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Global Climate Change as a Driver of Bottom-Up and Top-Down Factors in Agricultural Landscapes and the Fate of Host-Parasitoid Interactions

Frank Chidawanyika[1]*, *Pride Mudavanhu*[2,3] *and Casper Nyamukondiwa*[4]

[1] Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa, [2] Plant Health Protection, Agricultural Research Council, Stellenbosch, South Africa, [3] Department of Conservation Ecology and Entomology, Stellenbosch University, Stellenbosch, South Africa, [4] Department of Biological Sciences and Biotechnology, Botswana International University of Science and Technology, Palapye, Botswana

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***Correspondence:**
*Frank Chidawanyika
Chidawanyikaf@ufs.ac.za*

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The global climate is rapidly changing and the evidence is increasingly manifesting across various biological systems. For arthropods, several studies have demonstrated how changing climates affect their distribution through phenological and physiological responses, largely focusing on various organismal fitness parameters. However, the net-effect of the changing climate among ecological communities may be mediated by the feedback pathways among interacting trophic groups under environmental change. For agroecosystems, the maintenance of the integrity of trophic interactions even under climate variability is a high priority. This is even more important in this era where there is advocacy for sustainable agriculture, with higher emphasis on environmentally benign methods. For this reason, pest management in food production systems using biological control (especially use of parasitoid antagonists) has come to the forefront. In this review, we give an overview of the diversity of physiological responses among host insect and parasitoid populations and how this may influence their interactions. We highlight how climate change may modify bottom-up and top-down factors among agroecosystems with a particular focus on plant-insect host-parasitoid tritrophic interactions. We also outline how habitat management may influence arthropod population dynamics and how it can be manipulated to improve on-farm climate resilience and parasitoid conservation. We wrap-up by highlighting how the application of knowledge of conservation biodiversity, designing of multifunctional resilient landscapes, and evolutionary physiology of arthropods under thermal stress may be used to improve the fitness of mass-reared parasitoids (*in* or *ex situ*) for the improvement in efficacy of parasitoids ecosystem services under thermally stressful environments

Keywords: arthropod assemblages, coevolution, ecosystem responses, ecosystem services, environmental change, habitat loss, tritrophic interactions

INTRODUCTION

The spatiotemporal modification of global biophysical landscapes due to climate change exerts novel challenges to various levels of biological organization. For both managed and natural ecosystems, changes in organismal phenology, and distribution due to altered mean and temperature variability, and precipitation patterns have been widely investigated in recent years (Parmesan, 2006; Lee et al., 2009; Calosi et al., 2010; IPCC, 2014). This is in addition to studies investigating changes in feeding and oviposition preferences of both herbivores (Chidawanyika et al., 2014; Mbande et al., 2019a,b) and natural enemies (Dong et al., 2018) as microcosms of various ecosystems undergoing environmental change. Another important consequence of changing climates is how it influences trophic cascades among food webs with sensitivity varying among different trophic groups (Voigt et al., 2003; Rosenblatt and Schmitz, 2016). Decoupling multitrophic interactions under environmental change is daunting due to the high complexities characteristic of mega biodiverse ecosystems, high resource demands and outright uncertainty in the feasibility of undertaking such studies (Schuldt et al., 2017). Hence, much focus has been placed on feeding preferences, organismal physiology and biogeography (Lee et al., 2009; Calosi et al., 2010; Burrows et al., 2014), and phenological synchronization (Singer and Parmesan, 2010). Significant strides have also been made in investigating thermal energetics underlying consumer-resource trophic interactions where an assumption is made that thermal variability alters resource abundance (Rosenblatt and Schmitz, 2016). The contribution of all these various study approaches to present day understanding of global change ecology is enormous. However, there have been increasing calls for integration of investigative approaches to increase predictive power among higher levels of biological organization under environmental change (Rosenblatt and Schmitz, 2016).

Focal to these integrative approaches is the investigation of how biomass patterns in different food webs (biomass pyramids) will respond to climate drivers (Leroux and Loreau, 2015). Two competing hypotheses have been brought forward to explain the potential outcomes. First is the bottom-up approach or resource-based hypothesis which suggests that resources such as nutrients and primary producers will be key in shaping the biomass pyramids up to higher trophic levels (Leroux and Loreau, 2015). This explanation also accounts for climate factors such as rainfall and solar radiation and their subsequent influence on energy flow among trophic levels. Furthermore, due to the alterations of plant defensive capacity by these climate factors, this standpoint also accounts for changes in trophic dynamics due to alterations in herbivory because of either enhanced or compromised plant defense (Raffa et al., 2013) or poor nutritional value (Leroux and Loreau, 2015). On the other hand, a consumer-based hypothesis has also been brought forward, which posits that the structure of such biomass pyramids will rather be determined by consumers at higher trophic levels (Madrigal et al., 2011; Leroux and Schmitz, 2015). In nature, more so under dynamic systems undergoing environmental change, such bottom-up and top-down factors are likely to interact and also vary along climate/environmental gradients. Nonetheless, climate change will directly influence both bottom-up and top-down factors to varying degrees among different ecosystems and across different trophic levels.

Here we present a synthesis of the impacts of climate change on both bottom-up and top-down factors with a particular focus on herbivorous insect pest host-parasitoid population dynamics and their efficacy in agroecosystems. Current literature is replete with several studies documenting similar effects on herbivorous insects, but little is reported on their antagonists e.g., parasitoids (Vidal and Murphy, 2018). First, we begin by describing how climate change may influence host-parasitoid phenology and subsequent interactions. Second, we address how temperature extremes can act as top-down factors leading to changes in host-parasitoid interactions. Third, we describe the implications of the parasitoid thermal responses to biological control of pests in agriculture. Fourth, due to the persistent exposure to ever transforming environments under climate change, arthropods, like many other organisms, are bound to respond through both transient plastic and long term evolutionary mechanisms (Chidawanyika and Terblanche, 2011; Sih et al., 2011), albeit to varying degrees thereby creating "winners" and "losers" under selection pressure from various climate stressors (Oostra et al., 2018). We therefore explore the potential role of evolutionary adaptive responses to mitigate impacts of climate change on parasitoid populations and provision of their ecological services. Lastly, since agroecosystems typify some of the most highly disturbed ecosystems, almost always succeeded by habitat and biodiversity loss, we outline how such disturbances may also influence both bottom-up and top-down factors for parasitoids. We also discuss how landscape management may be used to mitigate the impact of climate change to ensure stable agroecosystems.

TEMPERATURE EFFECTS ON PARASITOID PHYSIOLOGY AND IMPLICATIONS FOR THE EFFICACY OF BIOCONTROL

Thermal effects on insect performance traits within certain temperature tolerance ranges can be summarized using a thermal performance curve (TPC) (Angilletta, 2009; Furlong and Zalucki, 2017). TPCs tend to take a general generic shape, with performance typically increasing proportionally with temperature, reaching maximum at optimum temperature (Topt), beyond which any increase in temperature causes performance decline. In consequence, TPCs exhibit the effects of temperature on organismal fitness (Schulte et al., 2011). This often varies across taxa, ontogeny, metrics tested and with magnitude of climate variability (Deutsch et al., 2008; Kingsolver et al., 2013; Thompson et al., 2013; Clavijo-Baquet et al., 2014; Vasseur et al., 2014). For interacting species, e.g., herbivorous host-parasitoid interactions, this is highly critical as differential responses in TPCs may lead to decoupled phenological cycles (e.g., Hance et al., 2007; Furlong and Zalucki, 2017; Machekano et al., 2018), with resultant loss of parasitoid essential ecosystem services. Recent studies have documented that the estimated optimum temperatures for various parasitoids were consistently lower compared to their hosts (Furlong and Zalucki, 2017), suggesting that parasitoids maybe more vulnerable to climate warming compared to their hosts. In agro-ecosystems, this may mean an asymmetrical host-parasitoid interaction and reduced efficacy of parasitoids biological control with warming temperatures.

Parasitoids are ectotherms and thus their development, activity and survival is intimately correlated with ambient temperature (Hance et al., 2007). They can be classified as endoparasitoids and ectoparasitoids in reference to their development within or outside a host, respectively (Godfray, 1994). They are further classified as either koinobiont or idiobiont parasitoids. For koinobiont parasitoids, host development continues following parasitisation and host is only killed following completion of parasitoids development. However, idiobiont parasitoids kill their hosts immediately or shortly thereafter following parasite host entry (Hance et al., 2007). Temperature changes at this stage may differentially affect each trophic level, leading to a system decoupling (Van der Putten et al., 2004). Moreover, temperature variability is likely more significant for higher than lower trophic levels since the former depends on the latter to adapt to changing ambient temperatures. As such, parasitoids and hyperparasitoids (third and fourth trophic levels, respectively) may be the most vulnerable (Hance et al., 2007). Indeed, efficacy of biological control using parasitoids depends largely on (1) habitat location, (2) host location, (3) parasitoids' potential to effectively evade or manipulate host immune system, and (4) ability to constantly track changing host environment. All these attributes are highly temperature dependent, and thus unraveling temperature effects on parasitoids is critical for modeling pest management programmes using parasitoids (Harrington et al., 2001).

The consequences of subjection of parasitoids to temperature extremes are well-documented (Hance et al., 2007). Effects can manifest as lethal or sublethal but both contribute significantly to shaping parasitoid life history traits and efficacy of parasitisation in agricultural landscapes. Parasitoid exposure to extreme high and low temperature for example can result in mortality (Chown and Nicolson, 2004). This may be due to the irreversible damage to the cells, or in the case of extreme low temperatures, change in physical structures due to extra- or intracellular ice formation. Freezing may also be associated with disruption of metabolism and may manifest as osmotic or oxygen stress (Turnock and Fields, 2005). Depending on their cold hardiness, some parasitoids may also suffer lethal effects at temperatures above freezing points (Bale and Walters, 2001), and this mortality may decouple host-parasitoid interactions and the ecological services provided by the later.

Stressful temperature extremes can also have sub-lethal effects on parasitoids that may manifest as failed biological control efficacy. For example, low temperatures are associated with constrained degree day accumulation and longer generation times. For other species, the damage caused by exposure to stressful low temperatures has often been followed by an increase in the degree days needed to complete development (Lysyk, 2004). Moreover, low temperature extremes also change the number of larval developmental instars (see Denlinger and Lee, 1998), which may offset synchrony with host phenology and efficacy of parasitoids in biological control. Parasitoids that developed from lower temperatures generally develop bigger body size, following the temperature-size rule (see Angiletta and Dunham, 2003). Nevertheless, *Trichogramma carverae* reared at low temperatures developed smaller body size, while *Sarcophaga bullata* prematurely pupated at low temperatures. Such anomalies represent negative fitness consequences for parasitoids as biocontrol agents and suggests that parasitoids reared at low temperature may allocate resources to metabolism (for the maintenance of temperature), at the expense of body size (Rundle et al., 2004).

For parasitoids to be effective in regulating pest numbers, they should be highly fecund, have good host searching and finding abilities and have high longevity. However, extremes of temperature may offset these attributes, with negative consequences on biological control. Exposure of parasitoids to extremes of temperature e.g., low temperature has been reported to decrease adult longevity (Pandey and Johnson, 2005; Foerster and Doetzer, 2006) and fecundity (Levie et al., 2005; Pandey and Johnson, 2005) and hence their ecological services. Moreover, temperature stress during development also interferes with sex allocation, causing an adult sex bias toward males (Denlinger and Lee, 1998). It also decreases the mobility of either sex and therefore decreases their efficacy in mate and host finding (Denlinger and Lee, 1998). Parasitoids also possess endosymbiont bacteria, necessary for their function, for example *Wolbachia* and *Buchnera* species. These endosymbiont bacteria may be negatively affected, or in worst cases killed by extreme temperatures (Ohtaka and Ishikawa, 1991; Thomas and Blanford, 2003), affecting parasitoids fitness and thus activity. It is also increasingly becoming apparent that temperature stress may increase abnormal morphological deformations in insects. Low temperature impacts directly on insect differentiating tissues, affects hormonal balance and may cause deformities (Sibly and Atkinson, 1994). Indeed, a positive correlation has been reported between duration of temperature stress, and the magnitude of birth deformities (Tezze and Botto, 2004).

Climate change has also brought increased incidence of heat waves and cold snaps that have negative consequences on parasitoids behavior and activity. Insects exposed to sub-lethal low and high temperature may enter cold and heat stupor, respectively. During this period, activity, which may be anything from flying, mating, feeding, or host finding is decreased (Boivin et al., 2006). Moreover, these extreme temperatures also interfere with habitat, host finding, and evaluation (Herard et al., 1988). The failure to locate a host and parasitise it may be result from (1) failed parasitoids recruitment by host plant secondary metabolites, or (2) directly through temperature effects on the natural enemy. Most plants produce synomones in response to herbivore attack (Micha et al., 2000), which in turn attracts natural enemies of the herbivores. Increased temperatures associated with climate change have been reported to negatively affect the synomone blends, and thus failed parasitoid recruitment. Furthermore, most parasitoids optimally perceive synomones at narrow temperature ranges, e.g., *Cotesia* *plutellae* responds optimally between 30 – 35°C (Reddy et al., 2002). Thus, temperature extremes, and increased variability may limit parasitoids' potential to perceive habitat and host cues and consequently offset their ecological services. Similarly, it has also been shown in many studies that for insects, the cost of living is extremely high at stressful high temperatures (>35°C). For example, the efficiency of the mitrochondria in converting carbohydrate substrates into energy has been shown to drop significantly at stressful high temperatures in *Manduca sexta* (Martinez et al., 2017). This reduction in mitochondrial capacity is linked with reduction in juvenile stages e.g., larval growth rates, whereby in the case of parasitoids, this may affect their phenology, abundance, and efficacy of host parasitisation.

EVOLUTIONARY IMPACT AND DECOUPLING OF PARASITOID-HOST THERMAL PREFERENCE

Prediction of parasitoid-host responses to climate change is highly complex (Harrington et al., 1999; Thomas and Blanford, 2003), but association between the two, and any probable climate induced deviations may be unraveled by comparing thermal windows between the two systems (Brooks and Hoberg, 2007; Agosta et al., 2018). Generally, if parasitoids and hosts exhibit similar thermal tolerance, then, temperature variability associated with climate change may not decouple the long evolved relationships and hence efficacy of parasitoids ecological services. However, if parasitoids and hosts differ in their thermal preference, this may mean decoupled long co-evolved relationships with climate change and impacts on parasitoids-host population phenologies and abundance (Hance et al., 2007; Machekano et al., 2018; Mutamiswa et al., 2018). Furthermore, thermal preference is also highly subtle and varies with species, age and ontogeny (Bowler and Terblanche, 2008), thus adding complexity into predicting the effects of climate change on parasitoids-host population dynamics. Hance et al. (2007) documented the negative impacts of temperature differential effects on parasitoids and their herbivorous hosts. If TPCs do not directly superimpose, this may imply a negative effect on parasitism in the face of thermal variability. What worsens the situation is that parasitoids are generally reported to have lower temperature tolerance relative to their hosts, as such, they may likely be more affected critically by changes in their ambient environment (Karban, 1998). Moreover, for parasitoids to be efficient in host parasitisation, they should overcome, or take control of their host immune system. However, higher temperature and variability have been reported to improve host immune resistance, while the capacity of the host to overcome parasitism also increases at higher temperatures (Thomas and Blanford, 2003). For example, host *Spodoptera litolaris* has been reported to be more resistant to its parasitoids *Microplitis rufiventris* at higher temperatures (reviewed in Hance et al., 2007). This means that temperature increases associated with climate change decrease probability of parasitoid immatures to survive in herbivorous hosts and thus decreases efficacy of parasitoids.

CLIMATE CHANGE IMPACTS ON BIOGEOGRAPHY AND PARASITOID-HOST INTERACTIONS

As climate is key in defining the geographic range of insects, another important consequence of climate change is the change in their distribution (Parmesan, 1996, 2007). There is ample evidence of some insect taxa shifting their range to higher altitudes and latitudes, in response to particularly warming, followed by diminishing abundance in the unsuitable areas (Parmesan and Yohe, 2003; Parmesan, 2006). Such changes in distribution patterns have been widely reported in Lepidoptera (Parmesan et al., 1999; Battisti et al., 2005, 2006; Wilson et al., 2005, 2007; Franco et al., 2006). Other examples include the northward spread of the mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Curculionidae) (Weed et al., 2015; Burke et al., 2017) and *Dendroctronus frontalis* (Coleoptera: Scolytidae) (Ungerer et al., 1999), all in response to winter warming. Such evidence in parasitoids is scant. However, Delava et al. (2014) reported a northward range shift in parasitoids. Hence, in all likelihood, most parasitoid may have such climate-dependent shifts in geographic range depending on their physiology and dispersal propensity. For example, Bale et al. (2002) argued that, under climate warming, non-diapausing insects with rapid development are more likely to expand their geographic range compared to the diapausing and slow developing ones that require low temperatures for diapause induction. Other factors that may mediate the range shifts include the availability of resources, photoperiods, predation by natural enemies, and intra- and inter-specific competition (Walther et al., 2002; Gutierrez et al., 2010).

Whatever the mode and cause of changes in distribution patterns, and indeed for interacting food webs, populations ought to adjust to biogeographic shifts through a suite of mechanisms including demographic patterns, physiological and phenotypic plastic adjustments as well as natural selection (Webster et al., 2016) with consequences on parasitism (Feldman et al., 2017). Two hypothetical scenarios may occur among agroecosystems. First, the reduction in parasitoid diversity due to the migration of species to more suitable habitats may result in increased pest pressure in the cases where pests do not share similar range expansion patterns with their parasitoids. Similarly, such mismatches may lead to reduced population growth and ultimately extinction in the case of specialist parasitoids due to limited hosts. Second, changes in distribution patterns may be beneficial to agroecosystems where the introduction of new parasitoid species may increase parasitisation of pests. Migration of pests from agroecosystems with unsuitable climates may also lead to increase in yield due to reduced pressure. However, this is highly unlikely as some dormant species may become more prevalent due to reduced competition. Hence, the consequences of climate-induced biogeography among parasitoids and pests are multi-faceted and may have differential impacts on crop productivity and biodiversity conservation.

CLIMATE CHANGE EFFECTS ON HOST-PARASITOID PHENOLOGICAL RESPONSES

The modification of trophic interactions at both a spatial and temporal scale is another major consequence of climate change. Due to their higher position in the food web, the fate of parasitoids under changing climates is also very much dependent on the bottom-up factors in the form of responses of the organisms at the lower trophic levels (Jeffs and Lewis, 2013; Rosenblatt and Schmitz, 2016). Several studies have reported how abiotic stressors such as warming, elevated CO_2 and drought can mediate the interaction between parasitoids and their hosts (Buchori et al., 2008; Walther, 2010; Evans et al., 2013; Jeffs and Lewis, 2013). For example, climate change can lead to phenological asynchrony between parasitoids and their hosts in cases where the phenology of the interacting species respond differently to a climate-related cue or where one of the species does not rely on a climate-related cue (Walther, 2010; Jeffs and Lewis, 2013).

Climate warming has been associated with rapid rates of development and multivoltinism (i.e., the completion of several ($\geq$3 generations) per year). Indeed, evidence of multivoltinism has been reported in several agricultural insect pests of economic importance including the maize stemborer *Chilo partellus* (Mwalusepo et al., 2015), bark beetle *Ips typographus* (Jönsson et al., 2009), and mealybugs *Phenacoccus solenopsis* (Fand et al., 2014). For interacting hosts and parasitoids, temporal phenological asynchrony may also occur if one of the interacting species has an obligate seasonal diapause or rapidly develops in response to warming (Forrest, 2016). Such asynchronies can lead to the escape from parasitism pressure by insect pests in the cases where climate change leads to earlier development among host insect pest populations. Theoretically, temporal synchronies stabilize the host parasitoid interactions as complete synchrony may lead to depletion of host populations with subsequent extinction of the parasitoids (Godfray et al., 1994). Thus, even though the initial parasitism pressure is a classical top-down factor, the consequent extinction of the hosts exerts bottom-up effects that lead to extinction of parasitoid populations especially in the case of specialists (Jeffs and Lewis, 2013). Despite scant empirical evidence, some studies focusing on these interactions have reported such asynchronies following even minute climate variability. This is the case with the emerald ash borer *Agrilus planipennis* and its parasitoid *Oobius agrili* where small changes in severity and extreme climate events phenologically excluded emerging parasitoids from host eggs (Wetherington et al., 2017). In the Glanville fritillary butterfly *Melitaea cinxia* larvae, behavioral plasticity such as movement for basking in warm sunny spots enables temporal relief from parasitoids through rapid development to the insusceptible instar stages during spring. This will cost its parasitoid *Cotesia melitaearum*, which will be immobile during that season. However, such rapid development in insects may lead to small body size at maturity and reduced fecundity (Kingsolver and Huey, 2008) thereby impeding the positive demographic effects of shorter generations (Forrest, 2016). On the other hand, such behavioral plasticity in the warm season may not be beneficial to the hosts as there may be more synchronization with the parasitoids (Van Nouhuys and Lei, 2004). In this case, climate warming will, in all likelihood, result in increased parasitisation of *M. cinxia*. Interestingly, warming can also result in mismatches due to parasitoid advanced development relative to the host as is the case with cereal leaf beetles *Oulema melanopus* and its parasitoid *Tetrastichus julis* where warmer years result in phenological asynchrony and reduced parasitism (Evans et al., 2013). Hence, predicting the consequences of parasitoid-host relationships is complex partly due to non-climatic factors that may act as cues for phenological change and the potential disproportionate adaptive evolutionary responses that may occur among interacting species.

IMPACT OF PLANT NUTRITIONAL QUALITY AND FOOD WEB DYNAMICS

Apart from plant diversity and abundance, nutritional quality is also highly responsive to climate variability with cascading effects among higher trophic groups. Greenhouse-based studies have shown how elevated CO_2 and temperature are closely linked with a simultaneous increase in foliar non-structural carbohydrates and a decline in protein concentration among various plant functional groups (Rothman et al., 2015). This is also in addition to changes in plant chemistry owing to alterations in biogeochemical cycles due to land-use change. Other studies of tropical trees along a rainfall and temperature gradient attributed the decrease in foliar nitrogen content and nitrogen-to-fiber ratios to increased precipitation and temperature (Schuur and Matson, 2001; Weih and Karlsson, 2001; Santiago et al., 2004; Craine et al., 2010). Whilst the impact of nutritional variability on insect herbivores is widely documented (e.g., Mody et al., 2009; Gutbrodt et al., 2012; Mbande et al., 2019a,b), information of its impact on parasitoids remains scant (Safraz et al., 2009). Much of the current knowledge on the impact of nutritional gradients on food webs has been generated from phytoplankton-based model systems. Even though stark contrasts exist between the ecology of terrestrial and phytoplankton systems, what is apparent from these studies is that the ecological efficiency and energy transfer to higher trophic levels depends on food quality. For herbivores, stoichiometric constraints exist through the proportion of carbon and nutrients relative to respiratory demands, in addition to assimilation efficiency with potential carryover effects to carnivores (Dickman et al., 2008).

Prey (herbivore) diversity is another aspect that has been previously linked with plant nutritional quality (Marzetz et al., 2017). In the study, Martinez et al. (2017) postulated three hypothetical scenarios of herbivore response to nutritional quality. First, the growth of the herbivore populations is promoted in diverse communities by co-occurrence of species with complementary nutritional traits. Hence, a positive correlation between herbivore performance and food diversity would exist. Second, a single or a few species may possess superior nutritional attributes that enable herbivore growth which in turn may transform the relationship between producer diversity and consumer growth. In such a scenario, a positive correlation between consumer performance and food diversity would be promoted in a more diverse community due to increased likelihood of having the high quality species. Third, high diversity may also mask the relative contribution of the high quality species if they are not competitive. The net interactive effect of the above processes could result in both null and negative correlations (Marzetz et al., 2017). How such plankton-based herbivore responses are transferrable to terrestrial systems and higher trophic groups is debatable. However, Nitschke et al. (2017) reported contrasting responses in the abundance of parasitoids and herbivores in response to plant diversity. Assemblage of the herbivorous *Chaetorellia jaceae* decreased with increasing plant species and functional diversity whilst parasitism of the chalcid wasps *Eurytoma compressa* and *Pteromalus albipennis* increased with increased plant functional diversity. In another study, Safraz et al. (2009) reported improved performance in several fitness correlates in koinobiont parasitoids in response to increased nitrogen, phosphorous and potassium among host plants. These examples demonstrate how nutritional quality mediates the performance of parasitoids through both herbivore population abundance or nutritional value of the host as mediated by the host plants. Therefore, a plant's nutritive status may not only affect its suitability for herbivorous insects, but fitness parameters of organisms at higher trophic levels such as parasitoids (Olson et al., 2009; Chen et al., 2010; Han, 2014).

Overall, density dependent interactions in response to nutritional gradients caused by global change will play a central role in food webs. Factors that reduce parasitism efficiency weaken the top-down forces (Power, 1992). For example, intraguild predation among parasitoids and hyperparasitism, which may increase when herbivore populations are low, may result in reduced parasitoid abundance and diversity (Rosenheim et al., 1993) thereby counteracting conservation efforts (Snyder and Wise, 2001; Symondson et al., 2002). Host plant quality may also mediate the interaction between parasitoids and hosts through its influence on herbivore body size. For example Chen et al. (2010) reported that development time of immature parasitoids is positively related to host sizes due to the close link between host body size and nutritive value leading a compromise of size dependent individual and population level parameters, as earlier stated (Thompson, 1999). This further highlights the critical role of plant nutritive value on parasitoid population dynamics, demographics and efficacy of their ecological services (Han, 2014). Hence, climate variability induced nutritional gradients may, in all likelihood, affect both the herbivorous hosts and their antagonists e.g., parasitoids through both bottom-up and top-down effects.

LANDSCAPE MANAGEMENT AND PARASITOID RESPONSES TO HABITAT COMPLEXITY AND CONNECTIVITY

Agricultural intensification is typically characterized by a high rate of disturbances resulting in fragmented habitats, significant biodiversity loss and poor ecosystem function due to modification of bottom-up and top-down processes (Crowder and Jabbour, 2014). Perhaps the most direct impact of disturbances is the loss of habitats, which leads to a reduction in their population carrying capacity of various species thereby limiting the provision of ecosystem services (Cronin and Reeve, 2005; Holzschuch et al., 2010; Crowder and Jabbour, 2014). The consequent existence of smaller populations on small but fewer suitable patches makes them highly vulnerable to genetic, demographic and environmental perturbations such as climate change (Baguette et al., 2013). Indeed, several studies have reported a high extinction risk among small parasitoid populations occupying small patches (Bennett and Gratton, 2012). Parasitism and inbreeding depression are some of the demographic factors that limit population persistence, the extent, effect, and manifestation/expression of which are magnified in small populations on small fragmented patches (Coudrain et al., 2014; Start and Gilbert, 2016). Apart from this, adaptive evolutionary responses to environmental stressors in such smaller populations are known to be highly limited (Bay et al., 2017). Hence, climate change will further increase the pressure exerted by demographic parameters leading to potential extinction. Moreover, climate warming among interacting trophic levels has already been reported as a catalyst for extinction in species at higher trophic levels like parasitoids (Jones, 2008; Northfield and Ives, 2013; Mellard et al., 2015) with population sizes mediating the evolutionary dynamics (Oostra et al., 2018).

Habitat complexity is widely reported as a conduit for parasitoid assemblages together with other pest natural enemies (Langellotto and Denno, 2004; Buchori et al., 2008; Holzschuch et al., 2010; Pierre and Kovalenko, 2014) thereby maximizing the provision of their ecosystem services (Fiedler et al., 2008). Indeed, emperical evidence has shown how landscape complexity can aid conservation biological control through improved provision of resources to pest natural enemies (Jonsson et al., 2012). This is because, for many species, highly complex habitats give more resources which form broad niches that reduce niche-overlap thereby promoting species coexistence (Smith et al., 2014). However, such diversity has occasionally been cited as a disadvantage for parasitoids. For example, some studies have reported a decrease in their foraging efficiency under complex habitats (Gols et al., 2005; Kruidhof et al., 2015), even though this may be ameliorated by their high associative learning capacity of the emitted herbivore induced plant volatiles (HIPVs) (Meiners et al., 2003; Kruidhof et al., 2015). Such capacity for associative learning is of high ecological importance and contributes immensely to the evolutionary fitness of parasitoids in cases where conditions allow for rapid learning (Dukas and Duan, 2000). Kruidhof et al. (2015) attributed a 28% increase in foraging efficiency in *Cotesia glomerata* (Hymenoptera: Braconidae) to associative learning under controlled outdoor experiments. Furthermore, another study reported differential responses to polycultures (regarded here as complex habitats) in the foraging capacity of generalists and specialist parasitoids. Naïve generalist parasitoids had poor foraging efficiency under complex habitats compared to specialists (Perfecto and Vet, 2003). However, this poor performance among generalists was nullified when they had an opportunity for associative learning (Perfecto and Vet, 2003), thus underlying the ecological importance of such behavioral plasticity. Therefore, poor capacity for associative learning of odors may result in fitness costs including longer foraging durations and increased exposure to predation (Dukas and Duan, 2000). It is however likely that where odor cues may not be sufficient during associative learning, other cues such as visual may be employed (e.g., Desouhant et al., 2010). Likewise, push-pull strategies, a stimulo-deterrent cropping tactic consisting of intercropping cereals with legumes and surrounded by grasses, can also be incorporated for repulsion and attraction of stem borer pests and parasitoids, respectively (Cook et al., 2007; Kebede et al., 2018).

Another important challenge posed by disturbances and climate change in agricultural landscapes is poor habitat connectivity, at both spatial and temporal scales. Indeed, climate stressors among fragmented landscapes exacerbate the pressure on biodiversity due to the limitations they exert on metapopulation and biogeographical responses (Opdam and Wascher, 2004). Ecological landscape processes such as herbivory, dispersal, and gene flow are highly dependent on the connectivity of habitats with both geographic isolation and seasonal quality or availability of resources all being important for species persistence (Cronin and Reeve, 2005; Baguette et al., 2013; Smith et al., 2014; Maguire et al., 2015). For parasitoids, the functional connectivity of natural and semi-natural habitats with cropping systems ensures a continuum of suitable habitats where acquisition of critical resources such as nectar, pollen and sap is made possible with short-term improvement in crop yield through increased parasitism of pests (Gurr et al., 2003; Wilkinson and Landis, 2005; Cook et al., 2007). Such connectivity minimizes foraging time thereby reducing risk of predation (Weisser et al., 1994) or environmental stress, which becomes more frequent under changing climates (Mutamiswa et al., 2018).

By promoting the conservation and activity of natural enemies of insect pests, habitat connectivity is availed thereby contributing positively to agricultural landscapes (Jonsson et al., 2014). This includes the assemblage of outbreak herbivorous insect species, which contribute toward ecosystem services such as nutrient cycling, soil formation, and carbon sequestration (Isaacs et al., 2009; Maguire et al., 2015). However, it can also be detrimental in cases where connectivity aids the spread of crop pests and diseases (Margosian et al., 2009; Maguire et al., 2015). For example, increased connectivity is beneficial for the establishment and spread of the mountain pine beetle *Dendroctonous ponderosae* (Coleoptera: Curculionidae), an insect pest of the boreal forests of North America (Maguire et al., 2015). This connectivity has been reported as interactive with climate warming resulting in major pest outbreaks (Aukema et al., 2008; Raffa et al., 2008; Safranyik et al., 2010; James et al., 2011; Bone et al., 2013). Conversely, connectivity in other parts of that region results in the suppression of the forest tent caterpillar *Malacosoma disstria* (Lepidoptera: Lasiocampidae) due to increased predation pressure by parasitoids (Cooke and Roland, 2000; Maguire et al., 2015). Factors such as habitat fragmentation were cited as key for disrupting parasitoid assemblages in such cases (Cooke and Roland, 2000). Apart from affecting intra-population dynamics like abundance, low connectivity resulted in poor diversity of tachinid parasitoids in 18 different grasslands in agricultural landscapes (Inclán et al., 2014). This underlies the profound role that habitat complexity and connectivity plays in the community assembly of parasitoids. Other arguments against maintaining connectivity in agricultural landscapes is their potential for providing pathways for dispersal of invasive species and noxious weeds (Pringle, 2003). However, this is highly debatable considering invasive plants can be more successful in highly disturbed areas where succession easily occurs in the absence of competition from native plants (Theoharides and Dukes, 2007).

From the foregoing, it is apparent and widely documented that habitat complexity and connectivity provide both ecosystem services and "disservices" in agricultural landscapes (Zhang et al., 2007). These dissensions however need to be evaluated in a landscape context taking into consideration the ecological attributes and the desired ecosystem services (Maguire et al., 2015; Landis, 2017). Several conceptual frameworks for incorporating the provision of various ecosystem services in landscape planning and design of agroecosystems have been posed (e.g., Buchori et al., 2008; Maguire et al., 2015). Landis (2017) points out the need to merge fundamental and applied ecological principals with agroecosystem concepts. These calls are not new and have resulted in the birth of what is now described as "agroecology" with emphasis on biodiversity conservation and sustainable agricultural production systems (Jonsson et al., 2014; Altieri et al., 2015; Gliessman, 2017). When meticulously planned, incorporation of agroecology principles that maintain plant diversity and connectivity will also ensure the resilience of agroecosystems under changing climates through buffering of biodiversity against climate shocks (Altieri et al., 2015). This is in addition to other pro-climate resilient ecosystem services such as carbon sequestration, soil formation, and moisture conservation (Altieri et al., 2015), albeit the possibility of trade-offs due to competition in water usage between crops and non-crop plants (Zhang et al., 2007). This is common for agroecosystems with high tree abundance that can reduce the replenishment of aquifers important for irrigation (Zhang et al., 2007) and also increase water loss through evapotranspiration from streams and dams within agroecosystems (Zavaleta, 2000). Hence, landscape planning and design based on an in depth understanding of the ecological processes at both on-farm and area-wide level is required to enhance ecosystem services whilst minimizing trade-offs (Maguire et al., 2015). For parasitoids, landscape design should enhance the drivers for parasitoid assemblage and movement or dispersal at both farm and the entire landscape level (Mazzi and Dorn, 2011; Macfadyen and Muller, 2013). All these interventions can account for the metapopulation theory with improved resilience against climate change.

PROSPECTS FOR IMPROVING THE EFFICACY OF BIOCONTROL EFFICACY

It is increasingly documented that temperature fluctuations associated with climate change are shifting parasitoid-host phenologies and population dynamics (Agosta et al., 2018). As such, there is increasing interest on experiments elucidating effects of different trophic interactions (Machekano et al., 2018; Mutamiswa et al., 2018), and the most convenient indices to be employed (Agosta et al., 2018). A variety of simple matrices have been proposed, including warming tolerance (Hoffmann et al., 2013) and thermal safety margins (Kingsolver et al., 2013). Though diverse indices point to a potential asynchrony of interacting trophic levels with climate change (Hance et al., 2007), few studies have looked at the second to fourth trophic levels (but see Agosta et al., 2018).

Outside this, parasitoids may also adapt to changes in their thermal environment in order to conserve those co-evolved trophic relationships. Evolutionary physiology may potentially be used to enhance the efficacy of biological control in the face of climate change (Sgrò et al., 2010; Hoffmann and Sgrò, 2011). Hence, apart from improvement of *in situ* genetic diversity or conservation of *in situ* evolutionary adaptation focusing on physiological traits may be key (Pörtner and Farrell, 2008; Chidawanyika et al., 2012). For example, during extreme temperature stress, and depending on environmental predictability, parasitoids may undergo dormancy or quiescence (Tauber et al., 1986), and this may manifest at any stage of parasitoids development. When environmental thermal variability is predictability low, and temperature stresses are short and transient, parasitoids often use behavioral adjustments to cope with stress, e.g., insects may go into chill coma (Mutamiswa et al., 2018). Another form of behavioral host manipulation by parasitoids has been reported for koinobiont parasitoids (Lagos et al., 2001). Koinobiont parasitoids often induce behavioral changes in their hosts, so they move to habitats that ensure maximum survival chances. Induction of this behavior has been reported for parasitoids *Aphidius ervi*, (Lagos et al., 2001) *A. nigripes* (Brodeur and McNeil, 1989), and *Eucelatoria bryani* (Reitz and Nettles, 1994). Such behavioral adaptations form the first line of stress defense because they are energetically less costly, and are adaptive in the face of changing environments.

When faced with freezing low temperatures, parasitoids have also evolved freeze tolerance as a survival strategy (Vernon and Vannier, 2002). While freeze tolerance is rare in parasitoids, it means they will be vulnerable to freezing temperatures if their host bodily fluids freeze, for freeze tolerant hosts. However, a few parasitoid genera are reported to be freeze tolerant e.g., endoparasitoids *Ichneutes* (Braconidae) and *Syndipnus* (Ichneumonidae). These have evolved freeze tolerance to survive freezing when living within the freeze tolerant host larvae under freezing Arctic conditions (Humble and Ring, 1985). For freeze intolerant parasitoids (see Vernon and Vannier, 2002), parasitoids have often evolved manipulation of their hosts to avoid freezing. Parasitoids do this through physiological manipulation of the host following parasitisation. For example, unparasitised host *Diuraphis noxia* has a supercooling point (SCP) of $\sim -25^{\circ}$C. However, physiological manipulations of this host by parasitoids *Aphelinus asychis, A. albidopus,* and *Diaeretiella rapae* (Hymenoptera: Braconidae) have been reported to depress host SCP to temperatures below -30°C (Nowierski and Fitzgerald, 2002). This is also consistent with reports on other insect taxa (Parish and Bale, 1990; see Hance and Boivin, 1993), and such physiological host manipulations by parasitoids are adaptive and may conserve ecological services in the face of changing climates. Moreover, color also plays a significant adaptive mechanism for surviving stressful temperatures in parasitoids and indeed parasitoid color morphs have been reported (Schlinger and Hall, 1960; Langer and Hance, 2000; Legrand et al., 2004), which may compensate for thermally stressful environments.

Investigating the effects of environmental heterogeneity on parasite-host interactions and predicting consequences on ecological services is complex, but very significant in biology. We conclude that basic thermal physiology comparative experiments across interaction species (e.g., Agosta et al., 2018; Machekano et al., 2018; Mutamiswa et al., 2018) may be the first step in elucidating some of the complex drivers. Nevertheless, it is generally agreed that climate change may decouple long co-evolutionary relationships across interacting species (Hance et al., 2007). Such divergence between parasitoid-host phenologies may disrupt ecological equilibrium and may lead to rapid insect pest outbreaks consequent of a climate change induced failure in biological control.

CONCLUDING REMARKS

Climate change presents new challenges and limits in agriculture. Concerted efforts will be required to ensure that the integrity of trophic interactions are maintained *in situ*. Since the factors associated with poor parasitoid assemblages and performance are largely attributed to high disturbances in agricultural landscapes, management practices should take an integral role in order to maintain resilient farming systems, with emphasis on those that incorporate evolutionary capacity in landscape organization in order to maintain parasitoids genetic heterogeneity. Whilst such disturbances vary across spatial and temporal scales, improved landscape planning at both local and area-wide levels will be key in order to improve parasitoid effectiveness. For example, development of multifunctional landscapes that promote biodiversity whilst maintaining essential ecological services must be encouraged. This landscape planning will require robust ecological indicators for both evaluation and determination of interventions. Research should therefore potentially aim at identifying parasitoids that are winners under changing climates, in particular those using adaptive evolutionary potential. These adaptive processes should be incorporated in biocontrol strategies aimed at maintaining interacting species and their essential ecological services.

AUTHOR CONTRIBUTIONS

FC and CN conceptualized the scope of the paper. FC, PM, and CN contributed equally to writing and editing of the manuscript.

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