting or crawling along treated plants, living in the soil or water nearby, or flying by planted fields—would be unaffected. As long as they did not feed upon crop plants, any benign or beneficial organisms were free to live on or near neonicotinoid treated plants with no adverse effects. Even though similar approaches had been attempted (albeit on a much more limited scale) with carbamate insecticides and found to have undesirable non-target effects upon birds (Elliott et al., 1996), this seed-based approach was framed as a quantum leap, and a true paradigm shift and improvement from driftable liquid or powdered insecticides that are sprayed over entire fields. The low mammalian toxicity of neonicotinoids and enhanced worker safety were further selling points. Propelled by these perceived advantages, and rapid registration approvals in virtually every crop and ornamental system in North America, neonicotinoids rapidly became as ubiquitous as any insecticide class in history; neonicotinoids are currently deployed as seed coatings, liquid applications and occasionally as granular applications (Elbert et al., 2008) to a range of landscape, garden, and agricultural crops. Although restrictions in other jurisdictions have been imposed, use rates

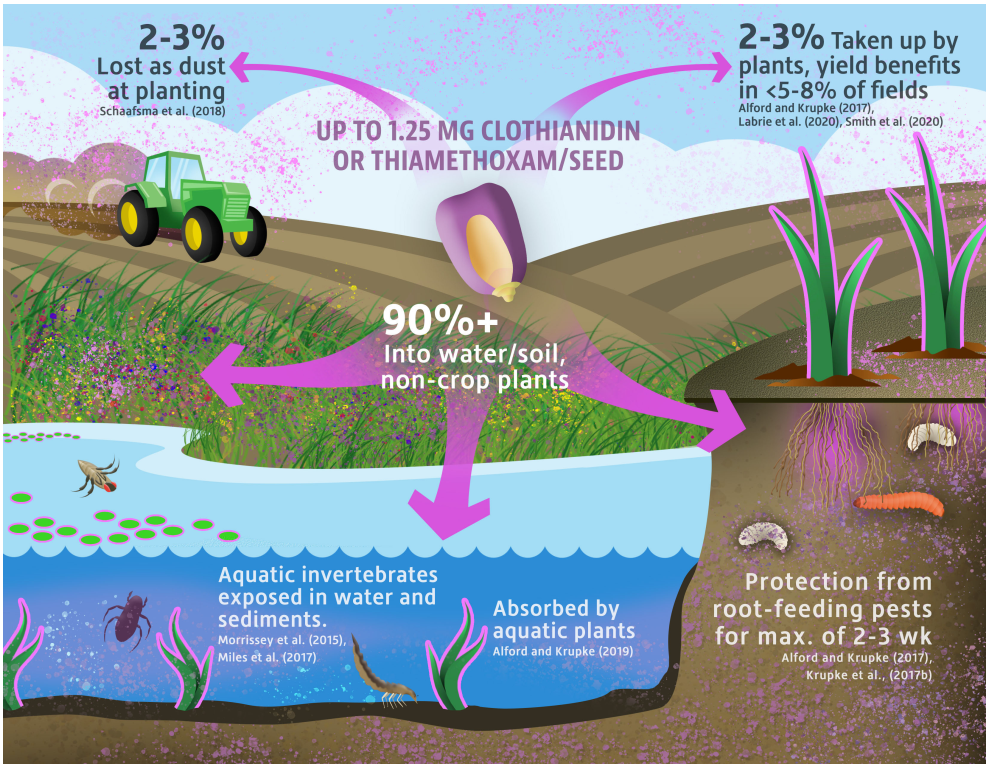

**FIGURE 1 |** A schematic representation of the environmental fate and transport routes of neonicotinoid active ingredients applied to crop seeds.

continue to rise each year in the U.S., providing an ongoing test case of this approach, with an ever-growing dataset to review. We qualitatively review some of these data here, both in terms of how well these compounds are delivering on their early pest management promise, but also in terms of their limiting effects on certain non-pest organisms that appear to have been largely overlooked during the registration and regulation processes.

## REALIZED POTENTIAL OF NEONICOTINOID-TREATED SEEDS FOR PEST MANAGEMENT AND YIELD PROTECTION IN FIELD STUDIES

If a specific pest management tool provides sufficiently high benefits to agriculture or society at large, some level of collateral damage to the surrounding environment may be deemed acceptable. Non-target effects are somewhat inevitable, and perhaps to be expected, in agricultural systems that rely heavily upon large, intensive monocultures and regular deployment of a suite of pesticides. It is striking, then, that a survey of the literature reveals no convincing or consistent demonstrations of economic benefits associated with neonicotinoid use in grain and oilseed crops. Small-plot field studies throughout North America (Seagraves and Lundgren, 2012; Bredeson and Lundgren, 2015; Krupke et al., 2017a,b; North et al., 2018), meta-analyses of trials in soybeans over multiple U.S. states (Mourtzinis et al., 2019), and multi-year larger scale trials conducted across dozens of commercial corn and soybean fields (Labrie et al., 2020; Smith et al., 2020) have all failed to detect clear or consistent economic benefits attributable to this widespread approach to pest management. Indeed, detailed surveys of pest infestations over several years in intensive corn and soybean producing area of Quebec and Ontario, Canada found that neonicotinoids had potential to protect yield in <5–8% of cases (Labrie et al., 2020; Smith et al., 2020). Populations of target pests were also documented in these studies and were low (often zero)—leading the authors to conclude that no pest management benefit was realized since pests were not present at damaging levels. It is notable that, unlike the situations reflected by meta-analyses of aquatic organisms (Chagnon et al., 2015; Sánchez-Bayo et al., 2016; Wolfram et al., 2018), there are no datasets showing long-term population trends for any of the pest species targeted by neonicotinoids. It is reasonable to suggest that, given the ubiquity of the seed treatment approach in North America over some 15 years, pest pressures may be expected to have dramatically declined. One of the experimental hurdles to carrying out such work is that there is no "untreated" refuge for the pest species targeted in the US, as almost all annual, or row crops, are treated every year. Despite this lack of biological or agronomic rationale, rates of active ingredient applied to crop seeds have steadily increased (Douglas et al., 2015; DiBartolomeis et al., 2019). Similarly, there are no data to support the hypothesis that novel pest pressures or changing economic considerations, such as commodity prices, are driving increasing rates of neonicotinoid active ingredient/seed. Given this lack of quantifiable justification, it seems likely that the trends of adding progressively more active ingredient on crop seeds is driven chiefly by considerations other than farmer or market demand or any readily quantifiable agricultural considerations. If pest pressures or economic considerations were driving higher application rates, it would be easier to reconcile some of the non-target effects of releasing progressively more neonicotinoids into the environment each year.

## THE FATE OF NEONICOTINOIDS FROM SEED COATINGS

The very properties that make neonicotinoids ideally suited for use as seed treatments—high water solubility and the potential for xylem transport in plant tissues—ensure that the majority of the neonicotinoid applied to crop seeds will, inevitably, wind up elsewhere (Hladik et al., 2014; Main et al., 2014; Long and Krupke, 2016; Mogren and Lundgren, 2016; Alford and Krupke, 2017, 2019). Chronicling the movement of these compounds from the seed coating, into the crop plant, and beyond, is a logical starting point in assessing the potential for effects upon non-target lands, waterways, and the organisms that live there.

Nowhere are neonicotinoids deployed more widely and thoroughly than annual production of corn, or maize in the United States, where virtually every non-organic seed grown for grain production is treated with thiamethoxam and/or clothianidin, and less commonly, imidacloprid (Douglas et al., 2015). During planting of corn seeds, neonicotinoids and other active ingredients are abraded from the seed coat and exhausted via pneumatic planting equipment typically used in modern North American planting operations. This dust moves out into the surrounding landscape (Krupke et al., 2012, 2017b; Stewart et al., 2014; Schaafsma et al., 2018), and presents a route of exposure via insecticide drift that has resulted in reports of honey bee mortality in multiple jurisdictions (summarized in Krupke and Long, 2015). Using honey bee foraging radii as a parameter, this airborne movement of active ingredient was found to have potential for lethal and sub-lethal effects extending hundreds of meters beyond each planted field, resulting in potential for lethal exposure of non-target organisms, in this case foraging honey bees (Krupke et al., 2017b). Although the environmental fate of dispersed particulates was not quantified in this study, these exposures are likely to be acute, in terms of toxicity, and relatively short in duration. One estimate concluded that planting of treated seeds typically results in 2–3% of the active ingredient applied to seeds being abraded and dispersed during planting, although the authors note that this percentage may range as high as 12% of the applied active ingredient (Schaafsma et al., 2018). Several potential solutions to address the release of this insecticide-laden dust have been proposed by the research groups referenced above and others (Biocca et al., 2017), and policies to reduce this non-target exposure route have been implemented in Canada (Health Canada, 2015). However, there are no indications that this route of exposure has been addressed or mitigated to any meaningful extent in the United States, where the majority of neonicotinoid treated seeds are planted even though initial reports first surfaced almost a decade ago (Krupke et al., 2012).

Once corn seeds are planted, concentrations of neonicotinoid active ingredients exhibit a typical exponential decay pattern, whereby there is a rapid initial uptake by plants following germination and movement into growing tissues, followed by a rapid decline (Alford and Krupke, 2017); the same pattern is found in rice treated with imidacloprid (Iwaya et al., 1998). This results in a potential "pest protection window" of a maximum of 2–3 weeks following planting. A similar pattern has been documented in soybeans, another key commodity planted using neonicotinoid-treated seeds (Krupke et al., 2017a). In fact, this pattern may be expected from any water-soluble compound—once plant tissues are saturated, any neonicotinoids remaining on or near the treated plant would be expected to demonstrate an affinity for unsaturated aqueous compartments, and not readily enter the plant. However, one surprising corollary of these results is the inefficiency associated with the seed-treatment approach; in corn, a maximum of 1.34% of active ingredient was recovered at any period in plant tissues, with a total of $<5\%$ of the initial application rate recovered from plants during the entire growing season. This raises obvious questions about the fate of the remaining active ingredient. Initial registration documents for both thiamethoxam and clothianidin reflect soil stability and persistence inherent in these compounds. Similarly, imidacloprid uptake by treated plants does not account for more than 2–20% of the applied amount (Goulson, 2013) with the remainder found in field soils and accumulating after successive yearly applications (Jones et al., 2014), effectively resulting in a reservoir of insecticide that may leach into surrounding waterways over months or years.

While not the only metric used to assess leaching risk, the Groundwater Ubiquity Score (GUS; Gustafson, 1989) relates the compound's soil organic carbon-water partitioning coefficient ($K_{oc}$), and its half life ($DT_{50}$) and assigns low, medium, and high leaching potentials to respective GUS values of $<1.8$, 1.8–2.8, and $>2.8$. Clothianidin and thiamethoxam have GUS values of 5.43–6.98 and 1.84–4.25, respectively, based upon respective $K_{oc}$ values of 60 and 68.4 (Alford and Krupke, 2017). These values reflect that both compounds are likely to be found in both ground and surface waters. Confining pesticide applications to the target crop and plant is a long-standing, elusive goal that was thought to be at least partially addressed by the seed treatment approach. However, we now know that neonicotinoid seed treatments can and do typically move beyond the planted field (Hladik et al., 2014; Samson-Robert et al., 2014; Morrissey et al., 2015; Chretien et al., 2017; Miles et al., 2017), and that leaching does occur when these compounds are used under field conditions (e.g., potatoes: Huseth and Groves, 2014; sugar beets: Wettstein et al., 2016). In one study, concentrations in tile-drained groundwaters peaked within several weeks following corn planting (Alford and Krupke, 2019). Similar results were found in no-till fields without tile drains, but this study also revealed that active ingredients with lower solubility left fields more slowly (Frame et al., accepted). In studies cited above (Samson-Robert et al., 2014; Alford and Krupke, 2019), spikes in detections of neonicotinoids from seed treatment in surface puddles and groundwater in and near fields corresponded with rainfall events, meaning that exposures are likely to be inconsistent, or pulsed, throughout the growing season and are likely to be most directly experienced by aquatic insects and other organisms in habitats that receive water running off of fields. This presents a challenge in replicating these exposures—that may include a mix of acute and chronic exposures—in controlled lab or semi-field settings.

## NEONICOTINOID INTERSECTIONS WITH AQUATIC COMMUNITIES

It is unsurprising that non-target effects have been documented for a range of organisms and systems, given the rapid, widespread "adoption" of neonicotinoid insecticides, albeit often without a clear consent from buyers (e.g., around 30% of farmers were not aware that insecticides were on their seeds; Hitaj et al., 2020). However, most research on non-target effects has focused upon honey bees and other pollinators, both in terms of documenting exposure routes, and lethal and sub-lethal effects. Indeed, it is clear that honey bees are exposed to neonicotinoid insecticides through a range of exposure routes (Wood and Goulson, 2017). However, we argue that because honey bees are an intensively managed, mobile, and resilient species, living in colonies of tens of thousands, honey bee health metrics are likely to dramatically underestimate the risk to more sensitive organisms with life histories that are more easily disrupted by exposure to a water-soluble insecticide. With mounting evidence showing that a significant portion of applied neonicotinoids end up in waterways, we would be wise to direct more attention toward the effects these water-soluble insecticides have upon aquatic environments.

While water-soluble insecticides are arguably the best place to start in assessing mortality factors for aquatic insects, we note also that there are important additional and overlapping stressors upon aquatic insect populations that may confound attempts to track the effect of neonicotinoids on aquatic systems (Beketov and Liess, 2008). As neonicotinoid adoption has increased, so have levels of other stressors associated with agricultural intensification, including habitat loss and climate change (Verberk et al., 2016; Cavallaro et al., 2018; Jourdan et al., 2019; Baranov et al., 2020). There are other challenges in tracking the effects of neonicotinoids in aquatic systems, largely due to aquatic insects' often-cryptic nature (many live under rocks, leaf debris, or within sediment) and a dearth of basic natural-history information or population data. This lack of baseline data for species diversity and abundance, relatively sparse quantitative data on aquatic insect sensitivity to neonicotinoids (e.g., Van den Brink et al., 2016; Rico et al., 2018; Macaulay et al., 2019) and a shortage of published protocols for rearing and maintaining colonies of aquatic insects, further exacerbate the challenge of quantifying the degree and effects of pulsed neonicotinoid exposures on the wide range of organisms living in aquatic environments.

This dearth of data highlights that trends in science research and education are not immune to economics: the demonstrable benefit that pollinators have for the agricultural food supply has led to a plethora of funding opportunities and research interest aimed at documenting threats to pollinator health, and the recent explosion of literature on this topic reflects this emphasis.

For most aquatic invertebrates, however, although they are key components of aquatic systems, the benefits for the public good are not as easily quantified and research funding options for studying them are consequently more limited. In short, many of these organisms have little readily demonstrable utility to the public. They are generally uncharismatic, often drab in color, and live under rocks, dead leaves, or in the mud. A layperson could be forgiven for having little interest or curiosity about these organisms. However, there is no doubt that they contribute to food-web stability and provide functional redundancy in the community (Polis and Strong, 1996) and unsurprisingly, a recent review of the data that is available clearly outlined the pervasive, negative effects of neonicotinoids upon aquatic systems (Sánchez-Bayo et al., 2016).

In response to threats of this nature, researchers have urged regulatory authorities and the agricultural community to embrace other approaches for pest management, ranging from stopping the sale of neonicotinoid insecticides altogether, to a more thorough implementation of pest management approaches that rely upon an IPM framework (Sánchez-Bayo et al., 2016). In recent years, neonicotinoid use in some jurisdictions has been curtailed via regulation, or stopped altogether, notably in the European Union (Stokstad, 2018). Conversely, in the U.S., use rates have continued to rise rapidly over the same time period (DiBartolomeis et al., 2019; Douglas et al., 2020). There is no reason to expect this trend to abate, and a recent review of pesticide concentrations in U.S. surface waters found that corresponding levels of neonicotinoids in these systems are increasing and are expected to continue to do so (Wolfram et al., 2018). A meta-analysis of published studies focusing on the effects of environmental neonicotinoids upon non-target terrestrial arthropods found that neonicotinoids negatively affected all performance variables measured (Main et al., 2018). The purpose of this paper is not to repeat aspects of these reviews, but rather to point out that some of the ecosystem-level effects that these and other authors have warned about are coming into clearer focus in the U.S. and elsewhere, while crop yield benefits remain elusive—providing even more impetus for necessary change.

A striking example of an ecosystem-wide influence of neonicotinoids emerged recently from Japan. In this example, neonicotinoid runoff from rice production into a large lake caused drastic and long-term reductions in key species of midge and zooplankton, which are prey of eels and smelts, important fish species for local fishermen. With large reductions in their food source due to neonicotinoids, the eel and smelt fisheries collapsed, with severe consequences for local economies (Yamamuro et al., 2019). This story is instructive for at least two reasons. First, introduction of imidicloprid into the system quickly decreased zooplankton populations, and continued presence of neonicotinoids in the water and their time-cumulative toxicity (Tennekes and Sánchez-Bayo, 2013) kept their populations low. This continual depression of invertebrate populations, with effects that ripple through higher trophic levels, should be expected in regions where neonicotinoids are routinely used—each growing season releases a new dose of the insecticides into the environment, potentially chronically suppressing sensitive invertebrate populations with potential repercussions for invertebrates that rely on these invertebrate populations (e.g., Hallmann et al., 2014; Chen et al., 2019). Second, while midge populations in this example would have been expected to be sensitive to neonicotinoids in water (Cavallaro et al., 2018; United States Environmental Protection Agency, 2019), based on limited toxicity work with aquatic crustaceans the zooplankton (a copepod species) would not have been expected to be highly sensitive to neonicotinoids (Sánchez-Bayo, 2006). Yamamuro et al. (2019) discuss the role of multiple active ingredients of neonicotinoids in the unexpected toxicity, but their data clearly show the decline of zooplankton began when just one neonicotinoid (imidacloprid) was being sold in the region. More recent research indicates that many aquatic species are more sensitive to neonicotinoids than the model toxicological organisms often used by regulatory authorities to assess potential harms to aquatic ecosystems. One notable example is the crustacean, *Daphnia magna*, which despite being orders of magnitude more tolerant of neonicotinoid insecticides than many aquatic insects (Raby et al., 2018), is the most frequently used aquatic invertebrate for aquatic toxicity testing and regulatory (i.e., U.S. Environmental Protection Agency) submission packages. This suggests that ecological thresholds for neonicotinoid concentrations in water must be lowered to avoid unanticipated impacts from acute and chronic exposure (Morrissey et al., 2015); there is a clear rationale for including additional, and possibly more sensitive species, in future assessments (Roessink et al., 2013). Chronic exposure is a particularly important aspect of the aquatic toxicological picture that is difficult to mimic experimentally with compounds, like neonicotinoids, that are systemic, persistent, and re-inundate the water supply constantly at sub-lethal levels while triggering cumulative toxicity (Tennekes and Sánchez-Bayo, 2013).

## ECOSYSTEM-WIDE EFFECTS OF INSECTICIDE USE: WHAT'S PAST IS PROLOG

Sixty years ago, we were confronted with similar stories, but with different players; environmentalists, including author Rachel Carson, were alarmed by the negative ecosystem-wide effects of synthetic pesticides, especially the organochlorine insecticide, DDT. One of the key themes that made Carson's *Silent Spring* so influential was the connection she drew between environmental and human health (Carson, 1962). A recent example from Africa illustrates this connection clearly and highlights the likelihood of unanticipated ecological disruptions when pesticides enter aquatic systems. This study found that relatively low concentrations of the neonicotinoid imidacloprid and the organophosphate diazinon reduced abundance of some of the more sensitive aquatic insect species, leading to larger aquatic snail populations because of reduced competition for food and less predation from insect species (Becker et al., 2020). Snails are intermediate hosts for parasitic flatworms that cause schistosomiasis in human populations, and their greater abundance increased the likelihood of flatworm transmission to the local population (Becker et al., 2020). Remarkably, Carson predicted these sorts of outcomes when insecticides are overused. She vividly described a scene from salt marshes treated with insecticides where snails were the only visible living animals, and explicitly warned of the risk to human health resulting from this abundance of snails, relating this to schistosomiasis outbreaks (Carson, 1962). While this human health issue may not be a large concern for individuals considering neonicotinoid use in the U.S., this example does show how humans, and not just wildlife, can be victims of subtle insecticide-driven changes in invertebrate community structure. Similar outcomes have been found in agricultural systems, where neonicotinoid-driven changes in the invertebrate predator community can reduce crop productivity (Douglas et al., 2015).

In Chapter 7 of *Silent Spring*, when lamenting the "needless havoc" on wildlife wrought by indiscriminate insecticide use, Carson wrote: "The entomologist, whose specialty is insects, is not so qualified by training, and is not psychologically disposed to look for undesirable side effects of his control programs." This is an unflattering, one-dimensional generalization of entomologists from the 1950s and early 1960s—rigid and myopic scientists focused on exterminating insect populations with no regard for non-target effects. Put into the perspective of that era, however, this is perhaps understandable as the responses of the Entomological Society of America to Carson reflected an initial hostility to her message (Krupke et al., 2007). This 2007 review of the response to Carson's work reflected that: "Today, we may be hard pressed to find a knowledgeable entomologist or toxicologist who would argue for a return to the widespread application of broad-spectrum, persistent pesticides," and yet, this is precisely the situation we find ourselves in today.

## SYNTHESIS

There is no doubt that the advances in chemistry and synthetic insecticides that emerged from World War II extended into everyday life to benefit farmers and consumers besieged by insect pests. Notably, USDA and its entomologists embraced and promoted insecticide use, with officials repeatedly assuring that there would be little or no cost to wildlife if the insecticides were used according to USDA recommendations (Mart, 2015). Then, as now, the trust in the environmental safety of proper insecticide use was believed to be justified at the time. But, thankfully, science is progressive by nature and new hypotheses and the tools to test them emerge continually. Through the work of entomologists, ecologists, wildlife biologists, toxicologists and other scientists, we learned that non-target effects were not only present, but pervasive. We now know that indiscriminate, often prophylactic, insecticide use can have significant non-target effects. In the current landscape, ample research has demonstrated that these effects are ubiquitous in association with widespread neonicotinoid use. Indeed, we are unaware of any recent reports of increases in abundances of aquatic species in agricultural regions of the U.S. where neonicotinoids are common. Interestingly, a recent meta-analysis focusing on the phenomenon of insect declines found that freshwater insect populations were actually increasing in abundance by about 15% between the 1960s and 2005, likely due to improvements in water quality (van Klink et al., 2020). However, because neonicotinoid use has increased most dramatically since 2006 (Douglas et al., 2015; Tooker et al., 2017), their potential influence on aquatic communities would not have been included in the data used in this meta-analysis.

Importantly, compared to the 1960s, we now have a better grasp of the ecological effects of food web simplification. Decades of theoretical and empirical work has demonstrated that removing the easily overlooked, apparently inconsequential species from terrestrial food webs can result in unexpected shifts in primary productivity and consumer performance (e.g., Polis and Strong, 1996; Scheu et al., 1999). However, neonicotinoids present a particularly thorny problem without a historical comparator; the persistent, ubiquitous and highly water-soluble nature of neonicotinoids has resulted in an ongoing logistical hurdle in finding truly "untreated" control sites for rigorous experimental work. We do know that in aquatic food webs, exposure of communities to very low concentrations of insecticides can have unpredictable and lingering effects on species abundance, phenology and ecosystem function (e.g., litter decomposition) with influences that ripple up through trophic levels to influence the whole ecosystem (Liess and Ohe, 2005; Sánchez-Bayo et al., 2016; Cavallaro et al., 2018; Yamamuro et al., 2019; Becker et al., 2020). If current trends continue, the fundamentals of ecology ensure that eroding the foundations of aquatic systems will eventually manifest in negative consequences for game fish, birds, and other species that do have clear monetary value.

Although we cannot ignore the trend toward monetizing and commoditizing insects and their activities in terms of ecosystem services (Losey and Vaughan, 2006), this approach leaves us with blind spots regarding many aquatic insects, which are difficult to place into a clear economic framework, but we know to be critical for ecosystem function (Suter and Cormier, 2015). Until fishery collapses (Yamamuro et al., 2019), bird declines (Li et al., 2020), or human disease outbreak (Becker et al., 2020) belatedly sound an alarm, we remain largely unaware of these effects. We argue that in the case of neonicotinoid seed treatments, where the benefits of the approach are elusive and inconsistent, and the negative effects on aquatic systems are pervasive, the case is clear and the need for changing the trajectory is evident.

## CONCLUDING THOUGHTS

Contrary to popular belief, insecticide use in the U.S. continued to increase after *Silent Spring*, and those increases continue today (Mart, 2015). In the U.S., where Bt corn is rightly hailed as a target-specific and largely environmentally benign breakthrough in terms of reducing pesticide use (Dively et al., 2018), it is not common knowledge that virtually every kernel of Bt corn is treated with at least one neonicotinoid insecticide, and at steadily increasing levels (Douglas et al., 2020; Hitaj et al., 2020). It is also not widely reported that: (1) these insecticides target a suite of secondary pests that have historically been of only minor and sporadic economic importance, (2) are effective in a relatively short window of a maximum of 14–21 days following planting (Alford and Krupke, 2019), and that (3) most of the acres planted with Bt hybrids that include a neonicotinoid seed treatment are also likely to receive one or more applications of pyrethroid insecticides (United State Geological Survey National Water-Quality Assessment Project, 2020). These are underlying mechanisms by which use of insecticides in the U.S., and the presence of toxic residues across the landscape, have increased dramatically in recent years.

Aquatic, benthic invertebrates are almost certainly the "canary in the coal mine" when it comes to chronicling the non-target effects of ubiquitous, highly mobile and water-soluble neonicotinoid insecticides (Chagnon et al., 2015; Morrissey et al., 2015; Sánchez-Bayo et al., 2016; Miles et al., 2017; Main et al., 2018). These organisms have been steeped in steadily increasing concentrations of neonicotinoids in watersheds across the country for well over a decade, and it is possible that some of the documentable effects have been lost with time. We argue that as effects come to light, they are not counterbalanced by convincing arguments based upon increasing insect pest pressures, novel pest threats, or increases in yield common fiber or food production. If any slowing of this trend is to occur, there is an urgent need to begin quantifying effects on these poorly studied species before the ecological consequences of their disappearance has catastrophic effects on higher trophic levels (e.g., Hallmann et al., 2014; Li et al., 2020). At the upper-most trophic levels, we have increasing documentation of neonicotinoids in our food and drinking water (Klarich et al., 2017), and studies are underway to determine what effects, if any, these exposures may have for human health (Cimino et al., 2017; Chang et al., 2018; Craddock et al., 2019).

The intense focus on neonicotinoid impacts upon honey bee and pollinator health, while it has resulted in a vast repository of novel scientific literature, has not bent the curve of neonicotinoid use across the landscape. On the contrary, as mentioned above, use rates in the U.S. have increased even as evidence of environmental harms has mounted (Douglas et al., 2015; Tooker et al., 2017). While there are advocates in both the public and private sectors for continuation of the status quo, in terms of ongoing intensification of insecticide use to protect crop yield, these claims are not supported by trends in pest damage or rigorous economic analyses. As Rachel Carson's initial documentation demonstrated, the effects of unchecked, prophylactic insecticide use often reveal themselves in unexpected ways. We submit that looking in and near crop fields and other terrestrial environments for non-target effects of neonicotinoid insecticides is likely to miss most of the story. In hindsight it seems clear that, far from an unexpected consequence, the erosion of aquatic ecosystems is entirely predictable when faced with steadily increasing concentrations of a broadly toxic, highly soluble and virtually ubiquitous class of insecticides.

Aquatic systems are a cornerstone for a wide range of economically significant fisheries, recreational activities, and are also treasured by citizens for their aesthetic value. We now know that they are the main environmental sink for neonicotinoid insecticides. This may present a new potential lever to effect change that is urgently needed in how we approach pest management in our largest commodities. Perhaps most importantly, we outline above the mounting evidence that this change can be accomplished without reducing yields and influencing the food supply. Although there is undoubtedly a need in the U.S. and elsewhere for wholesale changes in regulatory policy to address current and future unintended environmental consequences of pesticide use (Brühl and Zaller, 2019), a strategic approach to implement immediate change already exists: integrated pest management (IPM). If IPM is not re-embraced and use of neonicotinoids (and other pesticides) continues along the current trajectory, aquatic communities will continue to degrade (Beketov et al., 2013).

IPM was developed over 50 years ago as a response to a suite of non-target effects (Stern et al., 1959), but remains all but abandoned in modern pest management in oilseed and grain crops grown in the U.S., notably corn, even while pest pressures are at or near historic lows (Hutchison et al., 2010; Bohnenblust et al., 2014; Sappington et al., 2018; Tinsley et al., 2018; Veres et al., 2020). It is worthwhile to note that consistent plant breeding efforts have led to many plant commodities, including corn, that are more durable and competitive than ever (Duvick, 2005), yet this aspect of plant tolerance is largely ignored in modern pest management (Peterson et al., 2018) as we use ever-increasing levels of insecticides, in terms of insect killing power, than ever before (DiBartolomeis et al., 2019; Douglas et al., 2020). These trends are evident despite recent data demonstrating that an IPM approach offers clear economic advantages over the neonicotinoid seed treatment approach, for example, in the case of the soybean aphid, a key pest of US soybean production (Krupke et al., 2017a).

Given the increases in land devoted to agricultural production since the 1950's, and the more potent and persistent insecticide tools of the modern era, there is abundant rationale to re-introduce the IPM approach—including the notion of simply not applying pesticides where pest densities are not sufficient to cause economic harm. This requires that monitoring of pests and use of thresholds—critical elements of IPM—be re-introduced to protect natural enemies communities that can provide biological control, one of the original goals of IPM (Stern et al., 1959) that neonicotinoids work directly against (e.g., Douglas et al., 2015; Douglas and Tooker, 2016). In the case of many pests targeted by neonicotinoid seed treatments, these thresholds have not been revisited in decades, likely partly a result of both their low incidence and the ubiquity of preventative, prophylactic neonicotinoid seed treatment use. In the U.S., there are no modern datasets documenting where, or when, many of these pests are abundant, or if they are present at all, although recent analyses in Canadian corn and soybean production systems found remarkably few pests and a consequent limited pest-management benefit of neonicotinoid-treated seed (Labrie et al., 2020; Smith et al., 2020). These are readily accessible areas for future research in the U.S. that can give agricultural producers additional confidence in reducing their reliance on insecticides. Moreover, recent research has revealed that practices that form the core of conservation agriculture (e.g., no-till farming, cover crops, animal-based fertilizers, increased diversity) can, among other benefits, improve predator populations and associated top-down control; therefore, embracing these approaches, along with IPM, can help build biological control in fields and decrease reliance on insecticides (Schipanski et al., 2014; Lundgren and Fausti, 2015; Tamburini et al., 2016; Rowen et al., 2019, 2020; Busch et al., 2020; Tooker et al., 2020; Wyckhuys et al., 2020).

In the meantime, however, there is abundant evidence that the routine use of neonicotinoids on every hectare, every year, in many key commodities is an approach with mounting costs and few benefits. Considered within the backdrop of the multitude of environmental grand challenges facing our society (National Academies of Sciences, 2019), this issue stands out simply because the economic and food/feed production benefits of the current practice have been so difficult to document—this should be among the more solvable problems on the board, About 60 years ago, Carson (1962) documented a similar imbalance of costs and benefits, and that imbalance was addressed with regulation that has proven insufficient for dealing with the current ubiquity of neonicotinoid seed coatings. As the data reviewed above demonstrate, continuing along the current trajectory will result in mounting negative environmental consequences, with no consistent, demonstrable benefits. We submit that by ignoring the data, regulatory authorities and industry alike are unwittingly building a stronger case that neonicotinoid insecticides, and future offerings, must be more strongly regulated to prevent these entirely avoidable outcomes.

## AUTHOR CONTRIBUTIONS

CK initiated the contribution and developed the initial framework of the article. CK and JT contributed equally to writing the article. Both authors contributed to the article and approved the submitted version.

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REVIEW
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# Predators and Parasitoids-in-First: From Inundative Releases to Preventative Biological Control in Greenhouse Crops

**Juliette Pijnakker*, Dominiek Vangansbeke, Marcus Duarte, Rob Moerkens and Felix L. Wäckers**

*R&D Department, Biobest Group NV, Westerlo, Belgium*

Repeated mass introductions of natural enemies have been widely used as a biological control strategy in greenhouse systems when the resident population of natural enemies is insufficient to suppress the pests. As an alternative strategy, supporting the establishment and population development of beneficials can be more effective and economical. The preventative establishment of predators and parasitoids, before the arrival of pests, has become a key element to the success of biological control programs. This "Predators and parasitoids-in-first" strategy is used both in Inoculative Biological Control (IBC), and in Conservation Biological Control (CBC). Here, we provide an overview of tools used to boost resident populations of biocontrol agents.

**Keywords: biological control, conservation, standing army, bodyguards, predators, factitious prey, pollen, nectar**

***Edited by:***
*Helda Morales,*
*The South Border College (ECOSUR), Mexico*

***Reviewed by:***
*Charles MacVean,*
*York College of Pennsylvania, United States*
*Kris A. G. Wyckhuys,*
*Chinese Academy of Agricultural Sciences (CAAS), China*

****Correspondence:***
*Juliette Pijnakker*
*juliette.pijnakker@biobestgroup.com*

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## INTRODUCTION

Biological control in greenhouses dates back almost 100 years, when Speyer (1927) at the Cheshunt Experimental Station first described the control of greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) by the specialist parasitoid *Encarsia formosa* Gahan (Hussey et al., 1969). This example was followed in the fifties by the use of the natural enemies against mealybugs (Doutt, 1951) and in the sixties, by the introductions of the specialist predatory mite *Phytoseiulus persimilis* Athias-Henriot for the control of spider mites (Bravenboer and Dosse, 1962). Biological control in greenhouses has since been extended by the addition of generalist biocontrol agents to complement the specialist beneficials (Janssen and Sabelis, 2015). The release of generalists, that can feed on a range of prey, but may also exploit non-prey food, made it possible to maintain populations of natural enemies in crops in absence of the target pest, thus facilitating the preventative use of natural enemies.

Thirty years ago, Ramakers (1990) proposed the concept of "predator-in-first" and stated that the availability of supplementary foods, such as pollen and nectar, is essential for early establishment of generalist natural enemies. However, many cropping systems lack these floral resources (Wäckers et al., 2005). As a result, most biological control programmes rely on inundative release strategies, where natural enemies are periodically introduced in large numbers to control pest problems (Stinner, 1977; Van Lenteren et al., 2003; Collier and Van Steenwyk, 2004). The pest control in inundative strategies often relies on the released individuals, rather than their progeny (De Bach, 1964). In ornamentals especially, cheap predators and parasitoids are released weekly in crops without necessarily accomplishing establishment (Hoddle et al., 1997, 1998; Buitenhuis et al., 2014, 2015). Manual and automatized blowers of beneficials have been specially designed for that purpose

(Van Schelt et al., 2008). Inundative biological control strategies have among others the drawback to exclude more clostly, but more efficient natural enemies, like predatory bugs.

In recent years, there has been an increased interest in strategies to allow a preventative establishment of natural enemies (standing army) (Messelink et al., 2014; Pijnakker et al., 2017). Both Inoculative Biological Control (IBC), which aims at establishing mass-reared natural enemies, and Conservation Biological Control (CBC), that seeks to conserve or enhance naturally occurring biocontrol organisms, can benefit by providing natural enemies with missing resources (Hagen, 1986; Zemek and Prenerová, 1997; Wäckers, 2005). In biological control programs substantial advancements have been made in the use of factitious prey, pollen (extrafloral) nectar, and honeydew as food supplements (Van Rijn et al., 2002; Wäckers et al., 2005; Lundgren, 2009; Messelink et al., 2014). In addition, some predators can feed on plant tissues, which facilitates their establishment in periods of prey scarcity or in the absence of prey (Eubanks and Denno, 1999; Lucas and Alomar, 2001; Pappas et al., 2017). Besides the role of non-prey food, establishment of predators can also be supported through the provisioning of additional non-food resources, like shelter and oviposition sites (Messelink et al., 2014; Pekas and Wäckers, 2017). The advances in the use of supplementary resources to support early establishment of natural enemies in greenhouse crops are the focus of this review. Microbial control is not developed in this review, as preventative use of insect-pathogenic and antagonistic fungi is complex, there are few studies and results are inconsistent (Elliot et al., 2000).

## PLANT-TISSUE FEEDING

While plant feeding by omnivorous biocontrol organisms can potentially cause plant damage (see below), using tissue-feeding omnivores as biological control agents has many advantages. They have been traditionally underestimated in inundative release biocontrol strategies (Castañé et al., 2011); however, several recent studies emphasize its importance (Coll and Guershon, 2002; Eubanks and Styrsky, 2005; Wäckers et al., 2005; Castañé et al., 2011; Pappas et al., 2017). Plant-tissue feeding plays a major role in the survival of several omnivores, as it has been shown to occur broadly in heteropterans (Ridgway and Jones, 1968; Naranjo and Gibson, 1996), as well as in a number of phytoseiid mites (Tanigoshi et al., 1993). In Heteroptera it provides nutrients that are essential to successful development (Gillespie and McGregor, 2000; Sinia et al., 2004) and may help them persist in periods of drought. Plant-tissue feeding is also assumed to provide some crucial resources that facilitate prey consumption. When consuming prey, some predatory Heteroptera require a source of water to dilute the digestive enzymes they inject into their prey (Cohen, 1985). Plant-tissue feeding may allow the Heteroptera to balance nutrients, proteins, carbohydrates, vitamins and minerals that would otherwise be restricted in a carnivorous diet (Polis et al., 1989; Coll, 1998). Particular plant species allow a full development of omnivorous Heteroptera in absence of prey. As omnivores can rely on tissue feeding, the risk of dying or leaving the crop at low prey densities is probably limited (Crawley, 1975; Pimm and Lawton, 1978), but will depend on the plant species.

While the induction of plant resistance mechanisms in response to herbivore feeding has been widely studied, few studies have addressed the effect of plant-tissue feeding by omnivore natural enemies in terms of plant defense induction (Stout et al., 1997; Agrawal et al., 1999; Agrawal and Klein, 2000; Agrawal, 2005a,b; Pappas et al., 2017). Induced plant resistance mechanisms include the production of secondary metabolites, part of which are released as volatile chemicals (Herbivore-induced plant volatiles, HIPVs) (Paré and Tumlinson, 1999). HIPV's play an important role in protecting the damage sites against entry by pathogens. The induced change in plant chemistry can reduce plant attractiveness to herbivores, as well as herbivore performance (Turlings et al., 1990, Bolter et al., 1997; Karban and Baldwin, 1997; De Moraes et al., 2001; Kalberer et al., 2001; Wakefield et al., 2005), thus representing an important example of direct plant defense. An indirect defense mechanism is involved when HIPV's are used by the herbivore's natural enemies to locate their prey/hosts (Turlings and Wäckers, 2004). In addition, plant-tissue feeding also elicits the production of extrafloral nectar, an indirect defensive trait which allows plants to recruit ants and other nectar feeding omnivores, which in turn protect the plants by attacking the herbivores (Wäckers and Bonifay, 2004; Kost and Heil, 2005). Several studies have now demonstrated that plant-tissue feeding by predators also activates plant defense mechanisms (Pérez-Hedo et al., 2015a,b; Naselli et al., 2016; Pappas et al., 2016; Zhang et al., 2018). Plants with activated defense systems are less attractive to the tobacco whitefly *Bemisia tabaci* (Gennadius), but more attractive to the whitefly parasitoid *E. formosa*. Pappas et al. (2015) showed that the zoophytophagous predator *Macrolophus pygmaeus* Rambur induces defense of tomato plants, making them less susceptible to the two-spotted spider mite *Tetranychus urticae* Koch, but without affecting the greenhouse whitefly *T. vaporariorum*. Zhang et al. (2018) demonstrated that *T. urticae* and Western flower thrips *Frankliniella occidentalis* (Pergande) laid fewer eggs on sweet pepper plants previously inoculated with *M. pygmaeus*. As this also applied to newly produced leaves, which were not directly exposed to the omnivore, this suggests that the induced plant response is systemic. The development time of *F. occidentalis* larvae feeding on leaves previously exposed to *M. pygmaeus* was also prolonged.

The introduction of omnivores as biological control agents can create complex interactions. The ability of omnivores to feed on multiple trophic levels may not improve biological control. The possible benefits of plant-tissue feeding are omnivore specific and dependent on the developmental stage, prey availability and plant nutritional composition (Naranjo and Gibson, 1996). The complexity of food choice by omnivores remains poorly understood: in some cases, prey consumption is reduced when both prey and plant diets are available (Crum et al., 1998, Kiman and Yeargan, 1985, Weiser and Stamp, 1998). Feeding on high-quality plant food may provide a highly nutritious preferred food source and decrease the consumption of a particular prey species (Abrams, 1987). Omnivorous bugs consumed fewer prey on plants presenting lima bean pods in a study by Eubanks and Denno (1999). Plant-tissue feeding often facilitates survival rather than reproduction probably because of low nitrogen contents (De Clercq and Degheele, 1992). Population dynamics can be strongly influenced by the developmental stage (Coll and Guershon, 2002), the period of phytophagy of the omnivores (Cisneros and Rosenheim, 1997) or by the competition for plant food between omnivores and prey (Polis and Holt, 1992; Coll and Izraylevich, 1997).

Concerning the impact of induced changes in host plant chemistry on pests and beneficials, Ode (2006) underlined that this aspect has been insufficiently explored and reviewed negative tritrophic effects of inducible plant defenses on natural enemies. In a study by Agrawal et al. (2002), predatory mites were less attracted to plants that produced cucurbitacins than cucurbitacin-free plants and had a reduced fecundity when feeding on herbivores that feed on defended plants when compared to those that fed on plants free of cucurbitacins. Induced plant resistance is thus not always favorable to biological control.

Using phytophagous beneficials also has the consequence that their plant feeding exposes them to systemic pesticides (Coll, 1998; Smith and Krischik, 1999, Arnó and Gabarra, 2011; Prabhaker et al., 2011; Put et al., 2015). Plant feeding by omnivores can also result in crop damage or reduced crop growth, in particular at high omnivore populations. Omnivores can cause direct mechanical feeding injuries, injuries to plant vascular tissues or damage through the salivary enzymes killing plant cells (Castañé et al., 2011). Plant-tissue feeding heteropterans can also disturb plant hormonal balances (Zhang et al., 2018). In tomatoes, fruit damage by heteropterans is often reported, reflecting a preference for the more nutritious tomato fruit (Salamero et al., 1987; Alomar et al., 1991; Lucas and Alomar, 2002; Albajes et al., 2006; Castañé et al., 2011). *Nesidiocoris tenuis* (Reuter) is known to cause injuries on the aerial parts of tomato plants (necrotic rings on stems, shoots, leaf petioles and flower stalks), leading to flowers and fruits abortion, and, reduced growth (Arnó et al., 2010). Gillespie et al. (2007) reported damage on gerbera flowers, Castañé et al. (2003) and Sengonça et al. (2003) on cucumber and zucchini fruit.

Despite the above negative aspects, omnivores are crucial elements in biological control strategies, especially mirids in tomato crops and anthocorids in sweet pepper crops. Current biological control programmes are supported with different tools like smart-phone applications to register and follow crop injuries and sticky traps to monitor omnivores and the pests. This allows growers to maximize benefits of omnivores and avoid risks. Omnivorous predators are commonly used in greenhouse crops and their establishment is even stimulated by provision of alternative food (Lenfant et al., 2000; Castañé et al., 2006; Put et al., 2012; Moerkens et al., 2017; Brenard et al., 2019; Sade et al., 2019). Growers try to avoid applications of systemic pesticides, which are not compatible with omnivores. Resistance breeding does not yet take plant suitability for omnivores into account, but this might change as we gain further insights in the complex interactions involving omnivores.

## PEST FEEDING (PEST-IN-FIRST)

The "pest-in-first" (PIF) strategy is one of the oldest strategies to allow the establishment of a biocontrol "standing army" in greenhouses. Here an early introduction of natural enemies is combined with a controlled (pre-) release of the pest. This concept can also be used to allow early establishment of specialist natural enemies, which cannot be supported by factitious prey or pollen. One of the first examples of a successful PIF strategy is the release of two-spotted spider mites to reinforce the establishment of the predatory mite *P. persimilis* (Hussey et al., 1965; Gould et al., 1969; Markkula and Tiittanen, 1976; Havelka and Kindlmann, 1984; Waite, 2001; Bolckmans and Tetteroo, 2002). Other pest-in-first strategies have been evaluated, such as the introduction of low numbers of greenhouse whitefly *T. vaporariorum* in tomato followed by timed releases of its parasitoid *E. formosa* (Parr et al., 1976). Growers, however, are typically reluctant to release pests due to the risks of causing crop damage (Parr et al., 1976; Stacey, 1977, Starý, 1993). Instead, they prefer to wait until the pest develops naturally before introducing biocontrol, as releasing *P. persimilis* in naturally occurring *T. urticae* hot spots is often cheaper. Alternatively, they opt for calendar introductions of biocontrol agents.

## FACTITIOUS PREY

To allow early establishment of generalist predators, growers can use factitious prey (i.e., foods which the predators usually do not encounter in their natural habitat). Some factitious prey, such as eggs of the Mediterranean flour moth, *Ephestia kuehniella* Zeller, decapsulated cysts of the brine shrimp *Artemia* spp. and astigmatid mites (Hoogerbrugge et al., 2008; Midthassel et al., 2013; Nguyen et al., 2014a; Delisle et al., 2015a; Labbé et al., 2018) can be excellent food sources for a wide range of generalist predators. Studies on these supplemental foods are summarized in **Table 1**. Some of these factitious prey, especially *E. kuehniella* eggs and astigmatid prey mites, are also used in the commercial production of biological control agents.

### Astigmatid Prey Mites

In greenhouses, breeding sachets of *Neoseiulus cucumeris* Athias-Henriot have been developed to allow slow releases of predatory mites in the crop and thus reduce handling costs (Sampson, 1998). These rearing systems consist of predators, astigmatid mites as food and carrier material. They allow for a release of predators for periods up to four (sometimes even eight) weeks. In crops like roses or potted plants, that do not feature pollen, astigmatid prey mites do not establish on the plant, and where pests cannot be tolerated, predatory mite populations cannot build up on the crop and sachets need to be renewed regularly.

In potted plants, the spread of the predatory mites released from the breeding sachet is limited because plants are widely spaced; the majority of the predators remain on the plant, which received the sachet (Buitenhuis et al., 2010, 2014). To tackle these problems, strategies like using one (small) sachet per plant have been developed to provide each plant an open rearing system (Valentin, 2017) or predators and prey are blown over the crop

**TABLE 1 |** Examples of facticious prey.

| Factitious prey | Category natural enemy | Natural enemy | Source |
|---|---|---|---|
| Astigmatids: *Carpoglyphus lactis* L.; *Tyrophagus putrescentiae* (Schrank) | Anthocorids | *Orius naivashae* (Poppius); *Orius thripoborus* (Hesse) | Bernardo et al., 2017; Bonte et al., 2017 |
| Astigmatids: *Aleuroglyphus ovatus* (Troupeau); *Austroglycyphagus lukoschusi* (Fain); *Blomia tropicalis*; *Carpoglyphus lactis* L.; *Suidasia medanensis* (Oudemans); *Thyreophagus cracentiseta* Barbosa | Predatory mites | *Amblydromalus limonicus* Garman and McGregor; *Amblyseius eharai* Amitai and Swirski; *Amblyseius tamatavensis* Blommers; *Amblyseius swirskii* (Athias-Henriot); *Gaeolaelaps aculeifer* (Canestrini); *Neoseiulus cucumeris* (Oudemans) | Hoogerbrugge et al., 2008; Xia et al., 2012; Midthassel et al., 2013; Nguyen et al., 2013; Vangansbeke et al., 2014a; Barbosa and de Moraes, 2015; Ji et al., 2015; Ferrero et al., 2016; Massaro et al., 2016; Muñoz-Cárdenas et al., 2017; Rueda-Ramírez et al., 2018 |
| Cysts of *Artemia* spp. | Anthocorids | *Orius laevigatus* (Fieber); *Orius majusculus* (Reuter); *Orius naivashae* (Poppius); *Orius strigicollis* (Poppius); *Orius thripoborus* (Hesse) | Arijs and De Clercq, 2001; De Clercq et al., 2005a; Riudavets et al., 2006; Bonte and De Clercq, 2008; Bonte et al., 2012; Nishimori et al., 2016; Oveja et al., 2016; Sade et al., 2019 |
| Cysts of *Artemia* spp. | Coccinellids | *Harmonia axyridis* (Pallas); *Coleomegilla maculata* (DeGeer) | Hongo and Obayashi, 1997; Riddick and Wu, 2015; Seko et al., 2019 |
| Cysts of *Artemia* spp. | Mirids | *Dicyphus errans* (Wolff); *Macrolophus pygmaeus* Rambur; *Nesidiocoris tenuis* (Reuter) | Tavella and Arzone, 1996; Callebaut et al., 2004; Castañé et al., 2006; Riudavets et al., 2006; Vandekerkhove et al., 2006, 2009; Messelink et al., 2015; Hilgers et al., 2016; Oveja et al., 2016; Moerkens et al., 2017; Arvaniti et al., 2018; Brenard et al., 2018, 2019; Ghasemzadeh and Gharekhani, 2019; Owashi et al., 2020 |
| Cysts of *Artemia* spp. | Predatory mites | *Amblydromalus limonicus* Garman and McGregor; *Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Neoseiulus bicaudus* (Wainstein); *Neoseiulus cucumeris* (Oudemans) | Vantornhout et al., 2004; Oveja et al., 2012; Audenaert et al., 2013; Nguyen et al., 2014b, 2015; Vangansbeke et al., 2014b,c, 2016a,b; Leman and Messelink, 2015; Su et al., 2019 |
| Sterilized eggs of *Ephestia kuehniella* Zeller | Anthocorids | *Orius* spp.; *Orius albidipennis* Reuter; *0rius insidiosus* (Say); *Orius laevigatus* (Fieber); *Orius majusculus* (Reuter); *Orius naivashae* (Poppius); *Orius niger* Wolff; *Orius sauteri* (Poppus); *Orius strigicollis* (Poppius); *Orius thripoborus* (Hesse); *Orius tristicolor* (White) | Salas-Aguilar and Ehler, 1977; Richards, 1992; Tommasini and Nicoli, 1993; Chyzik et al., 1995; Richards and Schmidt, 1995; Schmidt et al., 1995; Cocuzza et al., 1997; Arijs and De Clercq, 2001, 2004; Van Lenteren and Tommasini, 2003; De Clercq et al., 2005a; Riudavets et al., 2006; Ferkovich et al., 2007; Bonte and De Clercq, 2008; Yano et al., 2009; Vandekerkhove and De Clercq, 2010; Bonte et al., 2012, 2017; Oveja et al., 2012; Pumariño and Alomar, 2012, 2014; Nishimori et al., 2016; Bernardo et al., 2017; Sade et al., 2019 |
| Sterilized eggs of *Ephestia kuehniella* Zeller | Chrysopids | *Chrysoperla carnea* (Stephens); *Chrysoperla externa* (Hagen); *Chrysoperla rufilabris* (Burmeister) | Zheng et al., 1993; Kathiar et al., 2015; Bezerra et al., 2017 |
| Sterilized eggs of *Ephestia kuehniella* Zeller | Coccinellids | *Adalia bipunctata* L.; *Coleomegilla maculata* DeGeer; *Cryptolaemus montrouzieri* Mulsant; *Harmonia axyridis* (Pallas) | Hongo and Obayashi, 1997; De Clercq et al., 2005b; Berkvens et al., 2007; Riddick, 2009; Attia et al., 2011; Maes et al., 2014; Riddick and Wu, 2015 |
| Sterilized eggs of *Ephestia kuehniella* Zeller | Mirids | *Campyloneuropsis infumatus* (Carvalho); *Dicyphus errans* (Wolff); *Dicyphus hesperus* Knight; *Dicyphus tamaninii* Wagner; *Engytatus varians* (Distant); *Macrolophus basicornis* (Stal); *Macrolophus pygmaeus* Rambur; *Nesidiocoris tenuis* (Reuter) | Fauvel et al., 1987; Grenier et al., 1989; Constant et al., 1996; Tavella and Arzone, 1996; Gillespie and McGregor, 2000; Iriarte and Castañé, 2001; Sanchez et al., 2003, 2004; Callebaut et al., 2004; Castañé and Zapata, 2005; Messelink et al., 2005; Alomar et al., 2006; Castañé et al., 2006; Riudavets et al., 2006; Vandekerkhove et al., 2006, 2009; Oveja et al., 2012; Put et al., 2012; Mollá et al., 2014; Van Holstein and Messelink, 2014; Hilgers et al., 2016; Perdikis and Arvaniti, 2016; Moerkens et al., 2017; Arvaniti et al., 2018; Brenard et al., 2018; Bueno et al., 2018; Ghasemzadeh and Gharekhani, 2019; Owashi et al., 2020 |
| Sterilized eggs of *Ephestia kuehniella* Zeller | Lygids | *Geocoris varius* (Uhler); *Geocoris proteus* Distant | Oida and Kadono, 2012; Igarashi and Nomura, 2013 |
| Sterilized eggs of *Ephestia kuehniella* Zeller | Predatory mites | *Amblydromalus limonicus* Garman and McGregor; *Amblyseius swirskii* (Athias-Henriot); *Euseius scutalis* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Neoseiulus barkeri* (Hughes) | Romeih et al., 2004; Vantornhout et al., 2004; Momen and El-Laithy, 2007; Audenaert et al., 2013; Nguyen et al., 2014a; Vangansbeke et al., 2014a,b,c; Leman and Messelink, 2015 |

with purpose built automatized blowers. Supplying predatory mites with factitious (astigmatid) prey mites as food has recently gained popularity among growers. The following feeding mites could be used to improve the reproduction and survival of predatory mites: *Tyrophagus putrescentiae* (Schrank) (Pirayeshfar et al., 2020), *Carpoglyphus lactis* (L.) (Nguyen et al., 2013), *Thyreophagus entomophagus* (Laboulbene), *Suidasia medanensis* (Oudemans) (Sánchez et al., 2019), and *Aleuroglyphus ovatus* (Troupeau) (Xia et al., 2012; Ferrero et al., 2016; Rueda-Ramírez et al., 2018). However, very few trials have been performed at plant level (Hoogerbrugge et al., 2008; Vila et al., 2017; Pirayeshfar et al., 2020) and studies on the actual effect of these strategies on pest control are limited. Pirayeshfar et al. (2020) succeeded in increasing *Amblyseius swirskii* Athias-Henriot numbers on chrysanthemum plants by providing living *T. putrescentiae* per plant, but failed to do so using frozen *T. putrescentiae*. Pirayeshfar et al. (2020) suggested that the different diets used to rear the prey mites may have an influence on the population increase of the predatory mites. Nowadays, some growers disperse the astigmatid mites *C. lactis* or *T. entomophagus* to supplement the released predatory mites with food. Ferrero et al. (2016) developed a gel product protecting astigmatid mites' eggs when they are dispersed, and increasing their shell-life on the crops. This product resulted in high population levels of A. swirskii on cucumber plants and a better biological control of sweet potato whitefly than with the use of breeding sachets. Using astigmatid mites as food supplement has the advantage that they are relatively cheap (Ramakers and van Lieburg, 1982; Castagnoli, 1989). The main drawback of mass application of astigmatid mites lies in the fact that they can cause health issues for users including dermatitis, allergies and anaphylaxis (Iglesias-Souto et al., 2009; Fernández-Caldas et al., 2014; Liu and Zhang, 2017; Mullen and O'Connor, 2019; Pirayeshfar et al., 2020). Furthermore, Tyrophagus spp. can cause plant damage (Czaikowska et al., 1988; Buxton, 1989; Fischer, 1993; Fan and Zhang, 2007; Yasukawa et al., 2011).

Muñoz-Cárdenas et al. (2017) proposed another approach using astigmatid mites in combination with mulch layers to provide food to crop-inhabiting predatory mites. Prey mites were introduced in the litter to stimulate the predatory mite *A. swirskii* on aboveground plant parts. In cage experiments with rose plants this increased predatory mite numbers 4-fold, as compared to control plants. Thrips control was increased and leaf- and flower damage was reduced as a result. It was shown that A. swirskii, which is usually considered to be a leaf-inhabiting species, actually moved between rose foliage and mulch to feed on the astigmatid mites. Similarly, Grosman et al. (2014) increased biocontrol of thrips and whiteflies with *A. swirskii* using mulch layers in different ornamental crops. Adding mulches with, for example bran, yeast or Biotop®, waste product of the potato industry (Grosman and de Groot, 2011), organic matter (Settle et al., 1996; Neves Esteca et al., 2020), animal manure (Navarro-Campos et al., 2012) to boost fungi, decomposers and plankton feeders can increase predators' population levels. Despite promising results in small-scale experiments, this strategy has not been adopted by growers. This is probably due to the increased labor when mulching, and the fact that the system is often effective on the short term only. Grosman et al. (2014) found that this approach produced predators for up to 6 weeks, which is comparable to the longevity of breeding sachets. These methods carry also the risk that the predators switch from feeding on herbivores to soil organisms (apparent mutualism, Holt, 1977) as reported by Birkhofer et al. (2008), or, are out-competed by other soil predators, that also benefit from the substrate manipulation (Messelink and Van Holstein-Saj, 2007, 2011).

## Mediterranean Flour Moth Eggs

To support establishment of predatory bugs, growers mainly use eggs of the Mediterranean flour moth *E. kuehniella*. The high nutritional value of *E. kuehniella* eggs ensures development, reproduction and survival of many arthropods (**Table 1**). In *M. pygmaeus*, higher reproduction rates were found when the mirids were fed on the moth eggs, as compared to whitefly pupae (Fauvel et al., 1987; Alomar et al., 2006). Sprinkling of *E. kuehniella* eggs on crop plants was the first supplemental food strategy widely adopted by growers on a large scale. They are typically used on the points where predatory bugs *Orius* spp. (sweet pepper) and mirid bugs *M. pygmaeus*, *N. tenuis*, and *Tupiocoris cucurbitaceus* (Spinola) (mainly tomato) are introduced (Put et al., 2012; Moerkens et al., 2017; Brenard et al., 2018).

The main factor limiting the use of *E. kuehniella* eggs is their cost, with prices of 400 EUR/kg (Nguyen et al., 2014a). They also need to be kept frozen. Furthermore, the eggs tend to dry out once applied on the crop, or when the relative humidity is too high, they become moldy on the leaves. Due to their cost, *E. kuehniella* eggs are not used to feed predatory mites. However, this food source was found to be suitable for oviposition of *Iphiseius degenerans* (Berlese) (Vantornhout et al., 2004), *A. swirski* and *Amblydromalus limonicus* Garman and McGregor (Nguyen et al., 2014a; Vangansbeke et al., 2014c), *Gaeolaelaps aculeifer* Canestrini and *Stratiolaelaps scimitus* (Womersley) (Navarro-Campos et al., 2016), as well as for the pest *F. occidentalis*. The performance of predatory mites on *E. kuehniella* eggs can vary (Vangansbeke et al., 2014c; Leman and Messelink, 2015) depending on egg storage conditions and ambient humidity in the crop. Liu and Zhang (2017) observed that immatures of *A. limonicus* exhibited difficulties to pierce the chorion of *E. kuehniella* eggs that hardened at low ambient humidity.

## Cysts of the Brine Shrimp

Several cheaper options have been investigated to replace the use of *Ephestia* moth eggs in commercial production as well as in field applications (**Table 1**). Out of the options tested, the most promising substitute of flour moth eggs for feeding generalist predators was found to be dry cysts of the brine shrimp *Artemia* spp. Having been used widely as fish food, *Artemia* cysts have the advantage that they can be stored for years in dry form, and do not require freezing as required for *E. kuehniella* eggs (Arijs and De Clercq, 2001). They keep their nutritional value longer than *E. kuehniella* eggs when applied on crops (De Clercq et al., 2005a; Messelink et al., 2016; Moerkens et al., 2017), they do not become moldy on plants (Vandekerkhove et al., 2009) and are, depending on the quality, up to 30 times cheaper than flour moth eggs (Nguyen et al., 2014a). However, *Artemia* cysts vary substantially in nutritional quality, and the high quality product is roughly the same price as *E. kuehniella* eggs. When used at high densities, *Artemia* cysts can leave a "fishy smell" on the crop. Brine shrimp cysts have been tested as prey for several natural enemies for production purposes (**Table 1**).

In field crops, Hoogerbrugge et al. (2008) and Leman and Messelink (2015) found either no or poor establishment of *A. swirskii* when fed with a commercial strain of *Artemia* sp. cysts alone in a chrysanthemum crop. In contrast, Vantornhout et al. (2004), Nguyen et al. (2014a) and Vangansbeke et al. (2014c, 2016b) showed in laboratory studies complete development of, respectively, I. degenerans, *A. swirskii* and *A. limonicus* on a diet of decapsulated cysts of a non-commercial *Artemia franciscana* Kellogg strain. Vangansbeke et al. (2016a) succeeded in establishing *A. swirskii* on chrysanthemum and ivy plants using this *Artemia* strain, but not when using a commercial decapsulated *Artemia* cyst product. Inconsistent results between studies might be explained by the incomplete decapsulation of the cysts or their level of hydration (Castañé et al., 2006) and by the substantial variation in *Artemia* product quality. De Clercq et al. (2005a) showed differences of composition and nutritional quality between *Artemia* cysts of diverse origins, which can have an impact on the nutritional value as well (Bloemhard et al., 2018; Sade et al., 2019). Overall, *Artemia* cysts have become a valuable complement in biological control programs in greenhouse vegetable crops, as most tomato and sweet pepper growers release *M. pygmaeus* with this alternative food, either by itself or in combination with *E. kuehniella*.

The provision of brine schrimp cysts and Mediterranean flour moth eggs is now a common practice on introduction points of predatory bugs in vegetable crops. As astigmatid prey mites are concerned, only ornamental growers release them weekly or biweekly, but generally additionally to predatory mites. They tend to use them within their inundative release strategies of predatory mites instead of seeking for an early establishment of predators after a few release. Besides their use to stimulate predatory mites, astigmatid mites might also hold potential to support field populations of predatory bugs, as they were found to be a suitable food source for *Orius* spp. (El-Husseiniak and Sermann, 1992; Husseini et al., 1993; Nagai et al., 1998; Gomaa and Agamy, 2002; Yang et al., 2009; Bernardo et al., 2017; Bonte et al., 2017; Song et al., 2018). This application is still at an experimental stage at growers.

## BANKER PLANT SYSTEMS

Supplementation of food resources and oviposition places for natural enemies can be done by providing secondary plants, so-called "banker plants" or "open rearing systems" (Bennison, 1992; Bennison and Corless, 1993). The principle of the banker plant system is the use of plants, usually different from the crop, to provide beneficials with alternative (non-pest) prey and/or plant-provided food resources. This method was developed for the introduction of parasitoid wasps to control aphids (Starý, 1969; Lyon, 1973) and whiteflies (Stacey, 1977). The banker plant method is often seen as a further development of the "Pest-in-first" method in greenhouses as the initial banker plant systems introduced additional crop plants carrying the target pest (**Table 2**) (Parr and Stacey, 1975; Stacey, 1977).

The advantages of using banker plants have been widely described. They aid survival, reproduction and development of naturally occurring or introduced natural enemies even in absence of pests (Pratt and Croft, 2000). When introducing beneficials, they can be released onto the banker plants where they find essential resources for survival and reproduction. Once the target pest appears, they then move from the banker plants into the crop. Successful banker plant systems allow for early season augmentation of beneficials and can replace "repeated inundative releases" (Hansen, 1983) thereby reducing costs (Huang et al., 2011). Furthermore, when using potted banker systems, these banker plants can be moved for "hot spot treatment" of pest colonies (Ramakers and Voet, 1995). When selecting banker plants, one should consider the natural enemies' affinity for the plant, as well as the plant's capacity to carry suitable alternative prey or other (food) resources (Jacobson and Croft, 1998; Goolsby and Ciomperlik, 1999). Nutritional, allelochemical and plant morphological traits (Price et al., 1980; Grevstad and Klepetka, 1992, Desneux and Ramirez-Romero, 2009) are taken into account when selecting candidate banker plant-prey combinations. It is known that morphological plant characteristics (e.g., toughness of leaves and stems, number of nectar glands, flowering period, number of flowers, plant pubescence, acarodomatia, trichomes) can be correlated with the dispersal, oviposition, developmental and reproductive success of arthropods (Walter and O'Dowd, 1992a,b; Pfannenstiel and Yeargan, 1998; Lucas and Brodeur, 1999, Lundgren et al., 2008; Parolin et al., 2012a). In addition, banker plants must be capable to survive temperatures and light conditions as the ones used in greenhouse production (Van der Linden, 1992).

Banker plant systems can be divided into two groups: (1) plants providing non-pest prey/host (2) plants producing non-prey food sources (pollen and nectar). Diverse publications provide complete inventories of the banker plant systems and their potential (Osborne et al., 2005; Frank, 2010; Huang et al., 2011; Ying et al., 2012; Miller et al., 2017; Miller, 2018; Payton Miller and Rebek, 2018). An overview of banker plant systems is given in **Tables 2–4**.

### Banker Plant Systems (Non-pest Prey)

Most banker plant systems using alternative prey/hosts (**Table 3**) were designed to control aphids, such as *Myzus persicae* Sulzer on sweet peppers or *Aphis gossypii* Glover on cucumbers. Hansen (1983) first evaluated a banker plant system using broad bean infected with *Megoura viciae* Bucken, to rear *Aphidoletes aphidimyza* (Rondani). Other banker plant systems consist of sorghum, rye, barley or wheat seedlings infested with cereal aphids which are harmless to greenhouse crops, such as *Rhopalosiphum padi* Linnaeus, *Sitobion avenae* Fabricius, *Metopolophium dirhodum* (Walker), *Melanaphis sacchari* (Zehntner), or *Schizaphis graminum* (Rondani) (Kuo-Sell, 1987; Abe et al., 2011; Nagasaka et al., 2011; Yano et al., 2011).

**TABLE 2 |** Examples of (pest prey) banker plant systems.

| Banker plant (common name) | Banker plant (Latin name) | Prey/host | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|---|
| Borage | *Borago officinalis* L. | *Myzus persicae* (Sulzer) | Parasitoids | *Aphidius colemani* Viereck | Fujinuma et al., 2010 |
| Bush bean | *Phaseolus vulgaris* L. | *Tetranychus urticae* Koch | Mites | *Phytoseiulus persimilis* Athias-Henriot | Matteoni, 2003 |
| Castor bean | *Ricinus communis* L. | *Bemisia tabaci* (Gennadius) | Parasitoids | Eretmocerus hayati (Zolnerowich and Rose); *Encarsia sophia* (Girault and Dodd) | Kidane et al., 2018 |
| Corn | *Zea mays* L. | *Tetranychus urticae* Koch | Mites | *Phytoseiulus persimilis* Athias-Henriot | Miller et al., 2017; Miller, 2018 |
| Kidney bean | *Phaseolus vulgaris* L. | *Tetranychus urticae* Koch | Mites | *Amblyseius fallacis* Garman | Lester et al., 2000 |
| Laurustinus | *Viburnum tinus* L. | *Tetranychus urticae* Koch | Mites | *Neoseiulus californicus* (McGregor); *Phytoseiulus persimilis* Athias-Henriot | Parolin et al., 2013; Bresch et al., 2015 |
| Melon | *Cucumis melo* L. | *Bemisia tabaci* (Gennadius) | Parasitoids | *Encarsia sophia* (Girault and Dodd); *Eretmocerus* spp.; *Eretmocerus hayati* (Zolnerowich and Rose) | Goolsby and Ciomperlik, 1999; Pickett et al., 2004; Kidane et al., 2018 |
| Pumpkin | *Cucurbita maxima* "Uchiki Kuri" | *Trialeurodes vaporariorum* Westwood | Parasitoids | *Encarsia tricolor* Foërster | Laurenz and Meyhöfer, 2017 |
| Rhododendron | *Rhododendron* sp. "Ana Kruschke" | *Oligonychus ilicis* (McGregor) and *Oligonychus ununguis* (Jacobi) | Mites | *Neoseiulus fallacis* (Garman) | Pratt and Croft, 2000 |
| Riverbank grape | *Vitis riparia* (Michx.) | *Tetranychus urticae* Koch | Mites | *Neoseiulus californicus* (McGregor); *Phytoseiulus persimilis* Athias-Henriot | Parolin et al., 2013; Bresch et al., 2015 |
| Rose | *Rosa* sp. | *Macrosiphum rosae* L. | Parasitoids | *Praon volucre* Haliday | Maisonneuve, 2002 |
| Swedes | *Brassicae napus rapifera* Metzg. | *Myzus persicae* (Sulzer) | Parasitoids | *Ephedrus cerasicola* Starý | Hågvar and Hofsvang, 1994 |
| Sweet pepper | *Capsicum annuum* L. | *Myzus persicae* (Sulzer) | Parasitoids | *Ephedrus cerasicola* Starý | Hofsvang and Hågvar, 1979 |
| Sweet pepper | *Capsicum annuum* L. | Aphids | Parasitoids | *Aphidius coleman*i Viereck; *Aphidius ervi* Haliday | Matteoni, 2003 |
| Sweet pepper | *Capsicum annuum* L. | Aphids | Gall midges | *Aphidoletes aphidimyza* (Rondani) | Matteoni, 2003 |
| Tobacco | *Nicotiana tabacum* L. | *Trialeurodes vaporariorum* Westwood | Parasitoids | *Encarsia formosa* (Gahan) | Schmidt, 1996 |
| Tomato | *Lycopersicon esculentum* Mill. | *Trialeurodes vaporariorum* Westwood | Parasitoids | *Encarsia formosa* (Gahan) | Parr and Stacey, 1975; Stacey, 1977; Rumei, 1991 |
| Watermelon | *Citrullus lanatus* (Thunb.) | *Bemisia tabaci* (Gennadius) | Parasitoids | *Eretmocerus hayati* (Zolnerowich and Rose) | Goolsby and Ciomperlik, 1999 |

Parasitoids, such as *Aphidius colemani* Viereck, *Aphidius ervi* Haliday, and *Aphidius matricariae* Haliday, and, the predatory gall midge *A. aphidimyza* can reproduce on these banker plant systems and thus be pre-established once crop aphids appear (**Table 3**). Abe et al. (2011) succeeded in maintaining *A. aphidimyza* for at least 3 months with such a system. Banker plant systems with non-pest prey used to be broadly implemented (Walters and Hardwick, 2000; Nagasaka and Oya, 2003; Yano, 2006). Some growers produce the banker plants themselves. However, a majority of growers are reluctant to adopt

**TABLE 3 |** Examples of (non-pest prey) banker plant systems.

| Banker plant (common name) | Banker plant (Latin name) | Prey/host | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|---|
| Arborvitae | *Thuja occidentalis* L. | *Oligonychus ilicis* (McGregor) and *Oligonychus ununguis* (Jacobi) | Predatory mites | *Neoseiulus fallacis* (Garman) | Pratt and Croft, 2000 |
| Barley | *Hordeum vulgare* L. | *Rhopalosiphum padi* L. | Coccinellids | *Scymnus creperus* Mulsant | Miller et al., 2017 |
| Barley | *Hordeum vulgare* L. | *Rhopalosiphum padi* L. | Gall midges | *Aphidoletes aphidimyza* (Rondani) | Ramakers and Maaswinkel, 2002; Yano et al., 2009; Nagasaka et al., 2010; Hemerik and Yano, 2012; Higashida et al., 2016; Miller et al., 2017 |
| Barley | *Hordeum vulgare* L. | *Rhopalosiphum padi* L. | Parasitoids | *Aphidius colemani* Vierec, *Aphidius matricariae* Haliday; *Syrphophagus* sp.; *Alloxysta* sp. nr victrix (Westwood); *Dendrocerus laticeps* (Hedicke) | Goh et al., 2001; Matsuo, 2003; Nagasaka and Oya, 2003; Ode et al., 2005; Saito, 2005 Van Driesche et al., 2008; Nagasaka et al., 2010, 2011; Jandricic et al., 2014; Prado and Frank, 2014; Miller et al., 2017; Miller, 2018 |
| Barley | *Hordeum vulgare* L. | *Rhopalosiphum padi* L. | Syrphids | Several hoverflies species | Pineda and Marcos-García, 2008 |
| Barley | *Hordeum vulgare* L. | *Rhopalosiphum maidis* (Fitch) | Parasitoids | *Aphidius colemani* Viereck; *Aphidius gifuensis* (Ashmead) | Goh et al., 2001; Ohta and Honda, 2010 |
| Barley | *Hordeum vulgare* L. | *Schizaphis graminum* (Rondani) | Parasitoids | *Aphidius colemani* Viereck; *Aphidius gifuensis* (Ashmead) | Kim, 2003; Kim and Kim, 2004; Ode et al., 2005; Sun et al., 2017 |
| Barley | *Hordeum vulgare* L. | *Sitobion akebiae* (Shinji) | Parasitoids | *Aphidius gifuensis* (Ashmead) | Ohta and Honda, 2010 |
| Black elder | *Sambucus nigra L.* | *Aphis sambuci L.* | Syrphids | Several hoverflies species | Bribosia et al., 2005; Wojciechowicz-Żytko and Jankowska, 2016 |
| Bluegrass | *Poa* spp. | *Rhopalosiphum padi* L. or *Schizaphis graminum* (Rondani) | Parasitoids | *Lysiphlebus testaceipes* (Cresson) | Miller et al., 2017; Miller, 2018 |
| Broad bean | *Vicia faba* L. | *Acyrthosiphon pisum* (Harris) | Parasitoids | *Aphidius gifuensis* (Ashmead) | Ohta and Honda, 2010 |
| Broad bean | *Vicia faba* L. | *Megoura viciae* Bucken | Gall midges | *Aphidoletes aphidimyza* (Rondani) | Hansen, 1983 |
| Buckwheat | *Fagopyrum esculentum* Moench | *Sitobion avenae* (Fabricius) | Syrphids | Several hoverflies species | Fischer, 1997 |
| Corn | *Zea mays* L. | *Oligonychus pratensis* (Banks) | Gall midges | *Feltiella acarisuga* (Vallot) | Xiao et al., 2011b |
| Corn | *Zea mays* L. | *Oligonychus pratensis* (Banks) | Predatory mites | *Amblyseius swirskii* (Athias-Henriot); *Neoseiulus californicus* (McGregor); *Phytoseiulus persimilis* Athias-Henriot | Parker and Popenoe, 2008; Popenoe and Osborne, 2010 |
| Corn | *Zea mays* L. | *Rhopalosiphum padi* L. | Parasitoids | *Aphidius colemani* Viereck | Jacobson and Croft, 1998; Payton Miller and Rebek, 2018 |
| European columbine | *Aquilegia vulgaris* | *Aleyrodes lonicerae* Walker | Parasitoids | *Encarsia tricolor* Foërster | Laurenz and Meyhöfer, 2017 |
| European black nightshade | *Solanum nigrum* L. | *Aphis fabae solanella* Theobald | Mirids | *Macrolophus pygmaeus* Rambur | Lykouressis et al., 2008 |
| Finger millet | *Eleusine coracana* Gaertn. | *Sitobion avenae* (Fabricius) | Parasitoids | *Aphelinus abdominalis* Dalman; *Aphidius ervi* Haliday; *Praon volucre* Haliday | Fischer, 1997; Fischer in Huang et al., 2011 |

*(Continued)*

**TABLE 3** | Continued

| Banker plant (common name) | Banker plant (Latin name) | Prey/host | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|---|
| Finger millet | *Eleusine coracana* Gaertn. | *Rhopalosiphum padi* L. | Parasitoids | *Aphidius colemani* Viereck; *Lysiphlebus testaceipes* (Cresson) | Delgado, 1997; Fischer and Leger, 1997; Schoen and Martin, 1997; Vergniaud, 1997; Martin et al., 1998; Schoen, 2000; Boll et al., 2001a,b |
| Finger millet | *Eleusine coracana* Gaertn. | *Sitobion avenae* (Fabricius) | Syrphids | *Episyrphus* sp. | Fischer, 1997 |
| Greater celandine | *Chelidonium majus* L. | *Aleyrodes proletella* L. | Parasitoids | *Encarsia formosa* Gahan | Van der Linden and van der Staaij, 2001 |
| Kale | *Borecole oleracea* L. | *Aleyrodes proletella* L. | Parasitoids | *Encarsia formosa* Gahan | Laska and Zelenkova, 1988 |
| Lucerne | *Medicago sativa* L. | *Acyrthosiphon pisum* (Harris) | Parasitoids | *Aphidius ervi* Haliday | Cameron et al., 1984 |
| Melon | *Cucumis melo* L. | *Bemisia tabaci* (Gennadius) | Parasitoids | *Encarsia sophia* (Girault and Dodd); *Eretmocerus* spp.; *Eretmocerus hayati* (Zolnerowich and Rose) | Goolsby and Ciomperlik, 1999; Pickett et al., 2004; Kidane et al., 2018 |
| Nipplewort | *Lapsana communis* L. | *Aleyrodes proletella* L. | Parasitoids | *Encarsia formosa* Gahan | Van der Linden and van der Staaij, 2001 |
| Oat | *Avena sativa* L. | *Metopolophium dirhodum* (Walker) | Gall midges | *Aphidoletes aphidimyza* (Rondani) | Götte and Sell, 2002 |
| Oat | *Avena sativa* L. | *Rhopalosiphum padi* L. or *Schizaphis graminum* (Rondani) | Parasitoids | *Aphelinus abdominalis* Dalman; *Aphidius colemani* Viereck | Andorno and López, 2014; Miller et al., 2017; Miller, 2018 |
| Papaya | *Carica papaya* L. | *Trialeurodes variabilis* (Quaintance) | Coccinellids | *Delphastus pusillus* (LeConte) | Osborne et al., 2005 |
| Papaya | *Carica papaya* L. | *Trialeurodes variabilis* (Quaintance) | Parasitoids | *Encarsia transvena* Timberlake; *Encarsia sophia* (Girault and Dodd) | Osborne et al., 2005; Xiao et al., 2011a |
| Persian buttercup | *Ranunculus asiaticus* L. | *Phytomyza caulinaris* Hering | Parasitoids | *Dacnusa sibirica* Telenga; Diglyphus isaea Walker | Van der Linden, 1992 |
| Potato | *Solanum tuberosum* L. | *Macrosiphum euphorbiae* (Thomas) | Parasitoids | *Aphelinus abdominalis* Dalman | Blümel and Hausdorf, 1996 |
| Rhododendron | *Rhododendron* sp. | *Oligonychus ilicis* (McGregor) and *Oligonychus ununguis* (Jacobi) | Predatory mites | *Neoseiulus fallacis* (Garman) | Pratt and Croft, 2000 |
| Rye | *Secale cereale* L. | *Rhopalosiphum padi* L. | Parasitoids | *Aphidius colemani* Viereck | McClure, 2014; McClure and Frank, 2015 |
| Rye | *Secale cereale* L. | *Rhopalosiphum maidis* (Fitch) | Parasitoids | *Aphidius colemani* Viereck; *Aphidius ervi* Haliday | Matteoni, 2003 |
| Rye | *Secale cereale* L. | *Rhopalosiphum maidis* (Fitch) | Gall midges | *Aphidoletes aphidimyza* (Rondani) | Matteoni, 2003 |
| Ryegrass | *Lolium multiflorum* L. | *Rhopalosiphum padi* L. | Parasitoids | *Aphidius colemani* Viereck | Jacobson and Croft, 1998); |
| Ryegrass | *Lolium multiflorum* L. | *Rhopalosiphum padi* L. or *Schizaphis graminum* (Rondani) | Parasitoids | *Lysiphlebus testaceipes* (Cresson) | Miller et al., 2017; Miller, 2018 |
| Savoy cabbage | *Brassica oleracea* L. | *Brevicoryne brassicae L.* | Parasitoids | *Diaeretiella rapae* McIntosh | Freuler et al., 2001, 2003 |
| Sorghum | *Sorghum bicolor* L. | *Rhopalosiphum padi* L. | Parasitoids | *Aphidius colemani* Viereck | Payton Miller and Rebek, 2018 |
| Sorghum | *Sorghum bicolor* L. | *Rhopalosiphum maidis* (Fitch) | Parasitoids | *Diaeretiella rapae* McIntosh | Ceballos et al., 2011 |
| Sorghum | *Sorghum bicolor* L. | *Schizaphis graminum* (Rondani) | Parasitoids | *Lysiphlebus testaceipes* (Cresson) | Rodrigues and Bueno, 2001; Miller et al., 2017; Miller, 2018 |

*(Continued)*

**TABLE 3 |** Continued

| Banker plant (common name) | Banker plant (Latin name) | Prey/host | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|---|
| Sorghum | *Sorghum bicolor* L. | *Melanaphis sacchari* (Zehntner) | Gall midges | *Aphidoletes aphidimyza* (Rondani) | Abe et al., 2011; Yano et al., 2011; Higashida et al., 2017 |
| Switchgrass | *Panicum virgatum* L. | *Rhopalosiphum padi* L. | Parasitoids | *Aphidius colemani* Viereck | Payton Miller and Rebek, 2018 |
| Triticale | *Triticosecale rimpaui* Wittm. | *Sitobion avenae* (Fabricius) | Parasitoids | *Aphidius ervi* Haliday | Jansson in Huang et al., 2011 |
| Triticale | *Triticosecale* sp. | *Metopolophium dirhodum* (Walker) | Gall midges | *Aphidoletes aphidimyza* (Rondani) | Götte and Sell, 2002 |
| Turnip | *Brassica rapa* L. | *Brevicoryne brassicae L.* | Parasitoids | *Diaeretiella rapae* McIntosh | Freuler et al., 2001, 2003 |
| Wheat | *Triticum aestivum* L. | *Diuraphis noxia* (Mordvilko) | Parasitoids | *Aphidius matricariae* Haliday | Miller and Gerth, 1994 |
| Wheat | *Triticum aestivum* L. | *Rhopalosiphum padi* L. | Parasitoids | *Alloxysta sp. nr victrix (Westwood); Aphidius colemani* Viereck; *Dendrocerus laticeps* (Hedicke); *Aphidius matricariae* Haliday; *Syrphophagus* sp. | Bennison, 1992; Lamparter, 1992; Albert, 1995; Conte, 1998; Jacobson and Croft, 1998; Van Schelt, 1999; Nagasaka and Oya, 2003; Saito, 2005 Nagasaka et al., 2010, 2011; Jandricic et al., 2014; McClure, 2014; McClure and Frank, 2015; Miller et al., 2017; Miller, 2018; Payton Miller and Rebek, 2018 |
| Wheat | *Triticum aestivum* L. | *Rhopalosiphum padi* L. | Coccinellids | *Scymnus creperus* Mulsant | Miller et al., 2017 |
| Wheat | *Triticum aestivum* L. | *Rhopalosiphum padi* L. | Gall midges | *Aphidoletes aphidimyza* (Rondani) | Bennison, 1992; Bennison and Corless, 1993; Albert, 1995; Miller et al., 2017 |
| Wheat | *Triticum aestivum* L. | *Schizaphis graminum* (Rondani) | Parasitoids | *Aphidius gifuensis* (Ashmead); *Aphidius colemani* Viereck; *Lysiphlebus testaceipes* (Cresson) | Starý, 1993; Miller et al., 2017; Sun et al., 2017; Miller, 2018 |
| Wheat | *Triticum aestivum* L. | *Sitobion avenae* (Fabricius) | Parasitoids | *Aphidius ervi* Haliday; *Aphidius gifuensis* (Ashmead); *Aphelinus asychis* Walker | Van Schelt, 1999; Wang et al., 2016; Miller et al., 2017; Miller, 2018; Sun and Song, 2019 |
| Wheat | *Triticum aestivum* L. | *Sitobion avenae* (Fabricius) | Syrphids | *Episyrphus balteatus* DeGeer | Ankersmit et al., 1986 |

the system, due to inconsistent efficacy, labor (handling and maintenance), sink effects, and/or issues with hyperparasitoids (Jacobson and Croft, 1998; Van Driesche et al., 2008; McClure and Frank, 2015; Payton Miller and Rebek, 2018). Furthermore, the parasitoid species reared on banker plant systems are not necessarily efficient against all occurring target pest species, such as the potato aphid, *Macrosiphum euphorbiae* (Thomas), and the foxglove aphid, *Aulacorthum solani* (Kaltenbach) (Van Driesche et al., 2008; Nagasaka et al., 2010; Prado et al., 2015). Development of parasitoid wasps (Jandricic et al., 2014) on the banker plant systems may be insufficient due to the provided aphids being of insufficient size. This can lead to a reduction of survival and male biased sex ratio of the parasitoids (Hoddle et al., 1998; Chau and Mackauer, 2001; Henry et al., 2005). Gall midges produced on aphid species of poor nutritional value can also suffer in terms of size and fecundity (Kuo-Sell, 1989). Natural enemies may be reluctant to switch from aphids on the banker plant to the crop aphids (Lester et al., 2000; Coyle et al., 2011) which can hamper the establishment of beneficials on the crop. This can be due to an acquired adaptation to the banker plant aphid through associative learning processes (Hoddle et al., 1998, Keasar et al., 2001, Ode et al., 2005, Prado and Frank, 2014). For all these reasons, the use of non-pest prey banker plant systems is relatively limited, relative to other methods supporting preventative establishment.

## Banker Plant Systems (Nectar and Pollen)

Natural enemies can also be boosted by banker plants providing pollen and nectar (**Table 4**). The use of castor beans as banker plants has been based on this principle, as it provides a copious and steady supply of pollen and extra-floral nectar, making it a suitable host plant for generalist phytoseiid predatory mites, such as *I. degenerans* and *Euseius* spp. (Van Rijn and Tanigoshi, 1999b). Castor bean bankers hosting about 2000 predatory mites have been used by growers allowing growers to move the plants to crop spots where pests were detected or where predatory mites

**TABLE 4 |** Examples of (nectar-pollen) banker plant systems.

| Banker plant (common name) | Banker plant (Latin name) | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|
| African marigold | *Tagetes erecta* L. | Anthocorids | *Orius insidiosus* say | Bueno et al., 2009 |
| Apple mint | *Mentha suaveolens* Ehrh. | Anthocorids | *Orius laevigatus* (Fieber) | Cano et al., 2009, 2012 |
| Basil | *Ocimum basilicum* L. | Anthocorids | *Orius* spp. | Cano et al., 2012 |
| Bishop's weed | *Ammi majus* L. | Syrphids | *Episyrphus balteatus* (De Geer) | Wäckers and van Rijn, 2012 |
| Brown hemp | *Crotolaria juncea* L. | Anthocorids | *Orius* spp. | Calvert et al., 2019 |
| Buckweat | *Fagopyrum esculentum* L. | Chrysopids | *Chrysoperla carnea* (Stephens) | Wäckers and van Rijn, 2012 |
| Buckweat | *Fagopyrum esculentum* L. | Syrphids | Several hoverflies species | Colley and Luna, 2000; Wäckers and van Rijn, 2012 |
| Borage | *Borago officinalis* L. | Chrysopids | *Chrysoperla carnea* (Stephens) | Wäckers and van Rijn, 2012 |
| Borage | *Borago officinalis* L. | Syrphids | *Episyrphus balteatus* (De Geer) | Wäckers and van Rijn, 2012 |
| Castor bean | *Ricinus communis* L. | Anthocorids | *Orius insidiosus* Say | Waite et al., 2014 |
| Castor bean | *Ricinus communis* L. | Predatory mites | *Amblyseius andersoni* (Chant); *Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans) | Ramakers and Voet, 1995; Van Rijn and Tanigoshi, 1999b; Miller et al., 2017; Miller, 2018 |
| Chamomile | *Matricariae camomilla* L. | Chrysopids | *Chrysoperla carnea* (Stephens) | Wäckers and van Rijn, 2012 |
| Chamomile | *Matricariae camomilla* L. | Syrphids | *Episyrphus balteatus* (De Geer) | Wäckers and van Rijn, 2012 |
| Chenille bush | *Acalypha hispida* Burm. f. | Anthocorids | *Orius laevigatus* (Fieber) | Armando and Yates, 2011 |
| Chrysanthemum | *Chrysanthemum segetum* L. | Chrysopids | *Chrysoperla carnea* (Stephens) | Wäckers and van Rijn, 2012 |
| Chrysanthemum | *Chrysanthemum segetum* L. | Syrphids | *Episyrphus balteatus* (De Geer) | Wäckers and van Rijn, 2012 |
| Cilantro | *Coriandrum sativum* L. | Syrphids | Several hoverflies species | Colley and Luna, 2000 |
| Coriander | *Coriandrum sativum* L. | Syrphids | Several hoverflies species | Pineda and Marcos-García, 2008 |
| Corn | *Zea mays* L. | Mites | *Amblyseius andersoni (Chant); Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans) | Miller et al., 2017; Miller, 2018 |
| Corn flower | *Centaurea cyanus* L. | Chrysopids | *Chrysoperla carnea* (Stephens) | Wäckers and van Rijn, 2012 |
| Corn flower | *Centaurea cyanus* L. | Syrphids | *Episyrphus balteatus* (De Geer) | Wäckers and van Rijn, 2012 |
| False yellowhead | *Dittrichia (= Inula) viscosa* L. | Mirids | *Macrolophus melanotoma* Costa; *Macrolophus pygmaeus* Rambur; *Nesidiocoris tenuis* (Reuter) | Vila, 2004; Perdikis et al., 2007; Cano et al., 2012 |
| Feverfew | *Tanacetum parthenium L.* | Anthocorids | *Orius insidiosus* Say | Waite, 2012; Waite et al., 2014 |
| Field Marigold | *Calendula arvensis* L. | Mirids | *Nesidiocoris tenuis* (Reuter) | Vila, 2004 |
| Floss flower | *Ageratum mexicanum* Sims | Predatory mites | Several predatory mite species | Huang et al., 2011 |
| French marigold | *Tagetes patula* L. | Anthocorids | *Orius* spp. | Imura and Kamikawa, 2012 |
| Geranium | *Geranium* sp. | Mirids | *Nesidiocoris tenuis* (Reuter) | Vila, 2004; Cano et al., 2012 |
| Gerbera daisy | *Gerbera jamesonii* L. "Festival" | Anthocorids | *Orius insidiosus* Say | Waite, 2012, Waite et al., 2014 |
| Golden Crownbeard | *Verbesina encelioides* Benth and Hook | Anthocorids | *Orius laevigatus* (Fieber) | Armando and Yates, 2011 |

*(Continued)*

**TABLE 4 |** Continued

| Banker plant (common name) | Banker plant (Latin name) | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|
| Great basil | *Ocimun basilicum* L. | Anthocorids | *Orius laevigatus* (Fieber) | Cano et al., 2012 |
| Gypsophila | *Gypsophila elegans* M. Bieb. | Chrysopids | *Chrysoperla carnea* (Stephens) | Wäckers and van Rijn, 2012 |
| Gypsophila | *Gypsophila elegans* M. Bieb. | Syrphids | *Episyrphus balteatus* (De Geer) | Wäckers and van Rijn, 2012 |
| Hidalgo Stachys | *Stachys albotomentosa* L. | Mirids | *Dicyphus hesperus* Knight | Sanchez et al., 2004 |
| Kale | *Brassica oleracea* L. var. Acephala | Parasitoids | *Diadegma insulare* (Cresson) | Gourdine et al., 2003 |
| Lance-leaf Coreopsis | *Coreopsis lanceolata* L. | Anthocorids | *Orius laevigatus* (Fieber) | Armando and Yates, 2011 |
| Male trees of blush macaraga | *Macaranga tanarius* Müll. Arg | Anthocorids | *Orius laevigatus* (Fieber) | Armando and Yates, 2011 |
| Marigold | *Tagetes patula L. "Lemon Gem'* | Anthocorids | *Orius insidiosus* Say | Waite, 2012; Waite et al., 2014 |
| Mint | *Mentha* sp. | Mirids | *Nesidiocoris tenuis* (Reuter) | Vila, 2004 |
| Mullein | *Verbascum thapsus* L. | Anthocorids | *Orius insidiosus* Say | Miller et al., 2017 |
| Mullein | *Verbascum thapsus* L. | Mirids | *Dicyphus hesperus* Knight | Matteoni, 2003; Sanchez et al., 2003, 2004; Lambert et al., 2005; Gillespie et al., 2012; Nguyen-Dang et al., 2016; Miller et al., 2017 |
| Mustard | *Brassica juncea* L. | Syrphids | Several hoverflies species | Colley and Luna, 2000 |
| Ornamental pepper | *Capsicum annuum* L. "Black Pearl," "Purple Flash" | Anthocorids | *Orius insidiosus* Say | Valentin, 2011; Wong and Frank, 2012, 2013; Brownbridge et al., 2013; Waite et al., 2014; Miller et al., 2017 |
| Ornamental pepper | *Capsicum annuum* L. "Masquerade," "Red Missile," "Explosive Ember," "Balck pearl" | Predatory mites | *Amblyseius andersoni* (Chant); *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans); *Amblyseius swirskii* (Athias-Henriot) | Popenoe and Osborne, 2010; Xiao et al., 2012; Avery et al., 2014; Kumar et al., 2014, 2015; Miller et al., 2017; Miller, 2018 |
| Parasol leaf tree | *Macaranga tanarius* L. | Anthocorids | *Orius* spp. | Calvert et al., 2019 |
| Parsnip | *Pastinaca sativa* L. | Chrysopids | *Chrysoperla carnea* (Stephens) | Wäckers and van Rijn, 2012 |
| Parsnip | *Pastinaca sativa* L. | Syrphids | *Episyrphus balteatus* (De Geer) | Wäckers and van Rijn, 2012 |
| Phacelia | *Phacelia tanacetifolia* Benth. | Syrphids | Several hoverflies species | Wnuk and Wojciechowicz-Zytko, 2007; Wojciechowicz-Zytko and Wnuk, 2012 |
| Perennial alyssum | *Aurinia saxitalis* L. | Syrphids | Several hoverflies species | Colley and Luna, 2000 |
| Pot marigold | *Calendula officinalis* L. | Anthocorids | *Orius sauteri* (Poppius) | Zhao et al., 2017 |
| Pot marigold | *Calendula officinalis* L. | Syrphids | Several hoverflies species | Colley and Luna, 2000 |
| Sage-leaved rock-rose | *Cistus salviifolius* L. | Mirids | *Nesidiocoris tenuis* (Reuter) | Vila, 2004 |
| Sesame | *Sesamum indicum L.* | Mirids | *Nesidiocoris tenuis* (Reuter) | Nakaishi et al., 2011; Biondi et al., 2016 |
| Sowthistle | *Sonchus* spp. | Anthocorids | *Orius* spp. | Ferragut and González-Zamora, 1994 |
| Spanish lupine | *Lupinus hispanicus* (Boiss and Reuter) | Anthocorids | *Orius majusculus* (Reuter) | Alomar et al., 2006 |
| Sunflower | *Helianthus annuus* L. "Choco sun" | Anthocorids | *Orius insidiosus* Say | Waite, 2012; Waite et al., 2014 |
| Sunflower | *Helianthus annus* L. | Chrysopids | *Chrysoperla carnea* (Stephens) | Wäckers and van Rijn, 2012 |
| Sunflower | *Helianthus annus* L. | Syrphids | *Episyrphus balteatus* (De Geer) | Wäckers and van Rijn, 2012 |

*(Continued)*

**TABLE 4 |** Continued

| Banker plant (common name) | Banker plant (Latin name) | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|
| Sweet alyssum | *Lobularia maritima* (L.) Desv. | Anthocorids | *Orius* spp.; *Orius laevigatus* (Fieber); *Orius majusculus* (Reuter) | Picó and Retana, 2000; Alomar et al., 2008; Bennison et al., 2011; Hogg et al., 2011; Pumariño and Alomar, 2012, 2014 |
| Sweet alyssum | *Lobularia maritima* (L.) Desv. | Parasitoids | *Dolichogenidea tasmanica* (Cameron) | Berndt and Wratten, 2005 |
| Sweet alyssum | *Lobularia maritima* (L.) Desv. | Syrphids | Several hoverflies species, *Eupeodes fumipennis* (Thomson) | Colley and Luna, 2000; Pineda and Marcos-García, 2008; Hogg et al., 2011 |
| Sweet alyssum | *Lobularia maritima* (L.) Desv. | Parasitoids | Several parasitoids, *Cotesia marginiventris* (Cresson); *Diadegma insulare* (Cresson); *Trissolcus* spp.; *Gyron obesum* Masner | Johanowicz and Mitchell, 2000; Berndt and Wratten, 2005; Begum et al., 2006; Pease and Zalom, 2010 |
| Sweet pepper | *Capsicum annuum* L. | Anthocorids | *Orius laevigatus* (Fieber) | Van den Meiracker and Ramakers, 1991 |
| Tamarillo | *Cyphomandra betacea* (Cav.) Sendtn. | Mirids | *Macrolophus pygmaeus* Rambur | Fischer and Terrettaz, 2003 |
| Tobacco | *Nicotiana tabacum* L. | Mirids | *Dicyphus hesperus Knight; Macrolophus pygmaeus* Rambur | Arnó et al., 2000; Ridray et al., 2001; Fischer, 2003; Fischer and Terrettaz, 2003; Schoen, 2003; Sanchez et al., 2004; Bresch et al., 2014 |
| Tree marigold | *Tithonia diversifolia* (Hemsl.) | Anthocorids | *Orius laevigatus* (Fieber) | Armando and Yates, 2011 |
| Vetch | *Vicia sativa* L. | Anthocorids | *Orius majusculus* (Reuter) | Alomar et al., 2006 |
| Vetch | *Vicia sativa* L. | Parasitoids | Several species | Wäckers and van Rijn, 2012 |
| Vetch | *Vicia sativa* L. | Syrphids | *Episyrphus balteatus* (De Geer) | Wäckers and van Rijn, 2012 |
| White rocket | *Diplotaxis erucoides* L. | Anthocorids | *Orius* spp. | Ferragut and González-Zamora, 1994 |
| Wild carrot | *Daucus carota* L. | Parasitoids | *Diadegma insulare* (Cresson) | Idris and Grafius, 1995, 1996; Johanowicz and Mitchell, 2000 |
| Wild carrot | *Daucus carota* L. | Chrysopids | *Chrysoperla carnea* (Stephens) | Wäckers and van Rijn, 2012 |
| Wild mustard | *Brassica kaber* L. | Parasitoids | *Diadegma insulare* (Cresson) | Idris and Grafius, 1995, 1996; Johanowicz and Mitchell, 2000 |
| Yellow rocket | *Barbarea vulgaris* R. Br. | Parasitoids | *Diadegma insulare* (Cresson) | Idris and Grafius, 1995, 1996 |

were scarce (Ramakers and Voet, 1995). However, this banker plant requires a lot of maintenance due to its rapid growth and the predatory mites do not always move into the crop. Additionally, castor bean can become a source of certain pests. The usefulness of castor bean plants was also limited in sweet pepper crops, as pepper produces pollen and floral nectar. Only a limited number of ornamental growers is still using castor bean plants. Many banker plant systems were developed to maintain predatory bugs, especially the anthocorid *Orius* spp., primarily used for the control of thrips. Establishing this predator requires prey, and a range of plant derived food, including pollen (Kiman and Yeargan, 1985; Richards and Schmidt, 1996; Corey et al., 1998), nectar (Yokoyama, 1978), and plant sap (Kiman and Yeargan, 1985; Richards and Schmidt, 1996; Lundgren et al., 2008). In addition, the plant structures need to be acceptable as oviposition substrate (Lundgren et al., 2008). The predator establishes easily in sweet pepper crops where it utilizes the floral resources of the pepper plants. However, most ornamental crops lack these resources. This hampers establishment of beneficials as well as the short crop cycle of many ornamentals. As repeated introductions of *Orius* spp. are too onerous and expensive for growers, a range of banker plant systems have been designed to support establishment of the predator. Several studies have used ornamental peppers "Black pearl" or "Purple Flash" and the perennial Sweet Alyssum (Valentin, 2011; Wong and Frank, 2013). The use of Sweet Alyssum with its long lasting flowering period results not only in higher densities of *Orius* spp. (Picó and Retana, 2000; Alomar et al., 2008; Bennison et al., 2011; Hogg et al., 2011; Pumariño and Alomar, 2014), but also benefits hoverflies, predatory Heteroptera (Pease and Zalom, 2010) and several parasitoids (Johanowicz and Mitchell, 2000; Berndt and Wratten, 2005; Begum et al., 2006). However, the adoption of this method has been limited due to the fact that Sweet Alyssum is also exploited by pollen-feeding pest species, such as thrips. Several banker plant systems have also been designed to attract and sustain reproductive populations of predatory mirids. These include tobacco plants for *M. pygmaeus*, mullen for *Dicyphus hesperus* Knight and sesame for *N. tenuis* (**Table 4**). Fischer and Terrettaz (2003) managed even to successfully overwinter *M. caliginosus* on tobacco and tamarillo as banker plants, thus allowing the establishment of the predatory bug into the new tomato crops the next spring. Other examples of banker plant systems maintaining predatory bugs are summarized in **Table 4**. Addition of factitious prey on banker plants, as discussed earlier, is often suggested to increase survival, longevity and fecundity of the predatory bugs (Pumariño and Alomar, 2012, 2014).

The complexity of banker plant systems in greenhouse crops limited their adoption. Since the last decade, more straightforward methods have been developed to support the establishment and retention of beneficials in greenhouse. However, some sweet pepper growers still use them against aphids before the appearance of hyperparasitoids and there is an increased interest for banker plants to maintain predatory bugs in ornamental crops. Few attempts were made to use cover crops in or next to greenhouses and to grow combined crops, alternating rows of tomato, sweet pepper and egg plants in one greenhouse (Janmaat et al., 2014) to benefit from the vegetational diversity (Letourneau, 1983, 1990). Despite good technical results, these strategies failed in practice because of the complexity of their management. In open fields, we recently see an increased interest for the use of banker plant systems.

## POLLEN

Providing pollen as a protein rich food in crops is another approach to boost establishment of pollen-feeding natural enemies, especially predatory mites. Pollen has been used extensively to support populations of generalist predatory mites (McMurtry and Scriven, 1966; Kennett et al., 1979; Van Rijn and Sabelis, 1990, 1993; Van Rijn and Tanigoshi, 1999a; Messelink et al., 2009; Nomikou et al., 2010; Hoogerbrugge et al., 2011; Maoz et al., 2014; Ranabhat et al., 2014, Vangansbeke et al., 2016a).

In greenhouse crops, bee-collected pollen has been tested in a number of studies, either as dry pellets or in suspension (Ramakers, 1995; Kolokytha et al., 2011; Goleva and Zebitz, 2013; Montserrat et al., 2013; Duarte et al., 2015). However, as the grains absorb water and become moldy, bee pollen was judged inappropriate by growers for crop applications (Ramakers, 1995). Attempts of using pollen providing banker plant systems, like castor beans (Ramakers and Voet, 1995; Van Rijn and Tanigoshi, 1999b), also failed, for reasons described previously. Pollen started to be used on a large scale by growers in July 2013, when commercial supplements based on narrowleaf cattail pollen were made available for crops where pollen sources are lacking (Pijnakker et al., 2014). This allowed preventative establishment of predatory mites in crops like cucumbers (which are parthenocarp and do not produce pollen), as well as ornamentals where no pests are tolerated.

Pollen can provide proteins, free amino acids, lipids, and phytosterols, nitrogen, carbohydrates, vitamins, and other inorganic minerals for many arthropods (Goss, 1968; Standifer et al., 1968; Stanley and Linskens, 1974; Rabie et al., 1983; Day et al., 1990; Roulston and Cane, 2000; Patt et al., 2003; Somerville and Nicol, 2006; Li et al., 2007; You et al., 2007; Campos et al., 2008; Lundgren, 2009). Pollen supports development, survival, and longevity of a range of natural enemies (Fauvel, 1974; Overmeer, 1985; Wäckers and van Rijn, 2005). Many studies (**Table 5**) show that several natural enemies are capable of reproducing and developing solely on pollen or in combination with other plant material in the absence of prey (Cocuzza et al., 1997; Beckman and Hurd, 2003; Berkvens et al., 2007; Carrillo et al., 2010). Among many studies on predatory mites, Onzo et al. (2005) showed increased survival and longevity of predatory mites when corn pollen was supplemented to the prey diet. Cloutier and Johnson (1993) and Buitenhuis et al. (2014) suggested that pollen feeding can benefit juvenile stages of predatory mites, since it is more difficult for them to attack thrips larvae, which usually show aggressive defensive behavior (Bakker and Sabelis, 1989). The nutritional value of the pollen depends on the pollen type (Todd and Bretherick, 1942; Saito and Mori, 1975; Van Rijn and Tanigoshi, 1999a; Goleva and Zebitz, 2013) and can differ between pollen consumers (Van Rijn and Tanigoshi, 1999a; Delisle et al., 2015a,b). Lundgren and Wiedenmann (2004) demonstrated that pollen quality can also vary within a given plant species. Van Rijn and Tanigoshi (1999a) showed the benefits of feeding on different pollen for predatory mites in the absence of prey. Pollen of Betulaceae, Euphorbiaceae, Leguminosae, Rosaceae, and Typhaceae seem, in general, to be suitable food sources for predatory mites (**Table 5**). The variations in nutritional value of pollen can be partly explained by the differences in the content of amino acids and lipids of pollen (Stanley and Linskens, 1974, Wäckers, 2005; Goleva and Zebitz, 2013). Also, pollen may contain secondary metabolites, that can reduce their suitability as food sources for arthropods (Rivest and Forrest, 2020); some types of pollen can even be toxic (Ranabhat et al., 2014; Goleva et al., 2015; Rivest and Forrest, 2020). In addition to variation in pollen nutrient composition, differences exist between natural enemies in their utilization of pollen from different plant species (McMurtry and Scriven, 1964; Van Rijn and Tanigoshi, 1999a; Adar et al., 2012). Part of this variation can be explained by the degree in which the phytoseiids have adapted to pollen feeding. While some predatory mites are specialized pollen feeders; others use it to complement their diet, while some specialist predators like *Phytoseiulus* do not consume pollen (McMurtry and Croft, 1997). Van Rijn and Tanigoshi (1999a) showed that *I. degenerans* could develop and reproduce on Betulaceae pollens whereas N. cucumeris failed to do so. Both predatory species did not perform on pollen from the conifer Pinopsida, but reproduced well on common cattail pollen. Goleva and Zebitz (2013) suggested that the morphology of the different pollens and their odor (Dobson and Bergström, 2000) are likely to influence their acceptance as food by a predator. Among insects, the coccinellids *Coleomegilla maculata* (DeGeer) and *Harmonia axyridis* (Pallas) use pollen as a supplemental food, allowing the ladybugs to survive during prey scarcity (Smith, 1960a,b; Koch, 2003; Lundgren and Wiedenmann, 2004; Lundgren et al., 2005; Michaud and Grant, 2005; Berkvens et al., 2007; Hodek and Honěk, 2013). The predatory bug *Orius* spp. has been frequently shown to be able to reproduce and develop on a sole diet of specific pollen (Fauvel, 1974; Naranjo and Gibson,

**TABLE 5 |** Examples of suitable pollen types.

| Plant (common name) | Plant (Latin name) | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|
| African oil palm | *Elaeis guinensis* Jacq. | Predatory mites | *Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma | Ferreira et al., 2020 |
| Alfafa | *Medicago sativa* L. | Predatory mites | *Euseius scutalis* (Athias-Henriot) | Al-Shammery, 2011 |
| Almond | *Prunus amygdalis* Batsch; *Prunus dulcis* (Mill.) D. | Predatory mites | *Iphiseius degenerans* (Berlese); *Euseius stipulatus* (Athias-Henriot); *Euseius tularensis* (Congdon); *Neoseiulus californicus* (McGregor); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman | Ouyang et al., 1992; Van Rijn and Tanigoshi, 1999a; Bouras and Papadoulis, 2005; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011; Khanamani et al., 2017 |
| Amazonian palm | *Euterpe oleracea* Mart. | Predatory mites | *Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma | Ferreira et al., 2020 |
| Aninga | *Montrichardia linifera* (Arr.) Schott | Predatory mites | *Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma | Ferreira et al., 2020 |
| Annual mercury | *Mercurialis annua* L. | Predatory mites | *Typhlodromus pyri* (Sheuten) | Engel and Ohnesorge, 1994 |
| Apple | *Malus domestica* L.; *Malus sylvestris* Mill. | Predatory mites | *Amblyseius swirskii* (Athias-Henriot); *Euseius finlandicus* Oudemans; *Euseius tularensis* (Congdon); *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman | Ouyang et al., 1992; Van Rijn and Tanigoshi, 1999a; Broufas and Koveos, 2000; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011; Delisle et al., 2015a,b |
| Apricot | *Prunus armeniaca* L. | Predatory mites | *Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Euseius finlandicus* Oudemans; *Euseius stipulatus* (Athias-Henriot); *Neoseiulus californicus* (McGregor); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman | Van Rijn and Tanigoshi, 1999a; Broufas and Koveos, 2000; Bouras and Papadoulis, 2005; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011; Fadaei et al., 2018; Soltaniyan et al., 2018 |
| Avocado | *Persea americana* Mill. | Predatory mites | *Euseius hibisci* (Chant) | McMurtry and Scriven, 1964 |
| Bermuda buttercup | *Oxalis pes-caprae* L.; *Oxalis* sp. | Predatory mites | *Typhlodromus pyri* (Sheuten); *Cydnodromus picanus* Ragusa | Ragusa et al., 2000; Bermúdez et al., 2010 |
| Betulaceous plants (e.g., alder, birch and hazel) | *Alnus incana* (L.) Muench; *Betula pubescens* Ehrh., *Betula pendula* Roth.; *Carpinus betulus* L., *Corylus avellana* L.; *Corylus americana* Marsh.; *Alnus rubra* Bong.; *Turnera ulmifolia* L. | Predatory mites | *Amblydromalus limonicus* (Garman and McGregor); *Amblyseius andersoni* Chant; *Amblyseius largoensis* (Muma); *Amblyseius swirskii* (Athias-Henriot); *Euseius addoensis* (Van der Merwe and Rijke); *Euseius finlandicus* (Oudemans); *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus pyri* (Scheuten) | Saito and Mori, 1975; Overmeer, 1981; Englert and Maixner, 1988; Grout and Richards, 1992; Engel and Ohnesorge, 1994; Kostiainen and Hoy, 1994; Schausberger, 1997; Van Rijn and Tanigoshi, 1999a; Addison et al., 2000; Goleva et al., 2015; Ferreira et al., 2020 |
| Bitter melon | *Momordica charantia* L. | Anthocorids | *Orius sauteri* (Poppius) | Zhou and Wang, 1989 |
| Brazilian oil palm | *Elaeis oleifera* Cort. | Predatory mites | *Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma | Ferreira et al., 2020 |
| Broad bean | *Vicia fabae* L. | Predatory mites | *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans) | Van Rijn and Sabelis, 1990; Van Rijn and Tanigoshi, 1999a; Nomikou et al., 2001 |
| Castor bean | *Ricinus communis* L. | Predatory mites | *Amblyseius gossypi* Elbadry; *Amblyseius herbicolus* (Banks); *Amblyseius idaeus* (Denmark and Muma); *Amblyseius largoensis* (Muma); *Amblyseius zaheri* Yousef and El-Borolossy; *Euseius hibisci* (Chant); *Euseius mesembrinus* (Dean); *Euseius scutalis* (Athias-Henriot); *Euseius tularensis* (Congdon); *Euseius yousefi* Zaher and El-Borolossy; *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans); *Phytoseius plumifer* (Canestrini and Fanzago); *Typhlodromalus aripo* DeLeon; *Typhlodromus negevi* Swirski and Amitai; *Typhlodromus pyri* Scheuten | Dosse, 1961; McMurtry and Scriven, 1964; McMurtry and Johnson, 1965; Rasmy and El-Banhawy, 1975; Momen and El-Saway, 1993; Tanigoshi et al., 1993; Yue et al., 1994; Ramakers and Voet, 1995; Yue and Tsai, 1996; Van Rijn and Tanigoshi, 1999a; Van Rijn et al., 2002; Momen, 2004; Gnanvossou et al., 2005; Skirvin et al., 2006; Momen et al., 2009; Al-Shammery, 2011; Rodríguez-Cruz et al., 2013 |
| Cat grass | *Dactylis glomerata* L. | Predatory mites | *Typhlodromus pyri* (Sheuten) | Engel and Ohnesorge, 1994 |

*(Continued)*

**TABLE 5 |** Continued

| Plant (common name) | Plant (Latin name) | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|
| Cattail | *Typha* spp.*: Typha angustifolia* L.; *Typha domingensis* Pers.; *Typha latifolia* L.; *Typha orientalis* Presl. | Predatory mites | *Amblydromalus limonicus* (Garman and McGregor); *Amblyseius andersoni* Chant; *Amblyseius herbicolus* (Banks); *Amblyseius largoensis* (Muma); *Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Euseius concordis* (Chant); *Euseius finlandicus* (Oudemans); *Euseius gallicus* (KreiterandTixier), *Euseius hibisci* (Chant); *Euseius ovalis* (Evans); *Euseius stipulatus* (Athias-Henriot); *Euseius mesembrinus* (Dean); *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans); *Proprioseiopsis asetus* Muma; *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa | Kennett et al., 1979; Ouyang et al., 1992; Kostiainen and Hoy, 1994; Yue et al., 1994; Yue and Tsai, 1996; Van Rijn et al., 1999; Nomikou et al., 2002; Nomikou, 2003; Emmert et al., 2008; Messelink et al., 2008; Park et al., 2010, 2011; Tuovinen and Lindqvist, 2010; Kolokytha et al., 2011; Goleva and Zebitz, 2013; Nguyen et al., 2013, 2014a,b; Pijnakker et al., 2014, 2016; Vangansbeke et al., 2014a, 2016a; Nguyen et al., 2015; Duarte et al., 2015; Leman and Messelink, 2015; Samaras et al., 2015; Massaro et al., 2016; Beltrà et al., 2017; Liu and Zhang, 2017; Muñoz-Cárdenas et al., 2017; De Figueiredo et al., 2018; Liu et al., 2019; Ferreira et al., 2020; Pascua et al., 2020 |
| Cherry (sweet) | *Prunus avium* L. | Predatory mites | *Iphiseius degenerans* (Berlese); *Euseius concordis* (Chant); *Euseius finlandicus* Oudemans; *Euseius stipulatus* (Athias-Henriot); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman | Van Rijn and Tanigoshi, 1999a; Broufas and Koveos, 2000; Bouras and Papadoulis, 2005; Papadopoulos and Papadoulis, 2008 |
| Chili pepper | *Capsicum frutescens* L. | Predatory mites | *Amblyseius herbicolus* (Banks) | Duarte et al., 2015 |
| China rose | *Rosa chinensis* Rehder and Wils. | Anthocorids | *Orius sauteri* (Poppius) | Zhou and Wang, 1989 |
| Coconut | *Cocos nucifera* L. | Predatory mites | *Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma; *Neoseiulus paspalivorus* DeLeon; *Proctolaelaps bickleyi* Bram | Lawson-Balagbo et al., 2007; Ferreira et al., 2020 |
| Common henbit | *Lamium amplexicaule* L. | Predatory mites | *Neoseiulus californicus* (McGregor) | Gugole Ottaviano et al., 2015 |
| Common meadow-grass | *Poa pratensis* L. | Predatory mites | *Typhlodromus pyri* (Sheuten) | Engel and Ohnesorge, 1994 |
| Common mugwort | *Artemisia vulgaris* L. | Predatory mites | *Typhlodromus pyri* (Sheuten) | Engel and Ohnesorge, 1994 |
| Common sowthistle | *Sonchus oleraceous* L. | Predatory mites | *Neoseiulus californicus* (McGregor) | Gugole Ottaviano et al., 2015 |
| Common wild poppy | *Papaver rhoeas* L. | Predatory mites | *Euseius finlandicus* Oudemans | Broufas and Koveos, 2000 |
| Corn | *Zea mays* L. | Anthocorids | *Orius insidiosus* (Say); *Orius sauteri* (Poppius) | Richards, 1992; Funao and Yoshiyasu, 1995; Richards and Schmidt, 1995 |
| Corn | *Zea mays* L. | Coccinellids | *Coleomegilla maculata* (De Geer) | Smith, 1960a,b; Hodek et al., 1978; Lundgren and Wiedenmann, 2004; Lundgren et al., 2005; Michaud and Grant, 2005 |
| Corn | *Zea mays* L. | Predatory mites | *Amblydromalus limonicus* (Garman and McGregor)*; Amblyseius swirskii* (Athias-Henriot); *Euseius concordis* Chant; *Euseius hibisci* (Chant); *Euseius fustis* Pritchard and Baker; *Euseius scutalis* (Athias-Henriot); *Iphiseiodes zuluagai* Denmark and Muma; *Neoseiulus barkeri* Hugues; *Neoseiulus californicus* (McGregor); *Phytoseius plumifer* (Canestrini and Fanzago); *Typhlodromalus aripo* DeLeon; *Typhlodromalus manihoti* Moraes; *Typhlodromus pyri* Scheuten | McMurtry and Scriven, 1964; Engel and Ohnesorge, 1994; Gnanvossou et al., 2005; Weintraub et al., 2009; Onzo et al., 2012; Saber, 2012, 2013; Goleva and Zebitz, 2013; Khodayari et al., 2013; Adar et al., 2014; Vieira Marques et al., 2014; Leman and Messelink, 2015; Samaras et al., 2015; Palevsky, 2016; Rezaie and Askarieh, 2016; Khanamani et al., 2017; Rezaie, 2017 |
| Corn | *Zea mays* L. | Trichogrammatids | *Trichogramma brassicae* Bezdenko | Zhang et al., 2004 |

*(Continued)*

**TABLE 5** | Continued

| Plant (common name) | Plant (Latin name) | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|
| Date palm | *Phoenyx dactylifera* L. | Predatory mites | *Amblyseius swirskii* (Athias-Henriot); *Euseius scutalis* (Athias-Henriot); *Neoseiulus barkeri* Hugues; *Neoseiulus californicus* (McGregor); *Proprioseiopsis asetus* (Chant) | Fouly, 1997; Al-Shammery, 2011; Abou-Elella et al., 2013; Rezaie and Askarieh, 2016; Rezaie, 2017 |
| Echinocereus | *Echinocereus* sp. | Predatory mites | *Amblyseius swirskii* (Athias-Henriot) | Goleva and Zebitz, 2013 |
| Eucalyptus | *Eucalyptus* spp. | Predatory mites | *Euseius hibisci* (Chant) | McMurtry and Scriven, 1964 |
| False oat-grass | *Arrhenatherum elatius* L. | Predatory mites | *Typhlodromus pyri* (Sheuten) | Engel and Ohnesorge, 1994 |
| Field bindweed | *Convolvulus arvensis* L. | Predatory mites | *Neoseiulus californicus* (McGregor) | Gugole Ottaviano et al., 2015 |
| Fireweed | *Epilobium angustifolium* L. | Predatory mites | *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans) | Van Rijn and Tanigoshi, 1999a |
| Foxglove-tree | *Paulownia tomentosa* Steud. | Predatory mites | *Amblyseius swirskii* (Athias-Henriot) | Goleva and Zebitz, 2013 |
| Galega | *Galega officinalis* L. | Predatory mites | *Neoseiulus californicus* (McGregor) | Gugole Ottaviano et al., 2015 |
| Hazel | *Corylus avellana* L. | Coccinellids | *Adalia bipunctata* L. | Blackman, 1967 |
| Henbit dead-nettle | *Lamium amplexicaule* L. | Predatory mites | *Neoseiulus californicus* (McGregor) | Gugole Ottaviano et al., 2015 |
| Hoary mustard | *Hirschfeldia incana* (L.) Lagr.-Foss. | Predatory mites | *Typhlodromus pyri* (Sheuten) | Bermúdez et al., 2010 |
| Honey bee pollen | different plants | Anthocorids | *Orius laevigatus* (Fieber); *Orius albidipennis* (Reuter) | Cocuzza et al., 1997 |
| Honey bee pollen | (mainly Brassicaceae+Verbascum spp.) | Coccinellids | *Harmonia axyridis* (Pallas) | Berkvens et al., 2007 |
| Horse-chestnut | *Aesculus hippocastanum* L. | Predatory mites | *Amblydromalus limonicus* (Garman and McGregor); *Amblyseius swirskii* (Athias-Henriot); *Neoseiulus cucumeris* (Oudemans) | Goleva and Zebitz, 2013; Ranabhat et al., 2014; Goleva et al., 2015 |
| Ice plant | *Carpobrotus edulis* (L.); *Malephora crocea* (Jacq.); *Mesembrianthemum* sp. | Predatory mites | *Amblyseius similoides* Buchelos and Pritchard; *Cydnodromus californicus* (McGregor); *Euseius hibisci* (Chant); *Euseius mesembrinus* (Dean); *Euseius stipulatus* (Athias-Henriot); *Euseius tularensis* (Congdon); *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus exhilaratus* Ragusa; *Typhlodromus phialatus* Athias-Henriot | McMurtry and Scriven, 1964, 1966; Ferragut et al., 1987; Van Rijn and Sabelis, 1990; Castagnoli and Liguori, 1991; Flechtmann and McMurtry, 1992; Ouyang et al., 1992; Yue et al., 1994; Van Rijn et al., 2002; Villanueva and Childers, 2004; Ragusa et al., 2009; Pina et al., 2012 |
| Maple (honey bee pollen) | *Acer* spp. | Anthocorids | *Orius insidiosus* (Say) | Kiman and Yeargan, 1985 |
| Meadow foxtail | *Alopecurus pratensis* L. | Predatory mites | *Typhlodromus pyri* (Sheuten) | Engel and Ohnesorge, 1994 |
| Nettle-leaved Figwort | *Scrophularia peregrina* L. | Predatory mites | *Cydnodromus californicus* (McGregor) | Ragusa et al., 2009 |
| Norway spruce | *Picea abies* L. | Predatory mites | *Typhlodromus pyri* (Sheuten) | Engel and Ohnesorge, 1994 |
| Oak | *Quercus* spp.: *Quercus agrifolia* Nee., *Quercus ilex* L.; *Quercus ithaburensis* L.; *Quercus virginiana* Mill.; *Quercus macranthera* Fisch. and Mey; *Quercus robur* L. | Predatory mites | *Amblyseius andersoni* (Chant); *Amblyseius herbicolus* (Chant); *Amblyseius largoensis* (Muma); *Amblyseius swirskii* (Athias-Henriot); *Euseius hibisci* (chant); *Euseius mesembrinus* (Dean); *Euseius scutalis* (Athias-Henriot); *Euseius tularensis* (Congdon); *Metaseiulus occidentalis* (Nesbitt); *Neoseiulus barkeri* Hugues; *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans); *Neoseiulus longispinosus* (Evans); *Neoseiulus paraki* (Ehara); *Typhlodromus cryptus* Athias-Henriot; *Typhlodromus exhilaratus* Ragusa; *Typhlodromus pyri* (Sheuten) | McMurtry and Scriven, 1964; Swirski, 1967; Calvert and Huffaker, 1974; Saito and Mori, 1975 Castagnoli and Liguori, 1986; Duso and Camporese, 1991; Ouyang et al., 1992; Engel and Ohnesorge, 1994; Yue et al., 1994; Hodek and Honěk, 1996; Yue and Tsai, 1996; Castagnoli and Simoni, 1999; Preverieri et al., 2006; Carrillo et al., 2010; Adar et al., 2014; Goleva et al., 2015 |
| Oak | *Quercus* spp. | Coccinellids | *Adalia bipunctata; Harmonia axyridis* (Pallas) | Hodek and Honěk, 1996; Koch, 2003 |

*(Continued)*

**TABLE 5 |** Continued

| Plant (common name) | Plant (Latin name) | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|
| Oil palm | *Elaeis guineensis* Jacq. | Predatory mites | *Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma | Ferreira et al., 2020 |
| Olive | *Olea europaea* L. | Predatory mites | *Amblydromalus limonicus* (Garman and McGregor); *Amblyseius swirskii* (Athias-Henriot); *Euseius tularensis* (Congdon); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Neoseiulus cucumeris* (Oudemans) | Ouyang et al., 1992; Matsuo et al., 2003; Kolokytha et al., 2011; Kumar et al., 2014; Samaras et al., 2015 |
| Passion fruit | *Passiflora edulis* Sims | Predatory mites | *Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma | Ferreira et al., 2020 |
| Peach | *Prunus persica* L. | Predatory mites | *Euseius tularensis* (Congdon) | Ouyang et al., 1992 |
| Pear | *Pyrus communis* L. | Predatory mites | *Iphiseius degenerans* (Berlese); *Euseius finlandicus* Oudemans; *Euseius tularensis* (Congdon); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman | Ouyang et al., 1992; Van Rijn and Tanigoshi, 1999a; Broufas and Koveos, 2000; Matsuo et al., 2003; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011 |
| *Peltaea riedelii* | *Peltaea riedelii* (Gürke) Standl. | Predatory mites | *Iphiseiodes zuluagai* Denmark and Muma; *Euseius concordis* Chant | Vieira Marques et al., 2014 |
| Pine (black, turkish, calabrian) | *Pinus* sp.; *Pinus brutia* Ten.; *Pinus nigra* L. | Predatory mites | *Amblydromalus limonicus* (Garman and McGregor); *Amblyseius swirskii* (Athias-Henriot); *Iphiseius degenerans* (Berlese); *Neoseiulus cucumeris* (Oudemans); *Typhlodromus pyri* (Sheuten) | Engel and Ohnesorge, 1994; Van Rijn and Tanigoshi, 1999a; Samaras et al., 2015; Kütük, 2018 |
| Pistachio | *Pistachio vera* L. | Predatory mites | *Neoseiulus californicus* (McGregor) | Soltaniyan et al., 2018 |
| Plum | *Prunus domestica* L. | Predatory mites | *Euseius stipulatus* (Athias-Henriot); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudeman | Bouras and Papadoulis, 2005; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011 |
| Pygmy date palm | *Phoenix roebelenii* O'Brien | Predatory mites | *Amblyseius largoensis* (Muma) | Yue and Tsai, 1996 |
| Small nettle | *Urtica urens* L. | Predatory mites | *Neoseiulus californicus* (McGregor) | Gugole Ottaviano et al., 2015 |
| Sour orange | *Citrus aurantium* L. | Predatory mites | *Euseius scutalis* (Athias-Henriot) | Al-Shammery, 2011 |
| Spanish needle | *Bidens pilosa* L. | Predatory mites | *Euseius mesembrinus* (Dean) | Yue et al., 1994 |
| Spring crocus | *Crocus vernus* (L.) Hill | Predatory mites | *Amblyseius swirskii* (Athias-Henriot) | Goleva and Zebitz, 2013 |
| Squash | *Curcubita pepo* L. | Predatory mites | *Iphiseiodes zuluagai* Denmark and Muma; *Euseius concordis* Chant | Vieira Marques et al., 2014 |
| Strawberry | *Fragaria x ananassa* (West.) | Predatory mites | *Iphiseius degenerans* (Berlese); *Neoseiulus californicus* (McGregor); *Neoseiulus cucumeris* (Oudemans) | Van Rijn and Tanigoshi, 1999a; Shakya et al., 2009; Gugole Ottaviano et al., 2015 |
| Sunflower | *Helianthus annuus* L. | Predatory mites | *Amblyseius zaheri* Yousef and El-Borolossy*;* *Euseius yousefi* Zaher and El-Borolossy; *Iphiseius degenerans* (Berlese); *Neoseiulus barkeri* Hugues | Van Rijn and Tanigoshi, 1999a; Momen, 2004; Rezaie and Askarieh, 2016; Ferreira et al., 2020 |
| Sunnhemp | *Crotalaria juncea* L. | Predatory mites | *Amblyseius herbicolus* (Banks) | Rodríguez-Cruz et al., 2013 |
| Sweet orange | *Citrus sinensis* L. | Predatory mites | *Amblyseius aerialis* Muma; *Iphiseiodes zuluagai* Denmark and Muma | Ferreira et al., 2020 |
| Sweet pepper | *Capsicum annuum* L. cv. Mazurka | Anthocorids | *Orius albidipennis* Reuter; *Orius laevigatus* (Fieber) | Vacante et al., 1997 |
| Sweet pepper, ornamental pepper, peper | *Capiscum annum* L.; *Capsicum frutescens* L. | Predatory mites | *Amblyseius swirskii* (Athias-Henriot); *Euseius hibisci* (Chant); *Neoseiulus cucumeris* (Oudemans) | McMurtry and Scriven, 1964; Van Rijn and Sabelis, 1990; Kumar et al., 2014 |
| Tea | *Camellia sinensis* L. | Predatory mites | *Amblyseius sojaensis* Ehara; *Neoseiulus cucumeris* (Oudemans) | Osakabe et al., 1986; Matsuo et al., 2003 |
| Tulip | *Tulipa* sp.; *Tulipa gesneriana* L. | Predatory mites | *Neoseiulus cucumeris* (Oudemans); *Amblyseius swirskii* (Athias-Henriot) | Ranabhat et al., 2014; Goleva et al., 2015 |
| Turkish pine | *Pinus brutia* (Ten.) | Predatory mites | *Amblyseius swirskii* (Athias-Henriot) | Kütük and Yigit, 2011 |

*(Continued)*

**TABLE 5 |** Continued

| Plant (common name) | Plant (Latin name) | Category natural enemy | Natural enemy | Source |
|---|---|---|---|---|
| Walnut | *Juglans regia* L. | Predatory mites | *Amblyseius swirskii* (Athias-Henriot); *Euseius hibisci* (Chant); *Euseius finlandicus* Oudemans; *Neoseiulus barkeri* Hugues, *Neoseiulus californicus* (McGregor); *Typhlodromus (Anthoseius) athenas* Swirski and Ragusa; *Typhlodromus foenilis* Oudemans; *Typhlodromus pyri* (Sheuten) | McMurtry and Scriven, 1964; Engel and Ohnesorge, 1994 Broufas and Koveos, 2000; Papadopoulos and Papadoulis, 2008; Kolokytha et al., 2011; Rezaie and Askarieh, 2016; Rezaie, 2017; Fadaei et al., 2018 |
| Willow | *Salix* sp. | Coccinellids | *Adalia bipunctata* L. | Blackman, 1967 |

1996; Cocuzza et al., 1997; Coll, 1998; Lundgren, 2009). However, the development of *Orius* spp. was prolonged and reproduction and survival reduced on pollen only diet (Salas-Aguilar and Ehler, 1977; Kiman and Yeargan, 1985; Funao and Yoshiyasu, 1995; Richards and Schmidt, 1996; Cocuzza et al., 1997; Vacante et al., 1997,?). As with the phytoseiids, *Orius* performance is dependent on pollen type (Vacante et al., 1997). Pollen feeding also provides benefits for *M. pygmaeus* (Perdikis and Lykouressis, 2000; Vandekerkhove and De Clercq, 2010; Portillo et al., 2012; Put et al., 2012). Cattail pollen doubled the longevity of *M. pygmaeus* females compared to bugs provided only broad beans (Portillo et al., 2012) and promoted its establishment on tomato plants (Put et al., 2012). Also larvae of green lacewings can benefit from (bee) pollen (Patt et al., 2003). For syrphids, sexual maturation requires proteins that can be provided by pollen, allowing the females to mature successive batches of eggs (Schneider, 1948; Pineda and Marcos-García, 2008).

In biological control, pollen has been reported to support population densities of natural enemies when prey densities are low and improve control efficacy against pests. Most of these studies concern predatory mites. In the presence of pollen, predatory mites provided better control of phytophagous mites (McMurtry and Scriven, 1966; Kennett et al., 1979; Ferragut et al., 1987; Pina et al., 2012, 2015; Saber, 2013; Maoz et al., 2014; Duarte et al., 2015; Pijnakker et al., 2016), thrips (Ramakers, 1990; Van Rijn and Sabelis, 1993; Van Rijn et al., 1999) and whiteflies (Nomikou et al., 2001, 2002, 2010; Nomikou, 2003). Van Rijn et al. (1999) were the first to provide clear experimental evidence that supplementing pollen can be an efficient strategy to boost the biological control potential of predatory mites. By supplying the predatory mite species *A. limonicus* and *I. degenerans* with cattail pollen they were able to enhance population levels of the predatory mites, which resulted in increased thrips control and reduced plant damage. Kütük and Yigit (2011) succeeded in pre-establishing *A. swirskii* on sweet pepper by spraying suspensions of pine pollen, thereby maintaining *F. occidentalis*-numbers under the desired threshold. Provision of cattail or corn pollen increased densities of *A. swirskii* and improved thrips control on potted chrysanthemum (Leman and Messelink, 2015). Muñoz-Cárdenas et al. (2017) succeeded in establishing *A. swirskii* in roses before thrips release by weekly provision of cattail pollen and thus managed to realize a decrease of thrips numbers and damage. Nomikou et al. (2002, 2010) showed improved suppression of tobacco whitefly populations by *A. swirskii* on single cucumber plants treated with cattail pollen. Skirvin et al. (2006) achieved a higher density of *N. cucumeris* on chrysanthemum plants with an application of castor bean pollen. Still, it led to an increased infestation of western flower thrips, as only a few predatory mites were recovered. These examples give an idea of the potential of pollen as alternative food but the studies were often performed over short temporal scales and at pest densities higher than those found in commercial greenhouses. Since cattail pollen has been made commercially available in 2013, growers can now apply pollen as part of biocontrol programs. They typically apply pollen weekly (blown at 250 g/ha) or biweekly (at 500 g/ha) (Pijnakker et al., 2016). These dosages correspond to 2.5 to 20 mg per plant. Various devices are available to apply pollen to enhance the establishment of predatory mites on crops (Gan-Mor et al., 2003, 2011; Weintraub et al., 2009; Pijnakker et al., 2016). Other arguments in favor of the use of cattail pollen, next to its high nutritional value, are its low allergenic character (Weber and Nelson, 1985), its relatively low attractiveness to pests and poor nutritional suitability for thrips (Hulshof et al., 2003). The fact that cattail pollen is not attractive to (bumble) bees, means that it does not distract pollinators used in the crop (Schmidt et al., 1989).

However, the use of pollen can have some drawbacks as it can also benefit herbivores (Kirk, 1987; Van Rijn et al., 2002; Chitturi et al., 2006; Wäckers et al., 2007, Leman and Messelink, 2015; Vangansbeke et al., 2016b). Hulshof et al. (2003) showed at laboratory scale that *F. occidentalis* feeds on pollen, resulting in an enhancement of its growth rate and fecundity. Van Rijn et al. (2002), using simulation models, showed that availability of pollen benefits predators more than thrips and improved predator-prey ratios resulting in enhanced thrips control. This has since been repeatedly confirmed in studies showing the efficacy of the pollen supplementation at plant or crop level (see above). The high reproduction by *A. swirskii* on plants treated with pollen prevented the pest from developing, even if they can feed on the pollen. This represents an example of apparent competition, where the population development of a prey is suppressed by a shared predator when an additional prey or food supplement is present (Nomikou et al., 2010). Despite the fact that *Typha* pollen has been widely shown to be effective in supporting biological control, growers could still run a risk of damage when thrips are too numerous at the start of the crop or when predators do not establish because of pesticide residues. When applying any food supplement, including pollen, predation per predatory mite will go down due to satiation effects (Skirvin et al., 2007). In addition to predator satiation (Holt and Lawton, 1993, 1994; Shakya et al., 2009) a feeding-switch to pollen may occur. Both mechanisms may result in a temporary reduction in predation rate of the pest (so-called apparent mutualism, Abrams and Matsuda, 1996). High dosage of cattail pollen reduced the predation of thrips by individual *A. swirskii* by 50% on laboratory scale (Leman and Messelink, 2015). However, these effects are typically short term and are soon outbalanced by the augmentation of natural enemy numbers (Van Rijn et al., 1999).

The use of supplementary food, and pollen in particular, is a powerful tool to help establish predatory mites and improve biocontrol efficacy. The application of exogenous pollen as supplemental food source can be optimized by avoiding excessive doses, as overly high pollen levels may result in satiation of predatory mites and stimulation of thrips (Sabelis and van Rijn, 2006). The choice of the pollen type and the match with the predatory mite can also affect the outcome. However, *Typha* pollen has proved to be suitable for a broad range of predatory mites (**Table 5**). Growers succeed in building strong populations of predatory mites with feeding their predators before pest appearance and performing adjustments in their irrigation systems and their spraying data. Some persue the development of the application by automatizing the blowing of this alternative food.

## NECTAR/SUGAR SOLUTION

Many natural enemies depend on sugars as their main source of energy. This includes a.o. parasitoids (Wäckers, 2001), syrphids (Van Rijn and Wäckers, 2016), gall midges (Fratoni et al., 2020), chrysopids (Stelzl, 1991; Hogervorst et al., 2007), coccinellids (Pemberton and Vandenberg, 1993), mirids (Portillo et al., 2012), and phytoseiids (Van Rijn and Tanigoshi, 1999b). Natural enemies can feed from a range of carbohydrate sources. Besides floral nectar, they can also exploit extrafloral nectar, as well as honeydew.

Floral nectar has evolved as a food reward in the mutualism between plants and their pollinators. Even though natural enemies, with a few noticeable exceptions (Pekas et al., 2020), are most likely not necessarily effective in pollinating flowers, they, nevertheless, can collect floral nectar to provide for their energetic needs. As natural enemies tend to have short mouthparts, their nectar foraging is restricted to those plant species with open and exposed floral nectaries, such as Apiaceae, Euphorbiaceae, or buckwheat (Campbell et al., 2012; Wäckers and van Rijn, 2012; Van Rijn and Wäckers, 2016).

While accessibility of floral nectar can be a bottleneck for natural enemies, some plants also produce nectar outside of the flowers. These so-called extrafloral nectaries tend to be exposed and thus highly accessible. Furthermore, the nectar is often secreted over prolonged periods of time (Wäckers and Bonifay, 2004). These adaptations fit their ecological function, as extrafloral nectar is part of a defensive strategy, allowing plants to recruit ants and other sugar feeding natural enemies. They, in turn, protect the plants when attacking herbivores. Extrafloral nectaries have been described in more than thousand plant species, including a number of important crops, such as cotton, cassava, peaches, plums, cherries, pumpkins, roses, field beans. In a number of plant systems, it has been demonstrated that the presence of extrafloral nectar can translate into both reduced plant damage and increased plant reproductive fitness (Heil, 2015).

Honeydew is a generic term for sugar-rich excretions of phloem-feeding Sternorrhyncha. In agricultural ecosystems, honeydew is often the most prevalent sugar source (Wäckers and Steppuhn, 2003; Hogervorst et al., 2007; Tena et al., 2015). However, honeydew differs from the above-mentioned sugar sources, as it is primarily a waste product. This can reduce the nutritional value of honeydew (Wäckers et al., 2008).

Overall, the nutritional suitability of the above sugar sources depends on composition and concentration of carbohydrates (Wäckers, 2001; Azzouz et al., 2004; Fratoni et al., 2020). Sugar concentration is an important factor determining sugar uptake. At low concentrations, gustatory perception might be impeded (Wäckers, 1999), whereas viscosity at high sugar concentrations can interfere with sugar uptake (Wäckers, 2000; Winkler et al., 2009). Upon the time of nectar secretion, sugar concentrations can already range from 5 to 75% (Dafni, 1992). Environmental conditions may further affect nectar concentrations both indirectly through their effects on the nectar producing plant, and directly through evaporation, hygroscopy or rain dilution (Winkler et al., 2009). Sugar concentrations of undiluted extrafloral nectar range from 5 to more than 80% (Koptur, 1992a,b; Wäckers, 2001). In general, extra floral nectar shows much more variation in terms of sugar concentration than floral nectar from the same plant. Extrafloral nectar tends to be more concentrated, probably due the fact that its exposed nature increases evaporation. The fact that honeydew is typically available as little droplets or as a thin film on the substrate, means that it is even more subjected to evaporation. As a result, sugar concentrations are often at saturation. This is likely to be a limiting factor in honeydew uptake. This problem is accentuated by the specific tendency of the honeydew sugars: raffinose and melezitose, to crystallize rapidly (Wäckers, 2000).

### Providing Sugar Sources to Boost Biological Pest Control

It has long been recognized that the lack of sugar sources in agricultural systems can strongly undermine the efficacy of biological control. This problem could be overcome by introducing food sources into our agricultural systems. Recently, we have seen an increasing interest in the use of (flowering) non-crop plants in field margins as a tool to sustain predators and parasitic wasps. Specifically selected seed mixtures are available that are intended to attract natural enemies and provide them with nectar sources. When introducing nectar plants, the use of sugar sources is not restricted to beneficial insects. Many pest insects thrive on sweets as well (Wäckers et al., 2007). By choosing plants that primarily benefit natural enemies, the positive impact on pest control can be maximized (Gurr, 2005; Winkler et al., 2010). Banker plants can also be used to provide sugar sources, either in the form of (extra-) floral nectar as in the case of castor bean or broad bean or by providing honeydew (considering the caveats mentioned above). As an alternative to the introduction of nectar- or honeydew providing plants, sugar can also be applied as such. Sugar can be either sprayed onto the crop, or provided in so-called "feeding stations." Spraying sugar has the advantage that it is an easy and cheap application method resulting in an even coverage and providing an easily accessible sugar source for the predators and parasitoids. The quantity of the sugar applied can be controlled through the choice of sugar concentration, by adjusting the spray volume/spray nozzle, and by varying the walking/driving speed. Yet, there are also obvious drawbacks to the use of sugar sprays. Blanket sprays quickly result in the crop getting sticky. Certain sugars can cause phytotoxicity when sprayed directly on the foliage. In addition, sugars on the plant surface are prone to growth of sooty mold. These drawbacks can be avoided, either by using very weak sugar concentrations (e.g., 0.1–1%) or by applying a higher concentrated solution in a very fine and light mist. For the target arthropods, having minute sugar droplets is often better than having to deal with a sticky sugar layer, as the latter interferes with arthropod mobility. Biological control practitioners have attempted to incorporate artificial sugar sprays as a strategy to cater to the nutritional needs of parasitoids (Mandour et al., 2007; Wade et al., 2008). However, the efficacy of this form of sugar provisioning in biological control programmes has been limited and inconsistent (Heimpel and Jervis, 2005; Wade et al., 2008). Tena et al. (2015) studied the use of sugar sprays in combination with the release of the parasitoid *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) for the control of the California red scale *Aonidiella aurantii* in a commercial citrus orchard. They demonstrated that sugar supplementation increased the parasitoid population density 2-fold. Parasitoid fecundity on sugar treated trees was shown to be enhanced as well. Higher population densities and the increase in realized fecundity translated in a 2-fold increase in parasitism under crop conditions. The successful examples show that under certain conditions the use of sugars can be an effective element in a conservation biological control strategy.

## DOMATIA

Shelter and oviposition substrates are other resources that can be essential to successful establishment and efficacy of natural enemies (Gurr et al., 2017). Providing sites of refuge can support reproduction (Pemberton and Turner, 1989; O'Dowd and Willson, 1991; Grostal and O'Dowd, 1994; Walter, 1996) and development, overwintering or aestivation and can protect them from cannibalism (Ferreira et al., 2008; Lee and Zhang, 2016, 2018), predation (Roda et al., 2000; Norton et al., 2001; Faraji et al., 2002a,b; Romero and Benson, 2005; Seelmann et al., 2007; Ferreira et al., 2011) and unfavorable climatic conditions (Walter and O'Dowd, 1992a,b; Grostal and O'Dowd, 1994; Walter, 1996; Sabelis et al., 1999; Norton et al., 2001).

Some plants have special morphological structures, called domatia (from the Latin for home "domus"), that are targeted to either ants, or predatory/fungivorous mites. Ant domatia are represented by hollow thorns or stems and rolled leaf margins. Acarodomatia may take the form of either pits or (dense) tufts of leaf hairs, in which small arthropods may reside (Romero and Benson, 2005). Many studies have demonstrated that the presence of domatia increases the population of predators, that in turn protect the plant against herbivores and in some instances pathogens and weeds (Lundstrom, 1887; Rozario, 1995; Kreiter et al., 2003; Ferreira et al., 2008, 2011; Shenoy and Borges, 2010; Parolin et al., 2013). Predatory mites tend to occur more abundantly on plants bearing acarodomatia (O'Dowd and Willson, 1997; Norton et al., 2000; Roda et al., 2001; Romero and Benson, 2005; Avery et al., 2014) and their survival and reproduction on such plants is enhanced (Pemberton and Turner, 1989; Karban et al., 1995; Agrawal, 1997; Agrawal et al., 2000; Cortesero et al., 2000; Avery et al., 2014; Bresch et al., 2015, 2018). Domatia also act as oviposition substrate. Many predatory mite species show a preference to lay eggs on trichomes. Egg clusters can be frequently seen inside domatia, where predatory mites can molt protected from predators. Besides serving as shelters and oviposition sites, the hair-tufts may trap pollen and fungal spores that the mites can then consume (Roda et al., 2000; Romero and Benson, 2005; Loughner et al., 2008). Thus, acarodomatia can serve a function in providing food as well. Pekas and Wäckers (2017) showed a strong synergistic effect between the availability of fibers and food (pollen and sugar water) in affecting population growth of predatory mites on citrus plants. Romero and Benson (2004) demonstrated the protective role of domatia on the tropical tree *Cupania vernalis* L. By blocking domatia on part of the experimental trees, they showed that domatia increased predatory mite abundance and lowered herbivore damage from eriophyid mites. However, very few studies have investigated their long-term effect on predatory mites, pest or fungi under natural conditions (Norton et al., 2000; Monks et al., 2007; Ferreira et al., 2010). Norton et al. (2000) showed that acarodomatia increased the abundance of the mycophagous tydeid mite, *Orthotydeus lambi* (Baker), which resulted in the reduction of 48% of grape mildew infestation on the riverbank grape.

Domatia can be provided to beneficials by (1) selecting crop variety with the appropriate properties, (2) by adding suitable non-crop plants to crops (Skirvin and Fenlon, 2001; Van Rijn et al., 2002; Osborne and Barrett, 2005; Frank, 2010; Huang et al., 2011; Parolin et al., 2012b; Kumar et al., 2015), (3) or by using artificial structures (Loughner et al., 2011; Adar et al., 2014; Pekas and Wäckers, 2017). Crop varieties can differ substantially in domatia characteristics. Choosing crop varieties for their domatia traits could thus help to support establishment of natural enemies. Breeding programmes have actually started to include traits that determine suitability for beneficial organisms (Bottrell et al., 1998; English-Loeb et al., 1999). Some tomato varieties, for example, have been selected for their distorted trichomes to facilitate biological control of tomato russet mites (Van Houten et al., 2013; Legarrea et al., 2020). Another method for applying domatia can be the interplanting of domatia bearing banker plants between crop plants lacking domatia. Parolin et al. (2013) showed an increased spider mite control in roses using the predatory mites *P. persimilis* and *Neoseiulus californicus* (MCGregor) when adding lauristinus and frost grape bearing acarodomatia as bankerplants. Adding the banker plants in this system enhanced the establishment of predatory mites and increased their efficacy. The method can only be successful if natural enemies disperse from the manipulated habitat to the crop. In practice, growers tend to focus on commercial crops and are reluctant to introduce non-crop (banker) plants. A further strategy could be to use artificial domatia. Various types of artificial domatia have been used in studies to assess the benefits of natural dolmatia, but also, to improve biological control on crops (Loughner et al., 2010, 2011; Pekas and Wäckers, 2017). Rozario (1994) brought tufts of polyester fibers to grape varieties with low natural domatia to augment populations of *Galendromus occidentalis* Nesbitt. Agrawal and Karban (1997) supplemented cotton plants with artificial domatia, which enhanced spider mite control and fruit yields. However, thrips numbers were also shown to benefit from domatia. Kawashima et al. (2006a) reported laboratory experiments showing that textured urethane foam and polyethylene shading nets were suitable sites for the reproduction of *N. californicus*. Kawashima and Jung (2011) suggested using urethane foam as ground cover in apple orchards to increase the survival of *N. californicus* populations during the winter. Loughner et al. (2011) mimicked domatia on glabrous beans seedlings and Impatiens plants by adding cotton fiber patches and chopped acrylic yarn fibers and found more *A. swirskii* on plants provided with pollen and artificial domatia than on plants given solely pollen or fibers. In this study, cotton patches and paper pulp supplements augmented and maintained *A. swirskii* populations, whereas jute and celluflo were not effective. Adar et al. (2014) tested the "pollen on-twine" method (Gan-Mor et al., 2011), using fibers (rayon/viscose 80% and jute 20%) coated with pollen and succeeded in enhancing *E. scutalis* populations. Oviposition occurred on rayon rather than on jute. Bresch et al. (2018) found wool, silk, polyamide, viscose and polyester to be equally suitable as natural domatia for oviposition by N. californicus. However, none of them improved spider mite control by N. californicus and polyamide even benefitted the pest. Pekas and Wäckers (2017) showed that the combined use of fibers, pollen, and sugar generate synergistic benefits to population growth of *Euseius stipulatus* (Athias-Henriot) on bitter orange. In orchards, Koike et al. (2000) designed a Phyto trap, which contains wool yarn mimicking the microstructure of spider mites colonies. This tool aims at collecting predatory mites in pear trees to monitor their densities during the seasons and maintain populations (Kawashima and Amano, 2006; Kawashima et al., 2006b). This tool inspired Messelink et al. (2016) to test among others further material with Velcro tape in greenhouse crops, but found that using millet husk or jute both combined with pollen were more effective to enhance the establishment of *A. limonicus* on anthurium. In spite of these examples showing the potential of using artificial domatia, there are no commercial applications of these artificial domatia yet.

## CONCLUSIONS

This review presents the potential, advantages and risks of the concept of "beneficials-in-first" over augmentative biological control in greenhouses and aims at discussing tools thought to preserve natural enemies in biological control programmes. The studies described show that natural enemies' survival, development, reproduction and efficacy can be enhanced with the use of factitious prey, banker plant systems, pollen, sugars and manipulated habitats. This concept of "beneficials-in-first" is no longer a focus of researchers only, but has been explored by commercial growers over the past two decades. However, despite the trials demonstrating their benefit, some methods to enhance natural enemies' establishment are still excluded from biological strategies in practice, as they often lead to other issues at large scale. The development of hyperparasitoids or pests on banker plant systems, the possible molting of *Ephestia* eggs and *Artemia* cysts, the lack of survival of living factitious prey, the damages caused by *Tyrophagus putrescentiae* or by mirid predatory bugs when they are too numerous, are such examples. Overhead irrigation can hamper the application of alternative food and artificial domatia in some crops. Artificial domatia are also difficult for growers to introduce in their crop.

Further increasing the adoption of the "beneficials-in-first" concept by growers can be achieved by:

1. Clearly demonstrating efficacy on a larger scale and communicate if the selected resources benefit more natural enemies than the antagonists or pests, decrease pest damage and increase production quality or yield;
2. Increasing the involvement of growers in the process of such large-scale experiments, including costs and handling times;
3. Fine-tuning the amount of supplemental resources, the release techniques, the timing and the frequency with which the tools should be employed (Janssen and Sabelis, 2015; Madadi, 2018);
4. Automatization as it will be the key in expanding the scope of inoculative biological control, both in protected and open-field crops.

In the coming decade, we foresee more applications of feeding stations and nectar plants in crops to enhance the survival of natural enemies. Beside the tools of enhancement of beneficials, the use of methods limiting pest activity in greenhouses will gain more importance like tools of sexual confusion, distraction of pests such as "push-pull systems" or the use of "repellent substances."

## AUTHOR CONTRIBUTIONS

JP: conceptualization, supervision, writing original draft, review, and editing. FW: conceptualization, supervision, writing draft, review, and editing. DV, RM, and MD: review and editing. All authors contributed to the article and approved the submitted version.

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# Cascading Effects of Birds and Bats in a Shaded Coffee Agroforestry System

**Lauren Schmitt[1]*, Russell Greenberg[2†], Guillermo Ibarra-Núñez[3], Peter Bichier[4], Caleb E. Gordon[5] and Ivette Perfecto[1]**

[1] School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, United States, [2] Smithsonian Migratory Bird Center, National Zoological Garden, Washington, DC, United States, [3] Departamento de Agricultura, Sociedad y Ambiente, El Colegio de la Frontera Sur, Tapachula, Mexico, [4] Department of Environmental Studies, University of California, Santa Cruz, Santa Cruz, CA, United States, [5] Department of Biology, Lake Forest College, Lake Forest, IL, United States

Volant vertebrate insectivores, including birds and bats, can be important regulators of herbivores in forests and agro-ecosystems. Their effects can be realized directly through predation and indirectly via intraguild predation. This paper examines data from bird and bat exclosures in coffee farms in Chiapas, Mexico in order to determine their effect on herbivores. Arthropods were sampled in 32 exclosures (with 10 coffee plants in each) and their paired controls three times during 6 months. After 3 months, herbivore and spider abundance increased, underscoring the importance of both intertrophic predation between volant vertebrate insectivores and herbivores and intraguild predation between volant vertebrate insectivores and spiders. After 6 months, herbivore abundance increased in the exclosures, which is indicative of a direct negative effect of birds and bats on herbivores. We suggest that intraguild predation is important in this food web and that seasonality may change the relative importance of intraguild vs. intertrophic predation. Results suggest a dissipating trophic cascade and echo the growing body of evidence that finds birds and bats are regulators of herbivores in agro-ecosystems.

**Keywords: coffee agroecosystem, food web, intraguild predation, trophic cascade, spiders, parasitoids, biological control, ecosystem function**

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***Correspondence:**
*Lauren Schmitt*
*lschmit@umich.edu*

*† Deceased*

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## INTRODUCTION

Defining trophic levels and outlining the connections between them has long been a fundamental goal in ecology. Much theoretical and empirical work has gone into understanding the factors controlling dominant pathways and the immense complexity in terrestrial food webs (Schoener, 1989; Spiller and Schoener, 1990; Hairston et al., 1997; McCann et al., 1998; Oksanen and Oksanen, 2000; Yodzis, 2000; Lambers and Dickerman, 2003; Stouffer et al., 2007). Inter-trophic consumption (i.e., feeding between trophic levels, as when a predator eats an herbivore) is undoubtedly important in structuring food webs, but is complicated by intraguild predation. Intraguild predation (i.e., organisms in the same trophic level consuming one another) is also very common (Gagnon et al., 2011). The feeding bias of predators—that is, whether they are primarily predating within or outside of their guild or trophic level—can have important consequences on food web structure.

The relative importance of inter-trophic vs. intra-guild predation has particular practical significance in managed ecosystems (Montoya et al., 2003). Natural enemies in the food web represent one of many tools for holistic pest management. But, for natural enemies to contribute to biocontrol, it is essential to understand the relative strength of intraguild predation and inter-trophic predation in the food web. For example, land managers might be interested in increasing the density of a predator in an effort to control pests. This intervention implicitly assumes that the primary effect of the predator on the pest is through direct inter-trophic predation. Alternatively, if the predator is also practicing intraguild predation and predating upon other predators of the pest, the managed predator could indirectly facilitate the pest by reducing the overall number of predators. The widespread benefits of holistic pest management are well-known (Lewis et al., 1997), but effective implementation requires an in-depth understanding of not just the pest and potential predator, but the food web within which they are embedded.

Volant vertebrate insectivores (VVIs), which includes birds and bats, have received a great deal of attention within the food web literature, in an effort to both conserve VVIs and ascertain their impact on managed ecosystems (Greenberg et al., 2000; Van Beal et al., 2003; Perfecto et al., 2004; Philpott et al., 2004, 2009; Borkhataria et al., 2006; Whelan et al., 2008; Johnson et al., 2010; Mooney et al., 2010; Böhm et al., 2011; Karp and Daily, 2014; Maas et al., 2016; Nyffeler et al., 2018). Early studies on the effects of birds on arthropods in temperate ecosystems concluded that birds exert little control over most arthropod groups (Holmes et al., 1979). If true and birds have little impact, there should be little net effect of VVIs on plants, since the positive effects of predation on herbivores should be counterbalanced by negative effects of intraguild predation depressing arthropod insectivore populations (Pejchar et al., 2018).

More recent work has shown that VVIs can be important in controlling arthropod populations (Greenberg et al., 2000; Van Beal et al., 2003; Perfecto et al., 2004; Philpott et al., 2004, 2009; Borkhataria et al., 2006; Whelan et al., 2008; Johnson et al., 2010; Mooney et al., 2010; Böhm et al., 2011; Karp and Daily, 2014; Maas et al., 2016; Nyffeler et al., 2018). Furthermore, studies in tropical forests and coffee agroforestry systems have found the effects of birds and bats (Kalka et al., 2008; Williams-Guillén et al., 2008; Morrison and Lindell, 2012), and of birds and lizards (Borkhataria et al., 2006), to be additive. These and other studies argue that VVIs serve an important function as regulators of arthropods, including herbivores, in forested and agricultural systems (Sekercioglu, 2006; Mooney et al., 2010; Maas et al., 2016). The food web structure can determine the net effect of VVIs on herbivory if VVIs are consuming predators or mesopredators, as demonstrated in cereal systems (Grass et al., 2017). Maintaining VVI populations could be important for pest control in coffee agro-ecosystems, but VVIs are also associated with a host of other ecosystem goods and services including pollination, climate regulation, and nutrient cycling and carbon sequestration (Jha et al., 2014).

Intraguild predation could be important in determining the effects of VVIs on arthropod herbivores not only if VVIs consume other predators, but also if arthropod predators consume one another. For example, while VVIs tend to prefer larger arthropods (Holmes et al., 1979; Marquis and Whelan, 1994; Greenberg et al., 2000; Van Beal et al., 2003; Gruner, 2004; Philpott et al., 2004), parasitoids are consumed mainly by spiders, especially web weavers (Polis and Hurd, 1995; Ibarra-Núñez et al., 2001). Thus, the feeding behavior of VVIs and arthropod predators could shape food web dynamics and pest control dynamics in the coffee system. However, the effects of intraguild predation among arthropods are less frequently considered in VVI exclosure experiments [for exceptions, see Martin et al. (2013), Maas et al. (2013), Karp and Daily (2014)].

In a further complication, in systems with marked seasonal shifts, the dominance of a trophic scheme and the importance of intraguild predation could change with the season (Pejchar et al., 2018). In the tropics, where this study was carried out, distinct dry and rainy seasons could have major impacts on life cycle dynamics, migration, and foraging strategies (Greenberg, 1995). In the dry season, ants are less abundant (Philpott et al., 2006), spiders are more abundant (Rendón et al., 2006) and migratory birds join the year-long residents, nearly doubling overall bird abundances (Greenberg et al., 1997). Shifting abundances of predators and prey can alter feeding habits and thus the importance of intraguild predation.

Arthropods can represent a significant threat to yields in agroforestry systems, including coffee agro-forestry systems. The coffee leaf miner (*Leucoptera coffeella*) and the coffee berry borer (*Hypothenemus hampei*) are the predominant threats to coffee yields with the former reducing photosynthetic potential of plants (Borkhataria et al., 2006) and leading to less fruit production and the latter boring into fruits, eating the seed and rendering the coffee unsaleable (Damon, 2000). In intensified coffee systems, pests are often managed with chemicals, to varying levels of success and with a number of negative externalities (Staver et al., 2001). In less intensively managed coffee systems, namely shaded agro-forestry systems, a diversified food web is relied upon to keep pest densities below a problematic threshold (Staver et al., 2001; Jha et al., 2014; Vandermeer et al., 2019).

We conducted this study in coffee agroecosystems of southern Mexico to assess the effect of VVIs on arthropod herbivores—an outcome dependent, in part, on the relative importance of inter-trophic consumption and intraguild predation—by experimentally excluding VVIs from target coffee plants. We explore three hypotheses regarding the general structure of the system: (1) direct inter-trophic interaction between the VVIs and herbivores, (2) intraguild predation between VVIs and arthropod predators, and (3) intraguild predation between VVIs and arthropod predators plus intraguild predation among arthropod predators (**Figure 1**). The exclusion of VVIs will result in an increase in herbivores for #1 and #3, and a decrease in herbivores for #2. In our system, the arthropod predators include beetles, lacewings, wasps, robber flies, ants and spiders, with spiders being the most common (Perfecto, unpublished data). The vertebrate predators include frogs, toads, lizards, bats and birds, with bats and birds being the most common, and the ones addressed in this study.

In experimentally removing the effect of VVIs, we can infer the general food web structure based on the responses of herbivores and arthropod predators (particularly spiders). If inter-trophic consumption is controlling the net effect of VVIs on herbivores, we expect the exclusion of VVIs will lead to an

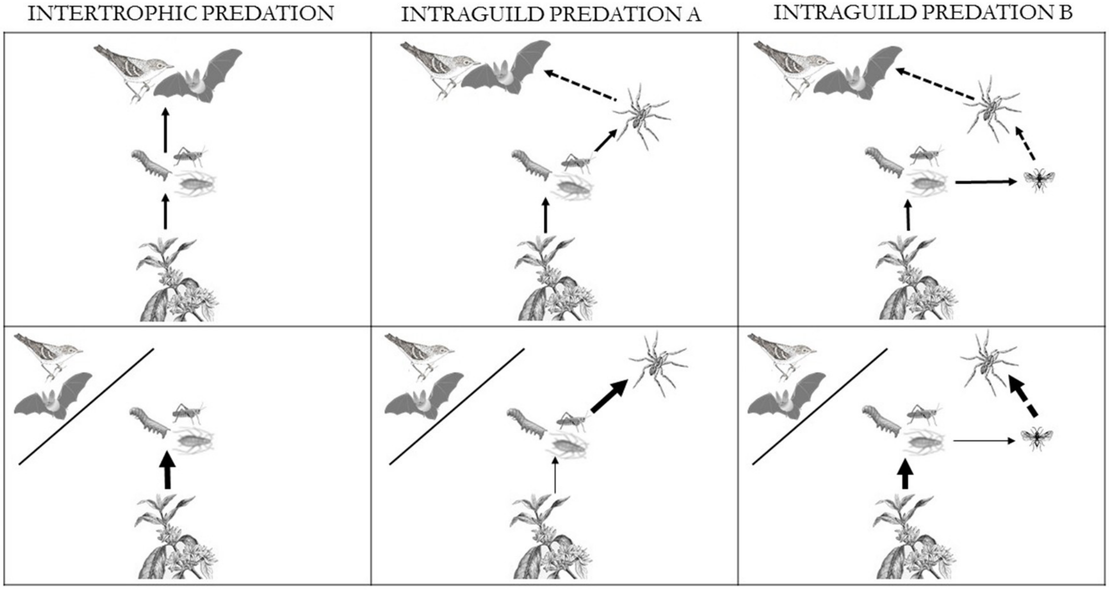

**FIGURE 1 |** Conceptual figure illustrating potential trophic dynamics with (1) only direct inter-trophic consumption, (2) intraguild predation between VVIs and arthropod predators, and (3) intraguild predation between both VVIs and arthropod predators and among arthropod predators. Intraguild predation is indicated by a dashed arrows and inter-trophic interactions are denoted with solid arrows. Modified from Perfecto and Vandermeer (2015) with additional vector elements from Tracey Saxby (Integration and Application Network, ian.umces.edu/imagelibrary/).

increase in herbivores. If intraguild predation is more important, we expect an increase in arthropod predators with the removal of VVIs, followed by a concomitant decrease in herbivores due to increased predation by arthropod predators. Further, we expect that effects of intraguild predation will be greater in the dry season vs. the wet season, because spiders and birds are both more abundant during this time.

## METHODS

Working on four coffee farms in the Soconusco region of Chiapas, Mexico, we established 32 large bird/bat exclosures (ten in each of two farms and six in the other two farms). The farms included *Finca Irlanda, Finca Hamburgo, Finca Bélgica*, and *Finca Belen*. The last two farms were united under the single name [*Finca Belén*] right before we started working there, but continued to be managed in different ways. All farms are located on the Pacific side of the Sierra Madre mountain range, in a region dominated by coffee farms [**Figure 2**, see Perfecto et al. (2003), Philpott et al. (2006), Gordon et al. (2009)]. They are managed under a gradient of management styles from rustic to commercial polyculture management (Moguel and Toledo, 1999). These differences were not taken into account in the analysis, which is a conservative approach, and are discussed elsewhere (Perfecto et al., 2003; Philpott et al., 2006).

Exclosures were constructed of transparent monofilamentous nylon (5 $cm^2$ mesh) fishing net. This mesh size is comparable to the mesh size used in other exclosure studies (e.g., Morrison and Lindell, 2012) and was chosen to exclude birds and bats, but permit most arthropods to pass through the cages (**Figures 2d,e**). They were established in November of 2000, and left for the duration of the experiment. Each exclosure enclosed 10 coffee plants [with the exception of five exclosures that enclosed seven (3), eight (1), and nine (1) plants] and each was ∼10 m long, 5 m wide, and 3 m high (**Figure 2e**). The same number of control plants were selected from a parallel row of coffee ∼2–3 m from the paired exclosure. Each pair was separated by at least 50 m, with the majority separated by more than 100 m. In total, 616 coffee plants were sampled, half of which were inside the exclosures and half outside. The coffee farms represented a variety of management systems, from shaded organic farms to unshaded conventional farms. Farm management can directly and indirectly influence VVIs and arthropods—some of the effects of management at these sites are discussed in relation to arboreal ants (Philpott et al., 2006) and ground foraging ants (Perfecto et al., 2003).

Arthropods were sampled using a D-vac (a reversed leaf blower modified with a fine mesh that allowed the collection of micro-arthropods), passed over a branch for a standardized amount of time. The contents of each sample were carefully transferred from the mesh and stored in 70% ethanol until identifications were made. Two coffee branches were randomly selected for arthropod sampling from each of 10 coffee bushes inside and outside exclosures (except in five exclosures and their controls where a lower number of plants were available for sampling). Samples were taken 2–3 days after the establishment of the exclosures (for baseline data) and at 3 and 6 months after establishment. This sampling method is destructive, with all arthropods on the two branches of the focal plants effectively removed; however, three months between sampling periods was

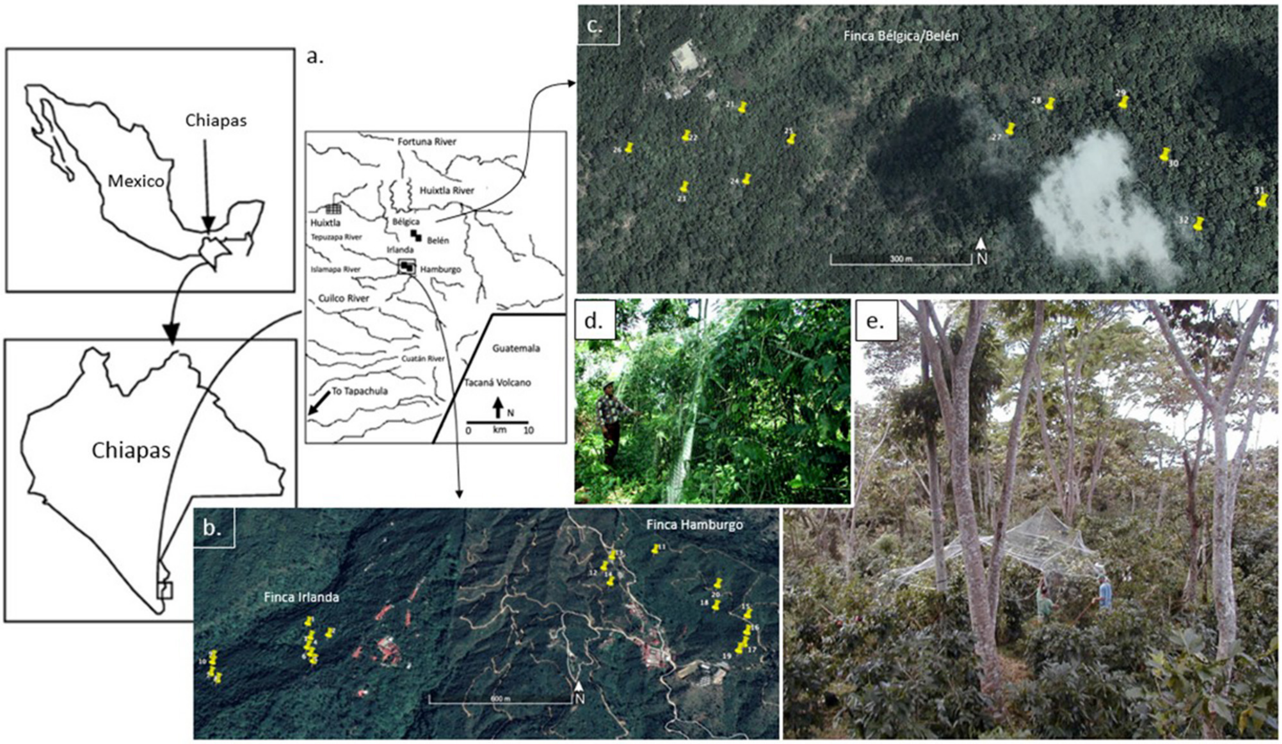

**FIGURE 2 |** Location of study sites and exclosures; **(a)** regional map indicating study sites; **(b)** location of exclosures in the Finca Irlanda and Finca Hamburgo sites; **(c)** location of exclosures in the Finca Bélgica/Belén sites; **(d)** photo from outside one of the exclosures; **(e)** setting up an exclosure.

assumed to be more than sufficient for arthropods to re-establish on the focal plants. The study site experiences distinct rainy and dry seasons. The 3 months sampling, in February, was in the middle of the dry season. The 6 months sampling in May occurred at the start of the rainy season.

Total foliar biomass on each sampled branch was estimated by measuring the length and width of each leaf and assuming the area results from an ellipsoid relationship between length and width (a justified assumption given the shape of coffee leaves). One hundred leaves from each farm (10 from 10 coffee plants) were collected at random. The area was estimated and the leaves were dried in an oven to constant weight. With that data, an empirically derived regression equation relating area with weight ($weight = (0.025^{*}area) - 0.08$) was used to estimate the biomass of each leaf.

Arthropods were sorted to order and some to family. The information at the family level was used to assign individuals to the herbivore trophic level (within Coleoptera, Hemiptera, etc.). Insects in the order Hymenoptera were separated into formicids (ants) and non-formicids (bees and wasps). Numbers of arthropods are presented as number per unit of foliar biomass. Our use of abundance, rather than biomass, as a measure of arthropod populations likely underestimates the effects of VVIs, given that they preferentially feed on larger arthropods. We did not estimate biomass because of the high variability and lack of precision associated with biomass estimation methods (Gruner, 2003).

A random sample of 15 leaves was taken from each sampled plant at the beginning of the experiment and after 6 months. Herbivore damage, approximated by leaf area loss, was estimated through image analysis using NIH-Image. Yield data were obtained by repeatedly harvesting all mature (red) berries for all the experimental plants from August 2001 to January 2002. Berries were counted and weighed for each individual plant.

We built generalized linear models using the "glmmTMB" function in the "*glmmTMB*" package in R (Brooks et al., 2017). Models for herbivores, spiders and parasitoids included the date (i.e., seasonality), treatment (control or exclosure), and interaction between date and exclosure, and farm. For the purposes of this analysis and paper, we were not interested in assessing the inter-farm differences in management, but with four farms, there were too few levels to include it as a random effect. We used exclosure replicate nested by farm as a random intercept to account for increased correlation between repeated measure at the exclosure (and control) sites. The data for herbivores, spiders and wasps was non-normal semi-continuous data, because it was adjusted by foliar biomass. We used a Gamma distribution and check the model fit using the "*DHARMa*" package in R (Hartig, 2019).

We used *post-hoc* tests to generate contrasts that allowed us to make pairwise comparisons between all three sampling points. We calculated the estimated marginal means, also known as least square means, using the "emmeans" function from the "*emmeans*" package in R (Lenth and Lenth, 2018).

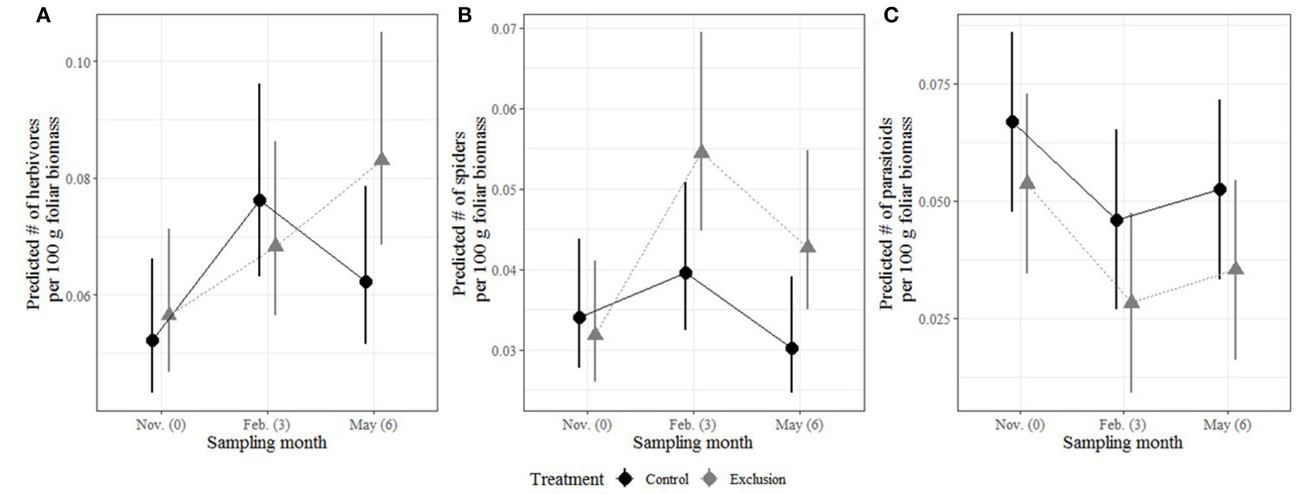

**FIGURE 3 |** Means and confidence intervals predicted from the GLMM output for herbivores **(A)**, spiders **(B)**, and parasitoids **(C)** per 100 g foliar biomass. Black circles represent the control treatment and gray triangles represent the exclosure treatment. Note that the y-axes are different in each panel.

This allowed us to compare across sampling dates and the factorial combinations of treatments. The model could be re-paramaterized using difference reference categories, but using contrasts provides comparisons between all levels of the factor with re-calculating the intercepts.

Similarly, we used generalized linear mixed models with the same random effects structure to assess the impact of treatment (control or exclosure) on herbivory and yield. This data was taken just once, so no effect of seasonality and no interaction with seasonality and treatment could be assessed.

To test the robustness of our results, arthropod, herbivory and yield data were also analyzed using non-parametric Wilcoxon paired tests. The non-parametric Wilcoxon test was used because the data failed to meet the assumption of normality required of parametric tests. Paired tests were executed between treatments (control and exclosures) at each time point.

## RESULTS

The vast majority of the herbivores collected were in two suborders of Hemiptera: Sternorrhyncha and Auchenorrhyncha (e.g., in the first sampling period 93% of all herbivores were in these two suborders). An overwhelming majority of the non-formicid hymenopterans (>95%) were parasitic wasps (i.e., parasitoids). There was high variability in ant abundances and our collection method was not well-suited to capture differences in ants, given their eusociality. The majority of the spiders captured in our study were web builders in the families Theridiidae (24%), Tetragnatidae (11%), and Araneidae (10.3%).

The three major groups of interest—herbivores, spiders and parasitoids—responded differently to the treatments over time (**Figure 3**, **Supplementary Figure 1**). There were no differences in the abundance of herbivores or spiders between treatments at the start of the experiment (*emmeans,* herbivore $p = 0.9949$, spiders $p = 0.9985$). GLMM results showed no difference between parasitoid abundances at the start of the experiment (*emmeans,* $p = 0.6686$). However, the non-parametric Wilcoxin test was marginally significant (**Supplementary Table 1**, $p = 0.0545$).

Three months after VVIs were excluded we found an increase in herbivore abundance across both treatments (*emmeans,* $p = 0.0178$). Spiders were also more abundant after 3 months (*GLMM,* $p = 0.0114$), and there was a significant interaction between treatments between November and February (*emmeans,* $p = 0.0467$). After 6 months, herbivore abundance increased (*emmeans,* $p = 0.0259$*)* in both treatments and there was a significant interaction between treatments in November and May (*emmeans,* $p = 0.0263$). Spider abundance did not differ between November and May (*emmeans,* $p = 0.79$) and there was a marginally significant decrease in abundance between February and May (*emmeans,* $p = 0.0621$). Parasitoid abundance was lower in exclosures after 3 (*emmeans,* $p < 0.001$) and 6 months (*emmeans,* $p = 0.0037$).

There were more spiders, regardless of time, in the exclosures (*GLMM,* $p = 0.0388$) and fewer parasitoids (*GLMM,* $p = 0.001$). Treatment alone was not a significant predictor of herbivore abundance (*GLMM,* $p = 0.428$). Model results (**Table 1**) are expanded upon with full pairwise interactions in **Supplementary Table 1**.

When summing all arthropods captures, there were season differences, but no differences between treatments (**Supplementary Table 3**, **Supplementary Figure 1A**). All arthropods captured are detailed in **Supplementary Table 4**.

Six months after the exclosures were established, foliar herbivory was an average of 0.17% lower in the exclosures (GLMM, *std error* = 0.04603, $p = 0.00013$). However, herbivory levels across both treatments were quite low (∼1–2%, **Supplementary Figure 2A**). Higher herbivory in the absence of VVIs did not translate into lower coffee yields (GLMM,

**TABLE 1 |** Generalized linear mixed model results and pairwise estimated marginal means contrasts of dates for herbivores **(A)**, spiders **(B)**, and parasitoids **(C)**.

| Predictors | Estimates | Std. Error | *P*-value |
|---|---|---|---|
| **A. Herbivores** | | | |
| (Intercept) | 9.7676 | 1.5774 | <0.0001 |
| Date | | | |
| February-May | −0.183 | 1.37 | 0.9902 |
| **February-November** | **−4.540** | **1.65** | **0.0178** |
| **May-November** | **−4.356** | **1.66** | **0.0259** |
| Treatment | 1.515 | 1.99 | 0.4280 |
| **B. Spiders** | | | |
| (Intercept) | 21.532 | 3.144 | <0.001 |
| Date | | | |
| February-May | −6.42 | 2.82 | 0.0621 |
| **February-November** | **−8.60** | **2.96** | **0.0114** |
| May-November | −2.18 | 3.33 | 0.7900 |
| **Treatment** | **−6.918** | **3.348** | **0.03880** |
| **C. Parasitoids** | | | |
| (Intercept) | 15.778 | 2.076 | <0.0001 |
| Date | | | |
| February-May | 4.41 | 2.44 | 0.1699 |
| **February-November** | **10.53** | **2.17** | **<0.001** |
| **May-November** | **6.12** | **1.87** | **0.0037** |
| **Treatment** | **12.452** | **3.778** | **0.001** |

*The reference treatment was control treament, the reference date was February. Significant factors at the 0.005 level are bolded. Full pairwise estimated marginal means for all combinations are provided in* ***Supplementary Table 2****.*

*std error* $< 0.001$, $p = 0.4987$, **Supplementary Figure 2B**) and there was no correlation between herbivory and yield (**Supplementary Figure 2C**).

## DISCUSSION

Our results highlight the role of intraguild predation in food webs with VVIs, as well as the direct role of VVIs in consuming herbivores. Our findings also support recent studies that indicate that VVIs can contribute to biocontrol, limiting arthropod populations in forests and agroecosystems (Greenberg et al., 2000; Kalka et al., 2008; Van Bael et al., 2008; Williams-Guillén et al., 2008; Johnson et al., 2010; Böhm et al., 2011; Morrison and Lindell, 2012; Karp and Daily, 2014; Gras et al., 2016; Maas et al., 2016). The implicit assumption of these and other exclosure studies is that vertebrate predators provide an important ecosystem function via inter-trophic predation. We do find evidence of direct consumption, but also suggest intraguild predation within the predator guild could be a key determinant in the net impact of VVIs on herbivores.

With significantly higher herbivore abundance inside the exclosures after 3 and 6 months, we find evidence of top-down control of herbivores by VVIs and of inter-trophic predation. A common concern in exclosure studies is that birds may use closures as a perch, artificially increasing the density of birds in the area. However, even the most intensified site in our study had a canopy of shade trees, so perch sites are unlikely to be limiting. While we find evidence of top down control by VVIs, higher spider abundance in the exclosures at both sampling points also underscores the role of intraguild predation. This is congruent with past work that finds intraguild effects of birds preying on spiders (Sherry, 1984; Burger et al., 1999; Greenberg et al., 2000; Strong, 2000; Van Beal et al., 2003; Gruner, 2004; Philpott et al., 2004; Gunnarsson, 2007; Karp and Daily, 2014) and spiders preying on parasitoids (Gunnarsson, 2007) can alter the net effect of VVIs on herbivores.

Our design does not allow us to disentangle the role of birds from bats, but each group is likely acting differently as predators. Other studies that have used diurnal and nocturnal exclosures have found a negative, additive effect of birds and bats on arthropod abundance (Williams-Guillén et al., 2008) and that bats can have a stronger effect than birds on arthropod abundances and resultant herbivory (Kalka et al., 2008). Exclosure studies suggest bats affect all arthropod groups, except spiders, though analysis of bird and bat feces in another coffee growing region found little evidence that bats are controlling the coffee berry borer (Karp et al., 2013). Unfortunately, the method we used for sampling arthropods is not good for sampling the coffee berry borer, which is found inside the berries, nor coffee leaf miners, which is inside the leaf tissue. Therefore, we cannot make inferences about the effect of VVIs on these two important coffee pests. Gut or fecal analysis would be useful in further defining these trophic relationships and determining the role of birds and bats broadly and determining which species are involved in these trophic relationships.

Parasitoid abundance was lower when VVIs were excluded, and parasitoid abundance was negatively correlated with spider abundance both in and outside of exclosures. This might suggest an indirect positive effect of VVIs on parasitoids, mediated by their consumption of spiders. Although the number of parasitoids was marginally lower within the exclosures at the initiation of the experiment (according to the Wilcoxin test, but not the *GLMM*), the difference between the controls and exclosures got larger and more highly significant both 3 and 6 months after establishment, which indicates that the exclosures had an important effect on the parasitoids. We know of no methodological bias that would lead to lower parasitoid numbers at baseline, but the baseline data was collected 2–3 days after the establishment of the exclosures, so it's possible that parasitoids were highly sensitive to any disturbance created during the establishment of the exclosures and therefore their numbers were marginally lower a few days after the disturbance. Physical structures are often limiting for web-building spiders (Uetz, 1991); the exclosure apparatus may have inflated the number of spider webs, and augmented the effect of spiders on parasitoids, but this is unlikely to have happened within 2–3 days of establishment. Regardless, this finding highlights the need to consider both arthropod predators and parasitoids together in food web studies and focus further research on the role of parasitoids.

Ants and beetles from this study design have been analyzed elsewhere (Philpott et al., 2006; Gordon et al., 2009) and showed no significant differences between exclosures and control. In another study conducted in some of the same sites as this study, Philpott et al. (2004) excluded VVIs from tree branches and found a marginally significant effect of VVIs on ants with VVIs reducing ants by 68% ($p = 0.07$). The main difference between these two studies is that in our study we excluded VVIs from coffee plants, while in the Philpott et al. study VVIs were excluded from branches on the shade trees. These are the sites where birds spend more time foraging and perching and therefore are more likely to affect the arthropod community, including ants. It has been shown that some resident birds shift their foraging from the shade layer to the coffee layer during the dry season, when the migratory birds arrive in high abundances (Jedlicka et al., 2006). However, that did not seem to be sufficient to cause a reduction of ants in the control as compared to the exclosures. Gordon et al. (2009) reported no effects of the exclosures on the beetle as a whole. However, they reported 293 morpho species of beetles belonging to 42 families, with representation of many predator families as well as herbivore families. Further research is needed to get a more complete picture of the role of these predator and parasitoid communities in the coffee food web and, as mentioned above, gut or fecal analysis would be useful in determining species-level trophic interactions.

Interpretation of results across all groups is complicated by seasonality. Sampling date, which could represent time from the treatment set up or seasonality, was significant for all of the major groups tested. Our exclosures were set up at the start of the dry season and the first sampling event after the baseline collection also took place during the dry season and our second sample, 6 months after set-up, occurred at the start of the rainy season. During the dry season (3 months survey, February), herbivore and spider abundance was higher in both exclosures and control. During the rainy season (6 months survey, May), herbivore abundance in the exclosures continued to rise, but abundances on the control plants decreased. The effect of the exclosures remained for spiders in the rainy season, though abundances decreased relative to the 3 months sample. Spiders in this system are key players in intraguild predation, as both prey of VVIs and predators of parasitoids. Thus, the overall importance of intraguild predation in structuring food web dynamics may be greater in the dry season when spiders are more abundant.

Seasonality can also alter foraging behavior (Philpott et al., 2004). For example, birds have been found to take more Lepidopteran prey, which tend to be larger in size, in the rainy season, though this seasonal difference is more pronounced in the shade layer of the agro-ecosystem than on the coffee plants themselves (Dietsch et al., 2007). Life cycle traits and migration could both contribute to seasonal effects. Williams-Guillén et al. (2008) found a greater impact of birds on arthropods in the dry season, when insectivorous overwintering migrants are present (Greenberg, 1995), and a greater impact of bats during the wet season, possibly due to more bat reproduction and higher abundances. If VVIs are predating upon more large herbivores in the rainy season, we might expect an increase in herbivore abundance (though not biomass) and less of a difference between the exclosure and control plants. We do find a higher abundance of herbivores in the exclosures during the rainy season relative to both the control plants during the rainy season and the exclosures during the dry season. Without finer scale time series data, it is difficult to parse apart the effects of seasonality and the exclosures, but foraging behavior provides another mechanism by which the relative importance of intraguild predation could be seasonally dependent.

Herbivory, as measured by leaf area loss, was significantly higher in the exclosures than controls after 6 months, which suggests a trophic cascade initiated by removal of the top predators. VVIs may preferentially be eating the relatively large leaf chewing herbivores, including Orthopteran and Lepidopteran, which more commonly cause leaf area loss. Given that large leaf chewing herbivores are known to be common in coffee agro-ecosystems (Dietsch et al., 2007), the lack of large herbivores in our samples is a bit surprising, even if VVIs are feeding preferentially. However, the lack of large leaf chewers and prevalence of hemipteran in our samples is consistent with the low documented levels of herbivory across treatments. Herbivory measures also may not have captured any damage caused by the coffee leaf miner, as coffee plants often respond to coffee leaf miner damage by dropping the damaged leaves (Guerreiro Filho, 2006). Thus, leaves sampled at the end of the experiment would have underestimated this damage. In previous work biocontrol services provided by VVIs were mediated by local and landscape level forest cover, but landscape level forest cover decreased leaf loss (Librán-Embid et al., 2017). Our study operates at the landscape level, with sites across farms in one coffee-growing region. Though pesticides were not used across all sites, usage may have decreased herbivory at some farms adding to some of the variability between farms.

We find the effect of top predators diminishes through the food web; we couldn't detect a significant effect of the exclosures on coffee yield. Other work in coffee systems has found a decrease in fruit set with the exclusion of vertebrates (Classen et al., 2014) and yield has been shown to decrease as much as 31% with the exclusion of VVIs in cacao systems (Maas et al., 2013). Still, our overall result is congruent with meta-analyses showing weak responses of terrestrial plants to the elimination of predators, even with a significant reduction of herbivores [Schmitz et al., 2000; Shurin et al., 2002; but see Croll et al. (2005) and Borer et al. (2005)]. However, herbivory levels found in this study were also very low (∼1–2%), so a lack of an effect on yield was not altogether surprising. In future studies, data should be taken on damage by the coffee berry borer, which affect coffee seed quality and weight rather than number of berries.

Shaded coffee farms have received much attention in the last 30 years because of their conservation potential (Perfecto and Vandermeer, 2015). High diversity and density of migrant and resident birds has become the basis for green certification labels, both to encourage conservation of migratory and resident species and in acknowledgment of the array of ecosystem services—including biocontrol—provided by birds and bats. This study provides empirical support of the role of VVIs in structuring the arthropod community in these managed agroecosystems. The response of herbivores, if not herbivory itself, does provide evidence that predators, including birds and bats, can contribute to preventative pest control in coffee agro-ecosystems. Most importantly, our results underscore the importance of considering intraguild predation between VVIs and spiders and spiders and parasitoids when investigating or managing for VVI control of arthropod herbivores.

## DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

## AUTHOR CONTRIBUTIONS

RG, GI-N, and IP conceived of the ideas and designed the methodology. RG, GI-N, IP, PB, and CG contributed to data collection and analysis. LS led the writing of the manuscript. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.512998/full#supplementary-material

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REVIEW
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# Terrestrial Slugs in Neotropical Agroecosystems

**Mariangie Ramos[1]*, Suzete Rodrigues Gomes[2], Yashira Gutierrez[1], Olgaly Ramos-Rodriguez[1] and Mariella Carmadelli Uzeda[3]**

*[1] Department of Agricultural Technology, University of Puerto Rico, Utuado, PR, United States, [2] Laboratório de Malacologia, Instituto Oswaldo Cruz, FIOCRUZ, Rio de Janeiro, Brazil, [3] Centro Nacional de Pesquisa de Agrobiologia, Empresa Brasileira de Pesquisa Agropecuaria, Rio de Janeiro, Brazil*

Slugs can be important agricultural pests in tropical regions. They are also intermediate hosts of parasitic nematodes, such as *Angiostrongylus costaricensis* and *A. cantonensis*, which can cause abdominal and cerebral angiostrongyliasis in humans. Management of slugs in conventional agriculture has relied heavily in the use of pellets containing metaldehyde. In this article, we review cases of slug problems and their management in neotropical agroecosystems.

**Keywords: terrestrial mollusks, pest management, organic agriculture, tropics, farmer knowledge, global change, Latin America**

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*Central University of Jharkhand, India*

***Correspondence:**
*Mariangie Ramos*
*mariangie.ramos@upr.edu*

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## INTRODUCTION

Terrestrial gastropods (land snails, semi-slugs and slugs) are a very diverse group, with ∼24,000 described species and 11,000–40,000 undescribed species worldwide (Lydeard et al., 2004). Several species of terrestrial gastropods are considered pests, however this fraction is small compared to the diversity of terrestrial Gastropoda (Neubert et al., 2019). Terrestrial gastropods contribute to litter decomposition (Meyer et al., 2013), and may even have roles in plant disease control in agroecosystems (Hajian-Forooshani et al., 2020).

Among the terrestrial gastropods, slugs have been identified as one of the most successful pest groups (South, 2012), especially in crops that require high physical disturbance (Port and Ester, 2002). For example, the Iberian slug *Arion vulgaris* (Moquin-Tandon, 1855) is a serious pest of vegetables and arable crops in Europe (Kozlowski et al., 2018; CABI, 2020), and is considered one of the top invasive species by the European Network on Invasive Alien Species (Slotsbo, 2014). In the US Midwest, slugs are one of the main pest problems for no-till growers (Douglas and Tooker, 2012).

Terrestrial slugs are not a monophyletic group, but a case of convergent evolution in which the slug form evolved from different lineages of land snails that gradually lost their shell, through a process called limacization (Simone, 2018). The slug body form is present in the Stylommatophora (land snails and slugs) and Systellommatophora (aquatic and terrestrial slugs) clades of the Eupulmonata (Schrodl, 2014). Thomé and Gomes (2011) cited 13 families of slugs in Brazil, of which only two of them are native to the Americas: Veronicellidae (common in tropical areas around the word) and Philomycidae (native from Asia and Northern America). Thomé (1993) reviewed the native Veronicellidae in the Americas, mentioning 144 species names classified in 18 genera.

Limacization resulted in adaptive radiation in land snail lineages, as slugs became adapted to diverse moist and protected spaces, such as crevices in rocks and wood debris (Hausdorf, 2001). The loss of the shell also allowed for more movement and less calcium dependence, making slugs more successful as pests (South, 2012). For example, in Venezuela, farmers do not consider snails pests but consider that slugs are a significant pest problem (Perichi, 2014).

Slugs in neotropical agroecosystems have been poorly documented in the literature. An exception to this, was the study of the bean slug, *Sarasinula plebeia* (Fischer, 1868), infestations in Central America in the 1980's. It was estimated that more than 400,000 farmers suffered economic losses due to this slug (Andrews, 1987a). Veronicellid slugs are also considered the main intermediate hosts of *Angiostrongylus costaricensis* (Morera and Céspedes, 1971), and can be naturally infected with *A. cantonensis* (Chen, 1935), which can cause abdominal and cerebral angiostrongyliasis in humans, respectively (Valente et al., 2020).

In this mini-review, we explore slug problems and management in the Neotropics. We review the literature: (1) to describe examples of slug infestations in the Neotropics and their potential causes; and (2) to explore preventive management strategies that have been used for slugs in this region. We expand on the review by Rueda et al. (2002), by including slug experiences from South America and the Caribbean.

## METHODS

We conducted a literature review using the following search terms in the topics category: slugs AND pest AND management. We used Web of Science All Databases, which include: WOS, BCI, CABI, KJD, MEDLINE, RSCI, SCIELO, ZOOREC. We search for all available years (1864- February 2020). A total of 1,320 records were obtained in 89 research categories. We refined research results to limit results to "Agriculture" research area, resulting in 866 records. Most records are from Europe (526 records) and North America (114 records). South America (16 records) and Africa (13 records) are the continents with the least number of records. In order to find more articles from the Neotropics, we conducted additional searches using the terms "babosas" (71 records), "lesmas" (13 records), and "limaces" (99 records). In addition, we used the term "babosas" and "lesmas" in Google search engine to find information in local management guides, thesis, or technical reports.

## SLUGS AS PESTS IN THE NEOTROPICS

The first reports of crop damage by slugs in the Neotropics are from Jamaica, where slugs were observed attacking coffee (Cockerell, 1893a) and strawberries (Cockerell, 1893b). In Trinidad, slugs caused significant damage to sweet potato plantations early in the 20th century (Callan, 1941). Pereira and Gonçalves (1949) later described slugs that affected bananas and vegetables in the coast of São Paulo state, Brazil. After a hiatus in publications, more articles about slugs in the Neotropics were published in the 1980's. Since the late 1960's, the bean slug *S. plebeia* started to cause severe damage to beans, a staple food, in Central America (Rueda et al., 2002). The Integrated Pest Management Project of Zamorano University (with financial support from USAID) conducted many studies to find suitable management practices to control *S. plebeia*. *Sarasinula plebeia* is believed to be native to the Americas despite its widespread distribution throughout tropical regions (Daglio et al., 2020). Andrews and Dundee (1987) studied the historic reports of the species and concluded that it was accidentally introduced to El Salvador, from where it spread throughout Central America, causing havoc to Central American farmers. In South America, *S. plebeia* is also known to cause damage to bean crops (Sannazzaro et al., 2000), but it is not considered a major pest (Cardona, 1994). Currently, *S. plebeia* is present in Central America, but farmers do not consider it a pest as important as whiteflies or leafhoppers in beans (R. Trabanino personal communication).

In the 1990's, the concern for slug damage intensified in Colombia, when higher than average rainfall was recorded, and significant coffee losses were experienced (Posada-Flórez et al., 2001). Slugs are considered pests in vegetable (Santacruz et al., 2011), flower and coffee production of Colombia. Martinez et al. (1994) first mentioned that slugs were problematic for flower production in Colombia, as they fed on the new shoots of plants and reduced flower production. Slugs are also problematic in flower production and many slugs are considered quarantine pests in importing countries (Robinson, 1999). Hausdorf (2002) identified *Deroceras invadens* (Reise et al., 2011), *Deroceras panormitanum* (Lessona and Pollonera, 1882), *Deroceras reticulatum* (Müller, 1774), and *Lehmannia valentiana* (Férussac, 1821) as serious pests in flowers of Colombia. The slug *Colosius confusus* (Gomes et al., 2013), a newly described species, was frequently intercepted by US authorities in fresh flowers coming from Colombia and Ecuador (Gomes et al., 2013). *C. confusus* also feeds and can be problematic on coffee plantations in Colombia and Peru (Constantino et al., 2010; Gomes et al., 2013). After 2000, researcher groups were formed to study the systematics, biology and management of terrestrial mollusks in Colombia (Moreno Suárez et al., 2008). Currently, slugs continue to be a problem in Colombian floriculture (mainly for *Alstroemeria, Dianthus* and *Hydrangea*), but are not perceived as major pests (A. Paez personal communication).

In recent years, slug species have been reported to cause damage in several crops in the Neotropics, including vanilla (Velazquez-Montes de Oca et al., 2014), passion fruit (de Oliveira and Frizzas, 2014), strawberry (Landal et al., 2019; Castellanos Gonzalez et al., 2020), and grapes (Baronio et al., 2014; Rodriguez et al., 2019). *Latipes erinaceus* (Colosi, 1921) and *Sarasinula linguaefomis* (Semper, 1885) are other species that are becoming problematic in the Neotropics. They are currently, one of the main pests of large-scale soy production in Brazil. Observations of *L. erinaceus* in the lab, have shown that it has a higher reproductive capacity than other species of the Veronicellidae family, spawning every month (S. R. Gomes unpublished).

From a food safety standpoint, the presence of slugs in leafy greens and fresh fruit production in the Neotropics is of particular concern. Slugs eat and leave secretions in leaves and fruits. Terrestrial mollusks, including slugs, are vectors of the parasite *A. costaricensis* and *A. cantonensis*. These parasites can survive in produce that is consumed raw (Kramer et al., 1998). In Santa Catarina, Brazil, *A. costaricensis* infection of 86% was observed in *S. linguaeformis* (Laitano et al., 2001). *S. linguaefomis* can be a pest of corn, beans, soybeans and leafy greens (Grisotti and Ávila-Pires, 2011; Moura et al., 2018). This slug is considered native to Brazil and it is widespread throughout the neotropical region (Valente et al., 2020). It usually occurs in low numbers in Rio de Janeiro State (Oliveira et al., 2015). However, in 2015, we studied an outbreak of this species in small scale vegetable farms of the Cachoeiras de Macacu Municipality (unpublished). In 2020, this species was also found in Puerto Rico, affecting small-scale agroecological vegetable production. Recently, the exotic Chinese slug *Meghimatium pictum* (Stoliczka, 1873) was associated to a case of abdominal angiostrongyliasis in a region where it is a grape pest (Rodriguez et al., 2019). This brings attention to the possible risk of human infection associated with accidental ingestion of contaminated fruit or vegetables containing larvae of the parasitic nematode *A. costaricensis*, the etiological agent of this parasitosis.

## SLUG MANAGEMENT IN THE NEOTROPICS

After examining abstracts and articles, we found 389 records that covered the topic of slug management. In general, seventy-five records (19% of records) covered metaldehyde use, and 55 covered other organic (i.e., with carbon) pesticides such as methiocarb. Records about metaldehyde use start in 1940 (with Gimingham, 1940), while records about organic pesticides start in the 1960's (with Henderson, 1968). Twenty-six records were about the use of inorganic compounds for slug management, which was the oldest slug management practice described in the literature (Baltet, 1889). Two studies in the Neotropics mentioned the use of lime for semi-slug and slug management (Bastos Garcia et al., 2012; Capinera, 2018). Literature about biological control of slugs is dominated by studies about carabid beetles (25 records) and nematodes (45 records). These records begin in the 1980's for carabids (Symondson, 1989), and early 1990's for nematodes (Wilson et al., 1994). Other slug management practices include the use of botanical extracts, traps, solutions of conspecifics, *Bacillus thuringiensis*, and barriers. Also, there were records that examined the effect of different farm management practices on slugs, such as tilling, use of cover crops, irrigation regimes and crop rotation. Most slug management records are from temperate areas and were recently reviewed by Le Gall and Tooker (2017).

The management of slugs (and snails) in conventional agricultural areas has relied heavily on the use of metaldehyde pellets. The use of metaldehyde ($C_8H_{16}O_4$) as a molluscicide began in the 1930's, after the discovery of its molluscicide properties by women gardeners in South Africa (Gimingham, 1940). In the Caribbean, it started to be used in 1937 (Callan, 1941). In South America, it has been known to be used since the 1940's (Pereira and Gonçalves, 1949). Slugs died 1–2 days after consuming metaldehyde pellets, but the adequate consumption of pellets does not always occur, making the method inefficient (Bailey, 2002). Metaldehyde is soluble in water, highly mobile in soils and generally stable to abiotic degradation (EPA, 2006). In Europe, it has been identified as a water pollutant, being frequently detected in surface waters above the EU Drinking Water Directive (Kay and Grayson, 2014). Metaldehyde was banned in 2018 in England because of its pollutant potential, however the ban was later overturned. Metaldehyde is commonly used by farmers in the Neotropics. Five (out of 11) management articles in the Neotropics examined the used of metaldehyde to manage slugs. Metaldehyde residue limits exists for the export of some products, such as legume foliage (EPA, 2015).

Pellets containing iron phosphate have been used since the 1990's as an alternative to metaldehyde pellets in some countries (EPA, 1998). Iron phosphate pellets can be an effective curative slug control method (Speiser and Kistler, 2002). Also, iron phosphate is non-harmful to humans or the environment (EPA, 1998) and can be used in organic agriculture (USDA-NOP). Recently, pellets containing ferric sodium EDTA have also become commercially available in some countries as another curative slug control method (Capinera and Rodrigues, 2015). Ferric sodium EDTA also has very low toxicity to humans and the environment (EPA, 2008). In the Neotropics, iron phosphate is commercially available but can be less accessible than metaldehyde molluscicides (slightly higher cost per gram and lower distribution to rural areas). Laboratory experiments in Brazil and Florida, showed that iron phosphate pellets can be more effective or slightly less effective than metaldehyde pellets, respectively (Baronio et al., 2014; Capinera and Rodrigues, 2015).

Several management practices were followed by farmers to manage *S. plebeia* in Central America. Beans are a staple food of family farmers in Central America, and are usually planted in a relay system with maize. Some of the management practices first implemented by Honduran farmers to deal with the new slug problem were: planting in slopes, burning maize residues before bean planting, deep tilling, and empirical pesticide use (Andrews, 1987a). From 1975 to 1987, the Honduran government subsidized the purchase of metaldehyde to distribute among farmers. Andrews (1985) argued that this subsidy resulted in less effective chemical control than that of Mexico or El Salvador, where private chemical companies lead control efforts. Several slug management techniques were evaluated at Zamorano, Honduras with farmer participation (Rueda et al., 2002). Some Honduran farmers preferred to combine different management techniques, including weed management, weed traps, night killing of slugs with a stake, and use of homemade baits (with *Jatropha curcas* seeds or metaldehyde) when there are more than 5 slugs per ten plants (FAO, 2005). Farmers using traditional "frijol tapado" systems in Costa Rica preferably use east-facing slopes and eliminate some of the plant species that favor slugs (Meléndez, 2004).

Agroecosystems in the Neotropics can range from small-scale highly diverse home gardens to large-scale conventional monocultures of crops such as sugar cane, soy, banana or palm oil. Family farming and agroforestry systems are also important in the region (Peters et al., 2016; Schneider, 2016), and can contribute to the conservation of biodiversity in these landscapes (e.g., Rooduijn et al., 2018). A comparison of slug abundance and plant damage in two agroecological and conventional farms in Colombia, showed that although slugs were more abundant in the agroecological farm, only one variety of lettuce had more damage in this system (Cordoba Vargas and Leon Sicard, 2010).

Agroforestry systems and landscapes with natural vegetation can benefit from higher predation of herbivores that feed on crops (Maas et al., 2020). Natural enemies of slugs include birds, reptiles, mammals, planarians, nematodes, insects, and mites, among others (Baker, 2004). In other regions, there has been an emphasis on the study of carabids and nematodes for slug biological control. In the Neotropics, natural enemies of slugs have not been studied in detail, but there are some documented and anecdotal examples. Firefly (Coleoptera: Lampyridae) larvae are known to feed on slugs (Viviani, 2001), but the rate of predation has been low under laboratory conditions (1 slug every 5 days; Rueda et al., 2002). Native planarians preferentially feed on introduced slugs and snails (Boll and Leal-Zanchet, 2015). Toads were used successfully in gardens of Colombia to reduce slug populations (Posada-Flórez et al., 2001). Since the Neotropics are very diverse, many natural enemies of slugs may remain to be discovered. For example, five new species of snakes that feed on terrestrial mollusks were recently discovered in Ecuador and Peru (Arteaga et al., 2018).

Nematodes and pathogens of slugs are also of interest for slug biological control efforts worldwide. The nematode *Phasmarhabditis hermaphrodita* (Schneider, 2016) is available commercially in Europe (Pieterse et al., 2016), and has been recently introduced to several countries (Howe et al., 2020). In the Neotropics, Mermithid and Rhabditid nematodes have been found parasitizing slugs (Thiengo, 1995; Posada-Flórez et al., 2001; Rueda et al., 2002; Moreno Suárez et al., 2008). In Brazil, we found Rhabditid nematodes parasitizing few slugs. Pathogenic bacteria and fungi can also infect slugs (Moreno Suárez et al., 2008; Galvis and Moreno, 2018).

## OTHER CONSIDERATIONS

### Global Change and Slugs in Agricultural Areas

The global distribution of terrestrial gastropods is changing. Humans have facilitated the dispersal of gastropod species across the globe, breaking geographic barriers and homogenizing global terrestrial gastropod diversity (Capinha et al., 2015). In this process, many species have become endangered, sometimes because of other mollusk pest biological control efforts (Lydeard et al., 2004). Other terrestrial gastropod species have benefited from human-facilitated dispersal, and have become invasive pests (Cowie et al., 2008). This was observed early on by Binnei (1871), when he described "All the species mentioned below are of foreign origin. They were imported from England. They are found only in close proximity to man. They have also been imported into other colonies of England, and probably are destined to become the most cosmopolitan of mollusks." There are at least 13 alien species of slugs in South America (Rumi et al., 2010; Gregoric et al., 2013). In Colombia, at least seven European slug species have been introduced in the highlands, some more than a century ago (Hausdorf, 2002).

Introduced non-native slug species can have detrimental effects in agricultural areas. This is the case of slugs such as *Deroceras reticulatum* in Australia (Nash et al., 2007), and the Cuban slug *Veronicella cubensis* (Pfeiffer, 1840) in the island of Rota (Robinson and Fields, 2010). We discussed examples in this article showing that this can also be the case in the Neotropics. Early on, Cockerell (1893b) described the introduction of European slugs in strawberries in Jamaica, stating that "They and their eggs come in the earth about the roots, and, in many cases, it must be practically impossible to detect them on arrival." In the case of the bean slug, the species was accidentally introduced from South America and caused damage to both conventional and diverse small-scale farmers in Central America (Andrews and Dundee, 1987). In the island of Puerto Rico, the non-natives *V. cubensis* and *S. linguaefomis* are causing problems to small-scale vegetable farmers. Introduced slug species are expected to thrive more in disturbed habitats, such as agricultural lands, than native slug species (Ryser et al., 2011). However, they can colonize natural areas and affect native plant communities (Shiels et al., 2014).

The range of invasive slugs may increase with climate change, since some species are favored by warmer conditions (Sommer and Cowie, 2020). Although terrestrial gastropods are susceptible to desiccation, they can also have costly behavioral and physiological mechanisms that help them cope with high temperature and drought periods (Nicolai and Ansart, 2017). Temperature increases, changes in rainfall patterns and increase of extreme weather events are expected for the Neotropics in the next 100 years. Traditionally, farmers associate periods of rains with higher slug abundance. Extreme rain events, such as hurricanes, decreased the abundance of the native semi-slug *Gaeotis nigrolineata* (Shuttleworth, 1854) in Puerto Rico (Willig and Camilo, 1991).

### Slug Identification and Monitoring

Slug diversity in agroecosystems in the Neotropics should be studied and considered more. This could be a first step to detect potential new slug invaders, and to better understand the drivers of sudden slug infestations in farms. A caveat to this is that slug identification can be difficult. A combination of external characters and internal anatomy is usually required to correctly identify species. Robinson (1999) presents the example of the process from the USDA Plant Protection and Quarantine Program, in which: (1) port inspectors find mollusks in arriving shipments; (2) port identifiers (PI) try to identify the species; (3) if the PI cannot identify the species, the PI dissects the individual and takes digital images of it; (4) the images are rapidly sent to the National Malacology Laboratory for identification; (5) if needed, the individual is sent for molecular analysis.

Recently, a new network of malacologists was created to track the presence of non-native mollusks in South America (Darrigran et al., 2020). The group is an important first step to increase awareness about this topic in our region. More attention should also be given to train extension and other agriculture professionals in slug identification, and to improve the identification (e.g., molecular) tools of slugs in the Neotropics. Participatory strategies may also help in the detection of new slug invaders or infestations. Knowledge dialogues or exchanges with and between farmers are an important agroecological practice in Latin America (Mier y Terán Giménez

Cacho et al., 2018). In the case of the bean slug in Honduras, farmers would prefer using "trash" traps (i.e., pilled plants residues from weeding and pruning) to monitor slug presence than other traps that required materials from outside the farm (Andrews, 1987b). Relying on damage observation was not recommended, as slug populations were difficult to manage at that point. In other regions, citizen science has been used to detect the occurrence of invasive slugs in private and public lands (Dorler et al., 2018; Morii et al., 2018). The participation of malacologists in social media groups, such as Facebook Groups "Moluscos del Ecuador" or "Biodiversidad de Puerto Rico," can make slug identification more accessible to the general public.

We found few initiatives that were testing unmanned vehicles for slug detection in farms. In Colombia, drones were experimentally used to determine the presence of slugs in flower cultivation (Caceres Florez et al., 2015). The drones detected leave damage, not slug individuals. Because slugs are frequently hidden in the soil, land unmanned vehicles have also been considered in other regions (Godeke et al., 2019).

## CONCLUSIONS

Slugs can be important pests in agricultural areas worldwide. In the Neotropics, reported examples of slug pests are fewer than in other regions such as Western Europe. Many factors could be hypothesized to explain this, starting with less abundance of malacologists studying terrestrial gastropods in the region. Also, the ecosystem service of natural pest regulation could be preventing slug populations to reach economic injury levels. Another possibility is that slugs are not considered pests by farmers, as observed for insect herbivores in traditional milpa systems of Guatemala (Morales and Perfecto, 2000). Alternatively, management of slugs is not studied extensively in the Neotropics because metaldehyde has been used to kill outbreaks of terrestrial mollusks for nearly 80 years. The examples presented in this article show that there are instances when slugs have been problematic in the Neotropics. It is important to understand these and other examples in order to prevent future slug pest problems in farms of our region.

Slugs and their management have been understudied in the Neotropics. More research is needed about their diversity and biology in our region. Weather extremes and international trade are expected with global change, and invasive slugs could benefit from these changes. Farmers already use a variety of techniques including barriers, traps and resistant crops, and socialize this information among themselves. However, these preventive management practices have not been sufficiently documented or validated in the scientific literature. The case of the bean slug provided important information about slug management in our region. However, these studies were conducted almost 40 years ago. New social and ecological technologies may exist to advance slug management in the Neotropics.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

OR-R and MR conducted the systematic literature review. SG contributed additional literature, slug infestation cases, and expertise on slug taxonomy and biology. All authors contributed to the writing of the manuscript, with MR and SG contributing the most.

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# Intercropping With Peppermint Increases Ground Dwelling Insect and Pollinator Abundance and Decreases *Drosophila suzukii* in Fruit

***Chelsea Megan Gowton*†, César Cabra-Arias† and Juli Carrillo†***

*Plant Insect Ecology and Evolution Lab, Faculty of Land and Food Systems, Centre for Sustainable Food Systems, Biodiversity Research Centre, The University of British Columbia, Unceded xʷməθkʷəýəm Musqueam Territory, Vancouver, BC, Canada*

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***Correspondence:**
*Chelsea Megan Gowton*
*cgowton@mail.ubc.ca*

**†ORCID:**
*Chelsea Megan Gowton*
*orcid.org/0000-0003-2443-0809*
*César Cabra-Arias*
*orcid.org/0000-0002-7164-9785*
*Juli Carrillo*
*orcid.org/0000-0003-4673-2875*

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Intercropping can be used to reduce pest insects within agricultural systems, e.g., through deterring pests directly or by increasing habitat for their natural enemies. For example, plant produced volatile organic compounds (VOCs) can deter or confuse host-finding by insects through olfactory disruption. *Drosophila suzukii* is an invasive fruit fly of agricultural concern as it can lay its eggs in both ripening and fresh fruits and, uses olfactory cues to identify its wide range of host plants. Peppermint plants (*Mentha* × *piperita*) produce high levels of VOCs while growing and may, therefore, be suitable as an intercrop to reduce *D. suzukii* infestations in the field, as peppermint essential oil VOCs have previously been shown to deter *D. suzukii* in olfactory trials. We conducted a field intercropping experiment to evaluate the effectiveness of peppermint plants compared to traditional ryegrass/clover mixes in reducing *D. suzukii* oviposition in the field, and the effect of peppermint intercrops on other invertebrates. In the field, we monitored sentinel fruit baits weekly for *D. suzukii* infestation. Additionally, we monitored intercropping effects on the invertebrate community through weekly pitfall trap collection and through a pollinator point survey. We monitored for local, farm level presence of *D. suzukii* through apple cider vinegar traps within crop fields and along hedgerows and found high abundance of *D. suzukii* (>3,000 individuals trapped). Peppermint intercrops had fewer *D. suzukii* emerge from fruit baits and supported greater beneficial insect abundance (predators and pollinators) compared to ryegrass/clover. However, levels of *D. suzukii* were low across both intercrop types. Overall, we found that peppermint intercrops could be a potential aromatic intercrop used to reduce *D. suzukii* adult emergence from fruit compared to conventional ryegrass/clover mixes, however this trial should be replicated over multiple growing seasons, geographic locations, and host fruits. Furthermore, further study should determine the effects of the intercrop on the focal crop of interest.

**Keywords: spotted wing drosophila (SWD), biological control, biodiversity, agroecosystem, organic, pest management**

# INTRODUCTION

Increased plant diversity on farms can improve ecosystem services such as nutrient cycling, soil conservation, pollination, and pest control (Isbell et al., 2017). Within a cropping system, including two or more crops (e.g., polyculture, intercropping, etc.), or utilizing companion plants (e.g., insectary plants Brennan, 2013, 2016) can support pest control goals in a multitude of ways. For example, including multispecies plantings may disrupt the ability of pest insects to find their host plants through changes in visual, olfactory, and other sensory cues (Cook et al., 2007; Pickett et al., 2012, 2014). Increasing plant diversity on farm, including through the use of intercropping systems, can increase the diversity and availability of resources (e.g., habitat, nectar, and pollen) for beneficial and predaceous insects, potentially supporting top-down control of pest populations (Root, 1973; Tscharntke et al., 2002; Kruess, 2003). For intractable pests, in which other control options have limited utility (e.g., due to the development of insecticide resistance or the inaccessibility of the pest to pesticide application) or are otherwise restricted (e.g., to maintain organic certification and/or to avoid negative interactions with pollinators), intercropping may present a more sustainable option for growers (Brennan, 2013, 2016; Pickett et al., 2014).

*Drosophila suzukii* Matsumura (Diptera: Drosophilidae) is an invasive insect pest accidentally introduced to the US in 2008 and has since become widely distributed across fruit growing regions including the USA (Lee et al., 2012), Europe (Asplen et al., 2015), Mexico and South America (Deprá et al., 2014), and Canada (Walsh et al., 2011; Thistlewood et al., 2013). *D. suzukii* females possess a serrated ovipositor which allows them to lay eggs in a broad range of ripening and fresh fruits, leading to larval presence within harvested fruit (Walsh et al., 2011; Anfora et al., 2012). Finding more effective and sustainable means of control for *D. suzukii* is of utmost importance due to the substantial losses experienced in berry and small fruit industries (Asplen et al., 2015; Haye et al., 2016) and the intensive management required to maintain marketable fruit.

Common management practices to prevent and reduce *D. suzukii* infestations include pesticide sprays every 4–7 days (Bruck et al., 2011), which can have numerous non-target effects (Desneux et al., 2006). Growers typically rely on pesticide sprays consisting of pyrethroids, carbamates, and spinosyns which target adults, which represent only about 10% of the populations (Anfora et al., 2012), whereas larvae are generally protected within developing fruit and pupae fall and burrow in the ground (Woltz and Lee, 2017). In Canada, two organic pesticides are registered for *D. suzukii* management, of which only one (spinosyn) is effective at reducing *D. suzukii* damage to crops (Bruck et al., 2011). Overall, the organic sector is more impacted by *D. suzukii* infestation due to the limited availability of effective and economically-feasible *D. suzukii* control solutions (Iglesias and Liburd, 2017). Although growers may also use cultural management practices such as rapid harvesting, removing damaged and dropped fruit, and the use of exclusion netting to manage *D. suzukii* (Leach et al., 2018), these practices can be economically unfeasible or provide limited control (Iglesias and Liburd, 2017). Both organic and conventional growers are impacted by the evolution of pesticide resistance in *D. suzukii* populations (Gress and Zalom, 2019), necessitating alternative control options and spurring research into the use of intercropping systems for *D. suzukii* control.

Of note, some intercrops release volatile organic compounds (VOCs) which can function in the attraction and deterrence of insect pests (Miller and Cowles, 1990; Khan et al., 2008). Utilizing plant-produced VOCs may be a less intensive way to manage pests compared to conventional pesticide application (Desneux et al., 2006; Khan et al., 2008), or could provide supplementary control. Plant-produced VOCs may disrupt host-finding behavior by either repelling or deterring pest insects from potential hosts (Miller and Cowles, 1990; Agelopoulos et al., 1999; Cook et al., 2007; Khan et al., 2008), or by attracting insects to traps (Burrack et al., 2015; Figueroa-Castro et al., 2017; Hasni et al., 2017). For example, VOCs from plant essential oils have been used to repel agricultural pests including codling moth (*Cydia pomenella* L.) (with oils of lavender, *Lavandula officinalis* L.; pennyroyal, *Mentha pulegium* L.; and cypress, *Cupressus sempervirens* L.) (Landolt et al., 1999), red bud borer midges [*Resseliella oculiperda* (Rubasaamen)] (with lavender essential oil, *Lavandula angustifolia* P. Mill.) (Van Tol et al., 2007) and western flower thrips [*Frankliniella occidentalis* (Pergande)] (with common thyme, *Thymus vulgaris* L. and winter savory, *Satureja montana* L.) (Picard et al., 2012). In the few instances where intercropping has been trialed in field systems, intercropping with high VOC-producing plants has been shown to reduce pests, either through direct repellent effects (e.g., Pickett et al., 2014) or through the attraction of natural enemies (Brennan, 2013, 2016). For example, intercropping maize with VOC-producing silverleaf desmodium (*Desmodium uncinatum* Jacq.) has been successful at reducing pests such as the stemborer moths (*Chilo partellus* Swinhoe) in sub-Saharan Africa (Khan et al., 2008; Vanlauwe et al., 2008; Pickett et al., 2014). Intercropping lettuce (*Lactuca sativa* L.) with sweet alyssum (*Lobularia maritima* L.) has also been successful at reducing currant-lettuce aphids (*Nasonovia ribisnigri* Mosley) by recruiting natural enemies such as hoverflies (Syrphidae) (Brennan, 2013); this pattern has also been observed in sweet alyssum intercropping of broccoli (*Brassica oleracea* L.) (Brennan, 2016). However, intercropping can also have neutral (Hodgkiss et al., 2019), or even positive effects on pest populations, e.g., through the creation of beneficial microhabitat that supports pest populations (Root, 1973). It is important to note that for intercropping practices to be successful, they must reduce pest populations while not impacting focal crop yield. Iverson et al. (2014) found diverse cropping systems, especially at high cropping densities, benefit pest biocontrol without affecting focal crop yield. However, they found that even when their results were consistent across geographical areas, the intercropping system could be affected by the type of plants used suggesting the need for intercrop trials with multiple plant types (Iverson et al., 2014). Furthermore, Letourneau et al. (2011) also found diversified cropping systems to benefit herbivore suppression through increased natural enemies, and that reductions in crop yield resulted from non-crop plants replacing those of agricultural importance.

Peppermint [*Mentha* x *piperita*, L. (pro. sp.)] is an aromatic crop for use in essential oil production as it yields high quantities of VOCs, including menthol (Santoro et al., 2011). In the laboratory, peppermint essential oil volatiles deterred *D. suzukii* adults up to 6 days after application (Renkema et al., 2016) and reduced adult emergence from pupae (Gowton et al., 2020). These results suggest that intercropping with volatile producing companion crops, such as peppermint, may similarly disrupt host finding or reproductive behavior of *D. suzukii*. Furthermore, growers may receive other benefits through intercropping practices such as diversified crops available to sell at market, reduction of other pests and weeds (Knörzer et al., 2010), and the attraction of beneficial insects. This reduction of pests by their natural enemies (i.e., predators and parasitoids) is expected to be more efficient in diversified crop habitats compared with simplified ones, as natural enemies may be more abundant in environments offering a greater diversity of prey/host species and microhabitats to exploit (Root, 1973).

Through a series of field assays at the University of British Columbia (UBC) Farm, we evaluated whether a peppermint intercrop could (1) reduce *D. suzukii* infestations in ripe fruit, (2) increase the number of beneficial ground dwelling invertebrates (potential pupal predators of *D. suzukii*), and (3) increase pollinators compared to the common alley groundcover of ryegrass and white clover.

## MATERIALS AND METHODS

### Site Description

On May 19, 2017, we initiated a field experiment at the Center for Sustainable Food Systems at UBC Farm (The University of British Columbia) to determine the efficacy of interplanting peppermint as a method to reduce *D. suzukii* infestations. UBC and UBC farm are located on the traditional, ancestral, and unceded territory of the xʷməθkʷəy̓əm Musqueam people, within a 90-year-old coastal hemlock forest (Centre for Sustainable Food Systems at UBC Farm, 2019). The UBC Farm is a 24-hectare, certified organic, diversified farm that grows over 200 varieties of fruits and vegetables, including blueberries and strawberries, common crop hosts of *D. suzukii* (Centre for Sustainable Food Systems at UBC Farm, 2019). The area surrounding UBC Farm includes alternative hosts of *D. suzukii*, such as elderberry (*Sambucus* L.), Himalayan blackberry (*Rubus armeniacus* Focke), salmonberry (*Rubus spectabilis* Pursh), trailing blackberry (*Rubus ursinus* Cham. & Shchldl.), and thimbleberry (*Rubus parviflorus* Nutt). The majority of BC blueberry production occurs within the lower Fraser Valley, which produces 90% of Canada's highbush blueberries (AgriService BC, 2018). The closest berry production operations are 12.64 km from UBC Farm. However, unlike much of the blueberry growing region of the lower Fraser Valley, the UBC farm is located on Bose-Heron soil (non-agricultural soil) with a sandy loam texture, characterized by poor water and nutrient-holding capacity but high soil organic matter (SOM) content due to management practices (Krzic et al., 2015).

### On-Farm Monitoring of *D. suzukii*

We monitored on-farm presence of *D. suzukii* with 10 apple cider vinegar (ACV) liquid bait traps located within hedgerows, 3 traps within a separate production planting of blueberries (Duke and Reka varieties) and 3 traps within a production planting of strawberries at the UBC Farm (**Supplementary Figure 1**). Each trap consisted of a 950 mL polypropylene deli container (Fabri-Kal) with ten 2.0 mm holes spaced 2.5 cm apart 10 cm from the top of the container filled with an ACV stock solution of 4-L of store-bought apple cider vinegar mixed with 0.1 g unscented detergent (Alconox, Inc.), and 0.05 g instant yeast. We placed 200 mL of the ACV solution in the trap and hung the trap on a 1.20 m U-Post (Peak Products) and collected it weekly. From the ACV traps, *D. suzukii* were sorted from other drosophilids and bycatch, counted and sexed. We conducted ACV trapping from April 12th to October 25th, 2018.

### Experimental Plot Establishment at UBC Farm

UBC Farm staff tilled the 31 by 7.5-m site (49.249845 N,−123.237734 W) prior to plot establishment in 2017. We obtained 36 Duke variety blueberry bushes (*Vaccinium corymbosum* L.) in 7.5 L pots (Sidhu Growers, Abbotsford, BC Canada). We sunk the pots into the ground at 1-m spacing (from pot center to pot center) to create two rows of 18, consisting of 6 blocks. We chose to sink pots in the ground to standardize root zone availability within the blueberry plants and reduce potential competition between blueberry plants and intercrops. Each block contained two rows of three blueberry plants, separated by three 1.5 × 5 m intercrop areas of either peppermint or ryegrass/clover control (**Supplementary Figure 2**).

Peppermint and ryegrass/clover blocks alternated within the field (not applied randomly), to reduce any density dependent effects of adjacent plots on volatile production and insect attraction. We used 1.0 m wide black landscaping cloth to create a buffer around the perimeter of the plot and between each intercrop block. On November 1, 2017, we seeded the control intercrop areas with white clover (*Trifolium repens* L.) (TerraLink Horticulture Inc.) and RichLawn Low-Maintenance Mix (TerraLink Horticulture Inc.) which contained a mixture of 20% perennial ryegrass (*Lolium perenne*), 30% hard fescue (*Festuca ovina*), and 50% creeping red fescue (*Festuca rubra*), a common alleyway cover crop on local Lower Fraser Valley berry farms. We seeded the white clover at 0.15 kg/92.90 $m^2$ and Low-Maintenance mix at a rate of 4.08 kg/92.90 $m^2$. Within each peppermint plot, we transplanted 25 clonal plants propagated from cuttings from a commercially purchased peppermint [*Mentha* x *piperita* L. (pro. sp.), no variety given], grown in 3.8 L containers. Throughout the duration of the experiment, we maintained peppermint plots by weeding non-peppermint by hand and by trimming and removing peppermint runners under the landscaping cloth. The ryegrass and clover plots did not receive mowing or weeding maintenance during the experimental period. Plots were watered using overhead sprinkler irrigation from April through the end of September for 15 min, four times per day.

## Intercropping Effects on *D. suzukii*

To test whether *D. suzukii* infestation differed between intercrop type (peppermint vs. traditional ryegrass/clover mix), we employed sentinel assays using fresh fruit baits within each intercrop type. In-field blueberry plants were too young in 2018 to produce enough mature fruit during this phase of the experiment to evaluate herbivory in a standardized method, however, the potted blueberry likely provided visual and olfactory cues of potential host plants.

To exclude bird and rodent damage or consumption of fruits, we constructed "fruit cages" (**Supplementary Figure 3**) to house fruit baits. Each week, we purchased fresh, organic blueberries to serve as bait for the fruit cages. We washed the fruit and placed five unblemished berries in each of the fruit cages. We placed a single baited cage at ground level within each of the 1.5 × 5 m intercrop plots of the field site ($n = 9$ for peppermint, $n = 9$ for ryegrass/clover control). Ground-based cages retained higher humidity (critical for *D. suzukii* survival) than traps placed at canopy level and *D. suzukii* will readily oviposit in both intact and abscised fruit. Baited cages remained in the field for 48 h to allow for wild *D. suzukii* oviposition. After the exposure period, berries were collected from each cage and placed in a 120 mL plastic solo cup (Uline, Model S-21201) with a perforated lid for airflow, and incubated in the lab for 2 weeks. Cages were reset with blueberries on a weekly basis and repeated over 18 weeks from May 1 to August 30, 2018. From September 11 to October 11, 2018, we followed the same protocol but used organic raspberries within the cages, due to commercial availability, and repeated this over a 5-week sampling period. Both blueberry and raspberry are commonly used in sentinel fruit assays with *D. suzukii* (Lee et al., 2011, 2016). Incubation in the lab occurred at ambient laboratory temperature and humidity (∼23°C and ∼45% RH) under cool white lights on a 16:8 h light:dark cycle. After 2 weeks of incubation, we counted all emerged drosophilids and identified adult *D. suzukii* and non-*D. suzukii* within samples. Additionally, each week we incubated 10 sets of "control" blueberries and raspberries (5 berries/incubation cup)—not placed in the field—to estimate base levels of *D. suzukii* from store bought fruit.

On May 29, 2018, we observed chewing damage from slugs, ground beetles and wasps on blueberry baits, despite our mesh cages. We recorded the number of blueberries receiving chewing damage and brought the damaged blueberries back to the lab with any intact berries for the incubation period. We did not record raspberry damage due to the friable structure of the fruit itself after being exposed in the field.

## Pitfall Trap Survey

We placed dry Vernon Pitfall Traps (Intko Supply Ltd.) in the center of plots along the top and bottom rows of the experimental planting on July 3, 2018 (**Supplementary Figure 2**). We collected pitfall traps weekly until a final sampling date on October 16, 2018 for a total of 16 weeks. For each sampling event, we froze individual pitfall samples for at least 24 h, before identifying each sample to family level, except for Collembola which we identified to order (**Supplementary Table 1**). We identified the insects in the pitfall traps through morphological characterization. We started identifying the taxonomical orders by their most recognizable traits, and then we used dichotomous keys (Borror and White, 1970; Bland and Jaques, 2010) to identify specimens to taxonomical families. We supported our findings by comparing our samples with entomology photographic atlas (Castner, 2000), the photographic records from the Spencer Entomological Collection in the Department of Zoology at the University of British Columbia, and the specialized literature. For every family that we identified, we corroborated its taxonomic status and hierarchy with the Integrated Taxonomic Information System (ITIS) online database. To establish the functional groups to which those specimens belonged, we searched in the specialized literature, and we assigned our specimens to three categories: predators, herbivores, and detritivores (**Supplementary Table 1**).

## Pollinator Survey

Midway through the growing season (July 13, 2018), we conducted a single pollinator survey across a subset of the experimental plots (six of each treatment) by sweep netting (Willmer and Stone, 2004). We counted all pollinators per plot including honeybees (Apidae, Hymenoptera), bumblebees, (Apidae, Hymenoptera), soldier beetles (Cantharidae, Coleoptera), butterflies (Hesperiidae, Lepidoptera), and hoverflies (Syrphidae, Diptera).

## Statistical Analysis

All analyses were conducted in R version 3.6.1. (R Core Team, 2014) and figures were drawn using ggplot 2 (Wickham, 2016). We used the glmmTMB package to analyze each response variable (Brooks et al., 2017), except total pollinators which used a linear model available in base R, and determined model fit through testing for overdispersion and comparing AIC scores (Blasco-Moreno et al., 2019, Bolker et al., 2009).

### On Farm Presence of *D. suzukii*

In order to run Tukey *post-hoc* test to compare trap locations, we filtered ACV trap data by sample date to create two data frames. The first contains samples across all three trap locations (hedgerow, blueberry production field, or strawberry production field) from April 19, 2018 through August 16, 2018. We analyzed the total number of *D. suzukii* caught in ACV traps with time (as continuous) and trap location (hedgerow, blueberry production field, or strawberry production field) as fixed effects. We then ran a *post-hoc* Tukey test to determine main effect differences between all three trap locations.

After August 16, 2018 the strawberry production field was tilled by the growers, and we stopped ACV trap sampling in the strawberry production. The second data frame contains ACV traps samples from hedgerows and blueberry production field from August 23, 2018 through October 18, 2018. We analyzed the total number of *D. suzukii* caught in ACV traps with time (as continuous) and trap location (hedgerow, or blueberry production field) as fixed effects. As trap counts were zero heavy, we specified a zero inflated negative binomial II distribution for both models.

### Adult *D. suzukii* Emergence From Fruit Baits

We analyzed the number of adult *D. suzukii* emerged from each fruit bait, with treatment (peppermint intercrop or ryegrass/clover control) and week (continuous) as fixed effects and plot as a random effect. As the emergence count data were zero heavy, we specified a zero inflated Poisson distribution for our model. Although we initially included fruit type (blueberry or raspberry) as a factor in the model, due to the abundance of zero counts, the fully parameterized model could not converge. Therefore, we excluded the fixed effect of fruit type to first evaluate the effects of intercropping across the full sampling period. We then filtered the data by fruit type which created two new data frames, the first being blueberry fruit bait samples and second raspberry fruit bait samples. In two separate models, we analyzed the number of adult *D. suzukii* emerged from (1) blueberry with treatment (peppermint intercrop or ryegrass/clover) and week (as continuous) as fixed effects; and (2) raspberry fruit bait with treatment (peppermint intercrop or ryegrass/clover) and week (as continuous) as fixed effects, and plot as a random effect, both with a Poisson distribution.

### Non-*D. suzukii* Damage of Berries

We analyzed the number of blueberries (zero through five) experiencing non-*D. suzukii* insect damage using a generalized linear model with a zero inflated Poisson distribution with intercrop and date (as continuous) as fixed effects and plot as a random effect. Although these data were proportional, analyzing the total number of berries with damage provided better model fit due to the large number of zeros within the data.

### Insect Groups Collected From Pitfall Traps

We classified insects captured within pitfall traps according to three functional groups: herbivore, predator, or detritivore (**Supplementary Table 1**). We analyzed pitfall trap samples (total insects, total predators, total herbivores (excluding *D. suzukii*), and total detritivores) using a generalized linear mixed model with intercrop (as categorical) and time (as continuous) as fixed effects and plot as a random effect. After assessing for overdispersion and normalcy, we fit our total insect model with a generalized Poisson distribution, total predator model with a zero inflated negative binomial I distribution, and the total herbivores and total detritivores models with a zero inflated negative binomial II distribution.

### Pollinator Survey

We analyzed the total number of sampled pollinators using a linear model with intercrop as a fixed effect.

## RESULTS

## On Farm Presence of *D. suzukii*

Apple cider vinegar traps captured *D. suzukii* across the landscape at UBC Farm (**Figure 1**). We captured a total of 3,063 individual *D. suzukii* adults within our ACV traps during our sampling period. From April 19 to August 16, 2018, we captured more *D. suzukii* in hedgerows compared to blueberry and strawberry production fields [trap location: $X^2{}_{(2,280)} = 48.10$, $p < 0.0001$], and captures depended upon sample date [$X^2{}_{(1,280)} = 102.47$, $p < 0.0001$], and the interaction between trap location and sample date [$X^2{}_{(2,280)} = 7.93$, $p = 0.02$]. After August 23, 2018, *D. suzukii* capture rates were higher in hedgerows than the blueberry production field [trap location: $X^2{}_{(1,111)} = 17.21$, $p < 0.0001$), and were dependent on sample date [sample date: $X^2{}_{(1,111)} = 101.17$, $p < 0.0001$] and the interaction between sample date and trap location [$X^2{}_{(1,111)} = 9.64$, $p = 0.002$]. We first detected *D. suzukii* in monitoring traps on April 19, with increasing ACV trap captures until July 26, 2018 (mean *D. suzukii*/trap ± SE: 24.4 ± 6.7) (**Figure 1**). During the month of August, we found decreased ACV trap captures of *D. suzukii* (**Figure 1**). The highest trapping of *D. suzukii* occurred on October 11, 2018 in traps located along the field hedgerows (mean *D. suzukii*/trap ± SE: 72.8 ± 13.89) (**Figure 1**).

## Adult *D. suzukii* Emergence From Fruit Baits

We observed low emergence rates of *D. suzukii* (between 0 and 5 flies per sample) from the fruit cages when using blueberries and raspberries as bait (**Figure 2**). Out of 414 berry bait samples, we recorded a total of 29 adult *D. suzukii* from 20 fruit bait samples. We observed our first emergence of *D. suzukii* on July 26, 2018 in ryegrass/clover intercrop (average flies/cage ± SE: 0.22 ± 0.12) (**Figure 2**). When comparing emergence across all fruit types, *D. suzukii* emergence was lower in peppermint intercrops than in ryegrass/clover intercrops [intercrop: $X^2_{(1,408)} = 5.00$, $p = 0.02$], and increased through time [date: $X^2_{(1,408)} = 15.71$, $p < 0.0001$]. Intercrop and sampling time did not interact to influence *D. suzukii* emergence [intercrop × date: $X^2_{(1,408)} = 0.09$, $p = 0.77$].

When we restricted the analysis to only the fruit cages baited with blueberry, adult *D. suzukii* emergence increased through time [date: $X^2_{(1,320)} = 6.78$, $p = 0.01$], but did not differ between peppermint and ryegrass/clover intercrops [intercrop: $X^2_{(1,320)} = 0.00$, $p = 1.00$] or the interaction with sampling time [intercrop × date: $X^2_{(1,320)} = 0.00$, $p = 1.00$; **Supplementary Figure 4**]. However, zero *D. suzukii* emerged from blueberry bait placed in peppermint intercrops (**Figure 2**; **Supplementary Figure 4**). When we restricted our analysis to only those fruit cages baited with raspberry, adult *D. suzukii* emergence decreased through time [date: $X^2_{(1,85)} = 17.25$, $p < 0.0001$], but emergence did not differ between intercrops [intercrop: $X^2_{(1,85)} = 0.30$, $p = 0.58$; **Supplementary Figure 4**] or depend upon an interaction between intercrop and sampling time [intercrop × date: $X^2_{(1,85)} = 0.16$, $p = 0.69$]. No *D. suzukii* emerged from the control berries that remained in the laboratory.

## Non-*D. suzukii* Damage of Berries

Fruit damage by other herbivores did not differ between intercropping type or over time [intercrop: $X^2_{(1,246)} = 0.55$, $p = 0.46$; date: $X^2_{(1,246)} = 2.59$, $p = 0.11$]. Damage by other

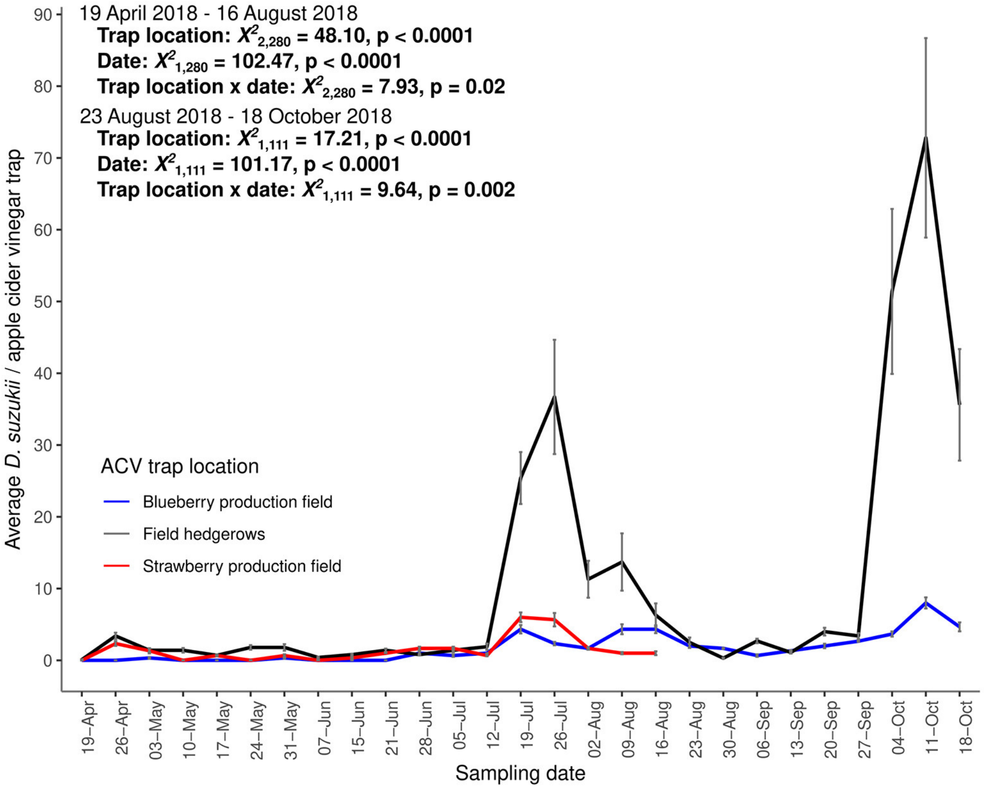

**FIGURE 1 |** Average counts of *D. suzukii* in apple cider vinegar traps in the blueberry production field (blue, $n = 3$), strawberry production field (red, $n = 3$) and field hedgerows (black, $n = 10$) sampled weekly from April 19, 2018 to October 18, 2018. Means and standard error shown.

herbivores varied in the interaction between intercrop type and sampling time [intercrop × date: $X^2_{(1,246)} = 5.04$, $p = 0.03$] (**Supplementary Figure 5**).

## Insect Groups Collected From Pitfall Traps

We captured 844 total insects within our pitfall traps, which included members of Hemiptera (Nabidae, Coreidae, Cercopidae, and Aphididae), Coleoptera (Staphylindae, Carabidae, Nitidulidae, Elateridae, Tenebrionidae, Curculionidae, Dermestidae, and Silphidae larvae), Hymenoptera (Braconidae, Cynipidae and Formicidae), Thysanoptera and Collembola. Total insect captures were affected by sampling date [date: $X^2_{(1,185)} = 21.01$, $p < 0.0001$; **Figure 3A**], but not intercrop type [intercrop: $X^2_{(1,185)} = 0.34$, $p = 0.56$; **Figure 3A**] or its interaction with date [date × intercrop: $X^2_{(1,185)} = 1.20$, $p = 0.27$; **Figure 3A**].

We additionally sorted trapped insects into predators, non-*D. suzukii* herbivores, and detritivores (**Supplementary Table 1**) to determine the effects of intercrops on these functional groups. Date and intercrop significantly affected the total number of predators [date: $X^2_{(1,185)} = 47.78$, $p < 0.0001$; intercrop: $X^2_{(1,185)} = 5.55$, $p = 0.02$]. We generally saw higher counts of predators in peppermint intercrop but this was variable across the sampling period [date × intercrop: $X^2_{(1,185)} = 6.74$, $p = 0.01$; **Figure 3B**]. Non-*D. suzukii* herbivores were more abundant in pitfall traps located in ryegrass/clover plots compared to peppermint intercrop plots [intercrop: $X^2{}_{(1,185)} = 20.53$, $p < 0.0001$; **Figure 3C**] with counts differing between sampling times [date: $X^2{}_{(1,185)} = 4.64$, $p = 0.03$; however, there was no interaction between date × intercrop: $X^2{}_{(1,185)} = 1.67$, $p = 0.20$]. We observed our highest non-*D. suzukii* herbivore counts on September 4, 2018 in our ryegrass/clover intercrops (average herbivores/trap ± SE: 9.50 ± 1.42) but counts within our peppermint intercrop traps were only 1.67 ± 0.34 (average non-*D. suzukii* herbivores/trap ± SE). Total detritivores caught in pitfall traps was dependent on sampling time [date: $X^2{}_{(1,185)} = 6.26$, $p = 0.01$] but not intercrop type [intercrop: $X^2{}_{(1,185)} = 0.07$, $p = 0.80$; **Figure 3D**]. There was a significant interaction between sampling date and intercrop type [date × intercrop: $X^2_{(1,185)} = 10.17$, $p = 0.001$].

## Pollinator Survey

Pollinators were more abundant in peppermint intercrops compared to ryegrass/clover plots [intercrop: $F_{(1,10)} = 20.12$, $p = 0.002$; **Figure 4**]. We observed honeybees, bumblebees, (Apidae, Hymenoptera), soldier beetles (Cantharidae, Coleoptera), butterflies (Hesperiidae, Lepidoptera), yellow jacket wasps (Vespidae, Hymenoptera), and hoverflies (Syrphidae, Diptera) visiting flowers while surveying the plots. In peppermint intercrops, we observed an average of 17.50 ± 1.93 pollinators

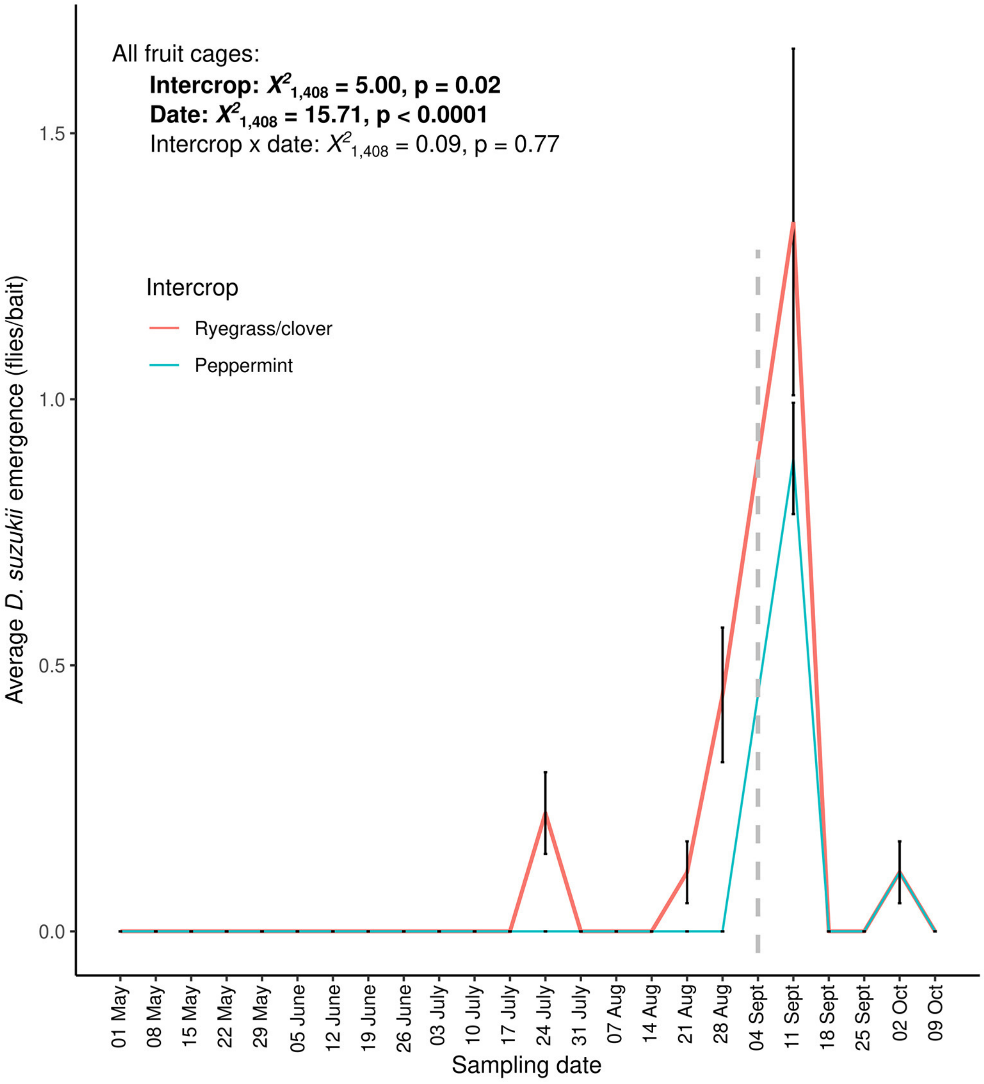

**FIGURE 2 |** *D. suzukii* emergence in weekly baited fruit baits with blueberries (May 3 to August 30, 2018) and raspberries (September 13 to October 11, 2018) in ryegrass/clover control (red) and peppermint (blue) intercrops. A dashed gray line on September 13, 2018 separates the two fruit types of fruit bait (blueberry and raspberry) used within the cages. Means and standard error shown.

per plot (average ± SE) compared to 3.00 ± 1.40 (average ± SE) within our ryegrass/clover control plots.

## DISCUSSION

Intercropping with peppermint reduced the number of *D. suzukii* adults emerging from fruit over the course of the season compared to the conventional ryegrass/clover mix (**Figure 2**), suggesting the potential for volatile intercrops to be used for *D. suzukii* management. Encouragingly, we found zero *D. suzukii* in blueberry baits within the peppermint intercrop (**Figure 2**), despite high levels of *D. suzukii* on farm (**Figure 1**). Indeed, we had generally low emergence of *D. suzukii* from all fruit baits.

*D. suzukii* prefer post-harvest fruit compared to ripening fruit (Keesey et al., 2015), and we expected *D. suzukii* emergence from fruit baits at higher levels than we observed. It could be that the microclimate of our experiment did not adequately support *D. suzukii. D. suzukii* prefer moist environments (Tochen et al., 2016; Rendon and Walton, 2019) and *D. suzukii* activity density has been shown to increase along the edge of large forest habitats compared to habitats with less edge (Santoiemma et al., 2019). The UBC Farm is a diversified agro-ecosystem and is situated within a 90-year-old hemlock forest habitat. The hedgerows consist of a wide variety of understory plants which can promote microhabitats suitable for *D. suzukii*. While no formal survey was done for the current study, the hedgerows of the UBC Farm were planted in 2005–2006 (Centre for Sustainable Food Systems at UBC Farm, 2021) and offer a wide array of

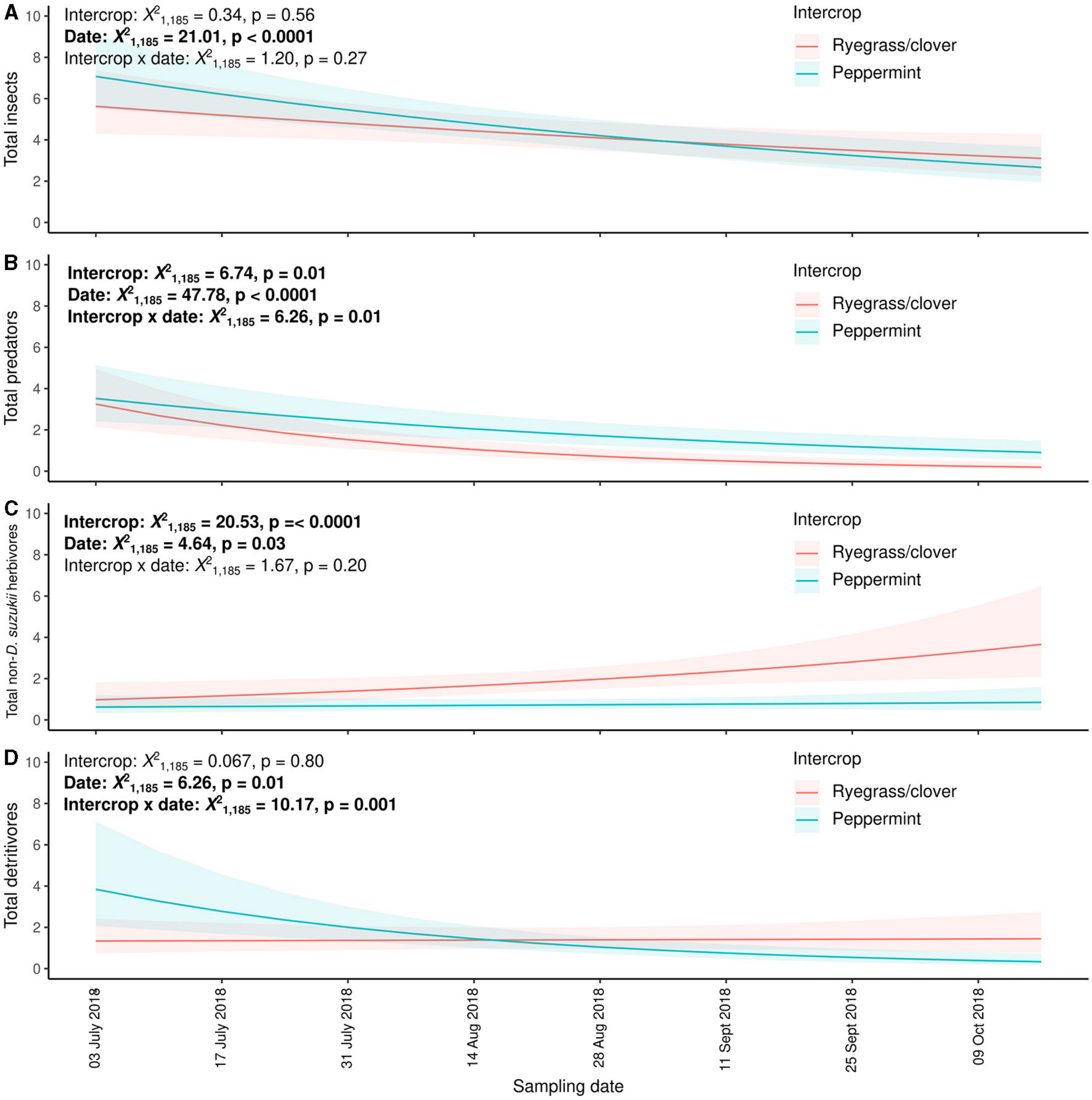

**FIGURE 3 |** The total insects **(A)** with functional groups being predators **(B)**, non-*D. suzukii* herbivores **(C)**, and detritivores **(D)** from pitfall traps ($n = 6$) collected on a weekly basis from July 3, 2018 to October 16, 2018 in ryegrass/clover control (red) and peppermint (blue) intercrops. Least square means with 95% confidence intervals shown.

alternative hosts for *D. suzukii* including salmonberry (*Rubus spectabilis* Pursh), thimbleberry (*Rubus parviflorus* Nutt.), salal (*Gaultheria shallon* Pursh), currant (*Ribes*), dogwood (*Cornus kousa* F.buerger *ex* Hance), Oregon grape (*Mahonia aquafolium* [Pursh] Nutt.), elderberry (*Sambucus*) and red huckleberry (*Vaccinium parvifolium* Sm.) (Lee et al., 2011, 2015). While not intentionally planted, of important note is the invasive species, Himalayan blackberry (*Rubus armeniacus* Focke), which has also colonized the hedgerows and provides numerous fruit for *D. suzukii* infestation. These hedgerow locations contain hosts that are more preferential for *D. suzukii* than the blueberries used within our field experiment (Olazcuaga et al., 2019). Furthermore, the lower mainland of Vancouver experiences a dry season during the summer months (Canada Environment and Climate Change, 2021). *D. suzukii* abundance increases in high humidity habitats which likely were present within the shaded hedgerows (Diepenbrock and Burrack, 2016; Tochen et al., 2016). To access the irrigated cropping areas, *D. suzukii* would have to leave these more preferential forested habitats and travel across dry exposed landscape to reach these agricultural hosts.

It could be that VOCs from our peppermint intercrop permeated the entire experimental area and reduced *D. suzukii* levels compared to overall farm levels. We assumed that any effects of VOCs would occur in the immediate area of the fruit baits, and that experimental plots could be considered independent as each of our plots were separated

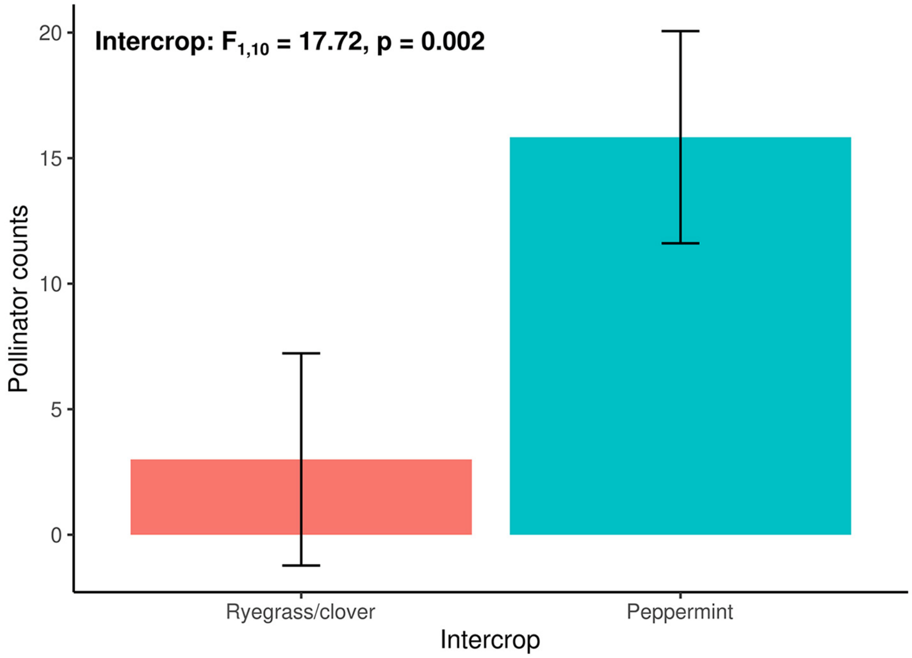

**FIGURE 4 |** Total pollinator counts per plot of ryegrass/clover control (red) and peppermint (blue) intercrops at one sampling event at 11:00 am. Least square means with 95% confidence intervals shown.

by one-meter landscaping cloth. However, during events that physically disturbed the intercrop (e.g., weeding or trimming), the smell of peppermint would diffuse a few meters away, however this appeared to occur infrequently. Nevertheless, this spatial effect may have completely disrupted *D. suzukii* host finding behavior within our whole experimental plot. Thus, it may be that our experimental spacing was not sufficient for *D. suzukii* to differentiate between fruit baits within the two intercropping types, resulting in overall low (or none) infestation rates in our fruit cages. However, because of the similarly low numbers of *D. suzukii* found in the blueberry production field and strawberry field on farm (**Figure 1**), it seems like the low numbers of *D. suzukii* observed within our experiment could be due to an overall preference of *D. suzukii* for hedgerows compared to crop fruit.

Pitfall trapping and a pollinator survey indicated that peppermint intercrops can support beneficial insects (**Figures 3**, **4**), with higher levels of natural enemies and pollinators observed in peppermint compared to the conventional ryegrass/clover mix. Woltz and Lee (2017) found exposure to predators in a blueberry field to decrease the abundance of pupae between 61 and 91% and to reduce larval survival by 19–49%, due to multiple predators, including ants and spiders (Woltz and Lee, 2017). Thus, increasing beneficial habitat, through peppermint intercropping, may further support *D. suzukii* pupae predation. For example, increasing floral resources and microhabitats increased counts of the beneficial hoverflies when intercropping *Phacelia tanacetifolia* (Benth.) in winter-wheat crops (Hickman and Wratten, 1996) and increased specialist parasitoids and parasitoid oviposition when intercropping *L. maritima* in grape vineyards (Begum et al., 2004, 2006). Intercropping collard greens with non-flowering parsley reduced aphid populations through recruitment of generalist predators but reduced specialist parasitoid emergence (Saldanha et al., 2019).

Despite only conducting a single pollinator survey, we consistently noticed higher pollinator activity in the peppermint intercrop throughout the baited fruit sampling period (C. Gowton, pers. obs.). This is to be expected as higher floral resources are associated with higher pollinator counts (Ebeling et al., 2008). For example, a greater number of pollinator visitors were observed in *Mentha arvensis* L. and *Coriandrum sativum* L. when intercropped in strawberries compared to *Myosotis arvensis* ([L.] Hill) or no intercropping treatments (Hodgkiss et al., 2019). While we did not specifically measure floral resources between the two intercrop treatments, we did conduct our survey while both clover and peppermint were flowering. However, to draw more accurate conclusions on how peppermint intercrops affect pollinator abundance and diversity, sampling should occur over multiple time periods and include floral surveys.

Economic costs associated with *D. suzukii* management are disproportionality experienced by organic compared to conventional growers (Farnsworth et al., 2017). Costs associated with increases in human labor associated with *D. suzukii* management in California organic raspberries decreased profit by 3.3% (Farnsworth et al., 2017). Growers may invest in expensive cultural controls such as netting or plastic tunnels (Rogers et al., 2016) and/or include rapid harvesting and sanitation of infested or fallen fruits (Leach et al., 2018). Allowing fruit to ripen to the point where fruit drop can occur may exacerbate the issue as these host sites may increase subsequent *D. suzukii* populations and disease incidence (Walsh et al., 2011). However, removal of overripe or dropped fruit often involves increases in human labor for hand picking and removal of these potential oviposition sites. We did not observe an effect of intercrop on non-*D suzukii* herbivory (**Supplementary Figure 5**); however, we only recorded the presence or absence of herbivory damage on berries and did not quantify this measure further (e.g., percent berry damaged, weight removed). As consumed berries cannot be used by *D. suzukii* as an oviposition site, increased herbivory of fallen fruit could reduce *D. suzukii* levels within adjacent crops. However, further study is needed to confirm the economic viability of such an option, including costs of peppermint control and maintenance, as well as the variability of this approach across in blueberries and other fruit systems in orchards across different locations and across multiple growing seasons.

Pest management decisions may not have immediate effects on insect pest populations. The effects may be present over longer time scales where the new techniques work to reduce pest populations between generations. Maintaining current use of insecticides is not ideal for the long-term management of *D. suzukii*, as decreased susceptibility to Spinosad (an organic pesticide) (Van Timmeren et al., 2019) and inherited Spinosad tolerance have been observed in a Watsonville, California *D. suzukii* population (Gress and Zalom, 2019), suggesting the need for more management options. Moreover, current pesticide regimes used to reduce *D. suzukii* are not sustainable as increased insecticide use decreases beneficial arthropod abundance (Desneux et al., 2006).

We show that intercropping can increase the number of natural enemies within the intercrop area, however it is unclear if this translates to increased control within the crop. In a seminal example of intercrop attraction and support for natural enemies, Brennan demonstrated aphid control in lettuce intercropped with sweet alyssum, which functioned to attract hoverflies (Syrphidae, Diptera) (Brennan, 2013, 2016). Similarly, it may be that even marginal plantings of insectary plants such as peppermint could increase predator populations enough to reduce *D. suzukii* numbers within crops or populations through control of pupal predation (Woltz and Lee, 2017). Indeed, methods which target larval or pupal stages of *D. suzukii* affect a greater proportion of the population compared to current chemical methods which only target gravid females, as adult *D. suzukii* makeup only 8% of the total population (Emiljanowicz et al., 2014). After this experiment was completed, Abram et al. (2020) reported the presence of larval parasitoids *Leptopilina japonica* Novkovic & Kimura and *Ganaspis brasiliensis* (Ihering) within the lower mainland in 2019 (Abram et al., 2020). This report includes capture of *L. japonica* at UBC Farm where we conducted this research (Abram et al., 2020). Further research is needed to determine the effects of floral resources (including peppermint) on the attraction of these parasitoids, but increasing habitat types (e.g., through intercropping) may increase natural enemies including parasitoids (Tscharntke et al., 2002; Kruess, 2003) such as *L. japonica* and *G. brasiliensis* parasitoids.

Although we managed the peppermint to prevent unwanted spread, there are several potential issues that require further study. Our experiment was not set up to test whether peppermint could increase competition for resources since our blueberries were grown in sunken pots and the intercrop was separated from the blueberries by landscaping fabric and had limited spread under the fabric. Since blueberries have a shallow rooting system contained within 0.4 m of the plant (Bryla and Strik, 2007), it is unlikely that competition for resources was an issue in this experiment. However, it should be noted that mint is characterized as an aggressive spreader without regular mowing (Lawrence, 2006) and further evaluation of its potential competitiveness with crops needs to be determined. In a field experiment near Simcoe, Ontario, Renkema et al. (2020) observed the lowest *D. suzukii* infestation rates in non-intercropped strawberries compared with trimmed and untrimmed peppermint intercropping (Renkema et al., 2020). That study was conducted later in the season when *D. suzukii* populations are at their highest and with more highly preferred fruits (strawberries). Critically, Renkema et al. (2020) observed a decreased in strawberry yield when peppermint intercrops were placed 0.6 m from strawberry plant center, and proposed this could be a result of shading and/or competition (Renkema et al., 2020).

Peppermint could also potentially result in an allelopathic effect which could reduce focal crop yield, as bioassays with mint leaf essential oils resulted in allelopathic effects due to menthone disrupting plant microtubule formation (Sarheed et al., 2020). However, further study is needed to determine if companion planting with peppermint will result in same allelopathic effects in the field. Mowing the peppermint to release VOCs during fruit ripening stages may help prevent and reduce further *D. suzukii* infestations, but could also increase potential allelopathic effects. Other potential economic factors to consider would be costs associated with maintaining a peppermint intercrop compared to the traditional grass/clover mixes as this was not addressed in our study but would be of concern for growers.

## CONCLUSION

We sought to determine whether peppermint could be used as an aromatic intercrop to reduce *D. suzukii* infestations in berry crops. We conducted an intercropping trial at UBC Farm to determine whether peppermint can be implemented in the field to reduce natural *D. suzukii* infestations. Peppermint intercrops reduced D. suzukii adult emergence from fruit baits compared to conventional ryegrass/clover mixes, indicating the potential to use aromatic intercrops within perennial berry plantings.

However, our experiment should be replicated over multiple growing seasons, field sites and berry crops to determine whether intercropping with peppermint can be successfully adapted across geographic regions and different berry growers. Further experimentation should be conducted to determine whether peppermint intercrops can reduce *D. suzukii* infestations in ripening berry crops as this is a more important factor for growers.

## DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found at: Center for Sustainable Food Systems at UBC Farm Dataverse doi: 10.5683/SP2/HMH80N.

## AUTHOR CONTRIBUTIONS

CG and JC conceived the research. CG and CC-A collected data. CG, CC-A, and JC analyzed the data. CG made the figures and wrote the first draft of the manuscript. All authors designed experiments and worked on later manuscript versions.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.700842/full#supplementary-material

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