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A research framework and a mechanistic host-interaction model for insects that use multiple host species: theoretical considerations and practical consequences

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Practical outcomes that are sought for various pest management systems involving insects are likely to be strengthened if the relevant underlying theoretical models and premises (which are often tacit) are taken into serious consideration. To illustrate this point, we revisit the research framework developed to help unravel the ecology of insects that use multiple host species, with a focus on herbivorous species (although the principles hold also for parasitoids and even predatory insects). The framework comprises four research questions that focus on the pattern of host species use (as quantified in the field) and the underlying mechanistic processes that result in the insects that use multiple host species being labelled as 'generalist'. Results that derive from these research questions have led to the development of a general model to explain how female insects (of any species) behave with respect to the different host species with which they interact, and in relation to the condition of the plants and the recent history of the ovipositing females. This background allows us to then explore the theoretical and practical consequences of the research framework and the mechanistic host-interaction model. We do so with reference to a particular area of applied entomology, that of classical weed biocontrol. Also considered are the historical outcomes from the practice of an applied entomological discipline that relies on the stability and accurate delimitation of the host recognition mechanism of biocontrol agents.

KEYWORDS

generalist, host repertoire, threshold, host-recognition and localisation, spatio-temporal dynamics, cryptic species, weed biocontrol

Introduction – the 'paradox' of generalism resolved?

Generalist insects are those recorded as using tens or hundreds of plant or insect species for their larval development, and this lifestyle is at variance with virtually all species being specifically adapted to particular ecological situations (Loxdale and Balog, 2025). Not only do such generalist insects provide a theoretical paradox, but they represent difficult practical problems in the derivative field of applied entomology. Indeed, many of the most serious agricultural pests have reputations as generalists (e.g., the moths *Helicoverpa armigera* and *Spodoptera frugiperda*, the mirid bug *Creontiades dilutus*, South African citrus thrips *Scirtothrips aurantii*, and silverleaf whitefly *Bemisia tabaci*). The diet of the predatory coccinellid *Cryptolaemus montrouzieri* is, incidentally, viewed in much the same way. Such generalist species are problematic from several perspectives:

1. Prevailing evolutionary theory explains multiple host use as a compensatory mechanism to maintain, enhance or optimise fitness using alternative hosts (e.g. Scheirs et al., 2000). Simultaneously, the use of multiple hosts is also theorised to impose biochemical and physiological costs on the generalist organism (e.g. Dall and Cuthill, 1997; Li et al., 2003; Braga and Janz, 2021).
2. From a practical perspective, observations in the field are often not consistent with the predictions or expectations of theory (Jones et al., 2022) and, somewhat surprisingly, generalist organisms are often extremely difficult to rear in the laboratory. Even then, once colonised in the laboratory, their responses in behavioural and physiological experiments are invariably not a reliable indicator of what they are observed to do in the field (Jones et al., 2020a).

We have reasoned that a new focus is needed if we are to understand the host use and spatio-temporal dynamics of insects that use multiple host species (Rafter and Walter, 2020) and, in this paper, we extend this to illustrate how the change in focus will help in the applied aspects of dealing with generalist insects.

The traditional focus in the investigation of generalist insects has tended to rely on the accumulation of host records and, in this respect, each observation and recorded host are treated equivalently (Rafter and Walter, 2020). Based on the number and diversity of host species included in the observations, an insect is labelled a generalist, and each host species on the list is assumed, perhaps tacitly, as an effective 'replacement' for any other host species in the field (Rafter and Walter, 2020). The problem is that this approach does not reveal much as to what are the primary influences on the underlying spatio-temporal dynamics of the species concerned, or even how to investigate them further to develop reliable management options or tools (Rafter and Walter, 2020). The consequence for the application of this theory is that it leads, for example, to the development of models that do not include the differences in host searching behaviour and oviposition across host species in the field in any realistic way (Jones et al., 2022). And it can also distort expectations of how mass-reared biological control agents will behave on release (Finlay-Doney and Walter, 2012) and how effective 'alternative hosts' will prove as trap crops of herbivorous pests (Rajapakse et al., 2006; Cook et al., 2007; Sarkar et al., 2018).

We therefore advocate a refocus on the pattern of host use, specifically that it should be quantified in the field for each insect species of interest. That would help expose the underlying behavioural and associated processes that result in the observed pattern in which the herbivore of interest deposits eggs across host plant species in the field. In brief, research on species seen as 'generalists' should focus on a research framework developed to help unravel the ecology of insects that use multiple host species (Rafter and Walter, 2020):

1. What is the relative frequency and intensity of host use across different plant or insect species (depending on whether one is dealing with a herbivore or parasitoid)? How consistent is this pattern spatially?
2. What is the species status of the various host-associated populations?
3. What does the spatio-temporal pattern of relative host use in the field reveal as to which are the primary and secondary host species?
4. How are primary and secondary host species recognised and localised before oviposition takes place in the field? And at what rates do different host species support larval development and survival?

What has been resolved empirically with respect to these questions in the framework has allowed a general model to be developed to explain how female insects (of any species) that use multiple hosts behave with respect to the different plant species, under what condition of the plants, and in relation to the recent history of the ovipositing females (Rajapakse et al., 2006; Jones et al., 2020a). The model is entirely mechanistic and focuses on the recognition of the various cues (mostly chemical compounds) that derive from the plants and the interaction with these as influenced by a system of underlying neurological and behavioural thresholds (Jones et al., 2022).

That is to say that even "generalist" insects have rather specialised host-interaction mechanisms. The ovipositing females are supposed to be attracted to particular hosts by a specific ratio of attractant chemical compounds or by the sum of multiple active compounds that activate various sensory receptors, each of which may individually contribute towards either enhancing or dampening a behavioural response (Jones et al., 2022). Experimental results on the relevant behaviour help explain why some host species (the primary host/s) are used routinely and by relatively large numbers of individuals, and why most recorded hosts of generalist species are used only incidentally. Some host species fall between these extremes, are best treated as secondary host species, and as such have a more substantial subset of the underlying cues that attract ovipositing females to primary host species routinely and in relatively high numbers (in relation to those of incidental host plant species).

The research framework and model detailed above remove the notion of herbivorous or parasitoid insects being arranged along a continuum from highly specialised to highly generalist, with selection acting on them according to their place relative to other species on the continuum (and with respect to their presumed relative competitive abilities) (see Walter, 2003). That is, natural selection does not operate on the species according to the number of host species used as resources; rather, it operates on the host location mechanism (including through the relevant recognition template and associated thresholds), oviposition behaviour, interaction of the egg with its environment and, ultimately, on the feeding and digestion physiology of the immature stages (Rafter and Walter, 2020; Braga and Janz, 2021).

The emphases detailed above are significant for they raise the question of why so many insect species have host-interaction mechanisms that respond to relatively few environmental cues and without the obvious mediation of thresholds, and why relatively few evidently respond to a greater diversity of cues and the perhaps periodic adjustment of thresholds. A strong argument can be made that these behavioural adaptations, involving thresholds of response being incorporated into the host interaction mechanism, are associated with species whose primary hosts are of unpredictable availability, both across space and through time. Such circumstances are associated with arid to semi-arid environments (Walter, 2003; Jones et al., 2022).

We believe that the above perspective explains, mechanistically, the use of multiple host species by insects, whether herbivores or parasitoids. And this implies that the paradox, really, is why it has taken so long to get away from the original paradox associated with generalist host use by insects. The full extent of an insect's host repertoire [a terminological shift from 'host range', as justified by Braga and Janz (2021)] is not acted upon directly by natural selection, which means it is a by-product of the mechanistic processes detailed above and how these are changed under selection, at speciation, in the original environment typically inhabited by the species of interest.

What does this change in theoretical perspective offer with regard to the point made by Andrewartha (1984), that any real test of theory is how well it works in practice? We therefore explore the theoretical and practical consequences of the research framework and the mechanistic host-interaction model, outlined above, in one area of applied entomology, that of classical weed biocontrol. We also consider the historical outcomes from the practice of an applied entomological discipline that relies on the stability, through time, of the host-interaction mechanism of biocontrol agents, as well as the accurate interpretation of that mechanism. We also review how outcomes from weed biocontrol can inform evolutionary and ecological theory as, after all, biological control is a large-scale field experiment in ecology (as recognised earlier by Myers, 1978).

A working example of the research framework in practice - classical weed biocontrol

Classical weed biocontrol is the scientific discipline of reuniting invasive alien plants (weeds) with host-specific herbivorous insects (called natural enemies and biocontrol agents) from the weed's native range (Schwarzlander et al., 2018). It is anticipated that natural enemies selected for release (after experimentally testing for their host-specificity, ability to damage the target plants, and their environmental safety) will impact the target weed sufficiently to maintain weed density across the landscape below a threshold that is acceptable environmentally and economically (Briese, 2000). Since weed biological control was developed as a management option in the early 1900s (Tryon, 1910), 262 invasive plant species, globally, have had biological control agents approved for release as part of targeted classical weed biocontrol programs (Winston et al., 2023). Weed biological control is underpinned by regulatory processes designed, through host-specificity testing protocols, to predict the risk of releasing that species or agent (as it becomes known at the time of release) in the new environment *a priori*, and this is a primary objective for weed biological control research (Raghu et al., 2007; Schwarzlander et al., 2018). It is worth noting that the obligation to assess risk through an understanding of the host-interaction mechanism of the species has not been explicitly specified.

Classical weed biocontrol thus provides an example in which a focus on the pattern of host use by the herbivorous insect species under consideration has environmentally significant practical implications, in the release of herbivorous insects (and insect predators and parasitoids) as biocontrol agents. In this section we discuss how current research in the investigation of herbivorous insects as potential biocontrol agents is structured, and its benefits. We argue that an understanding of the underlying behavioural processes that results in the observed pattern of host plant species use in the field are not fully resolved in general. And, specifically, with respect to candidate species for biocontrol release, the host localisation and recognition mechanism is not the primary focus of research once any particular insect species is deemed sufficiently host specific for use as a biocontrol agent. This omission reduces the pool of environmentally safe and potentially effective herbivore species available for weed biocontrol, for potentially useful and environmentally safe species may well be prematurely deemed to be too generalised in their host species use for further consideration for release (Rafter et al., 2008, 2013; Hinz et al., 2014).

Current risk assessment of herbivorous insects for weed biocontrol involves a progression of research steps. It starts with native range surveys in which biocontrol researchers routinely confront the first question of the research framework developed for generalist herbivore species (see above): 'What is the relative frequency and intensity of host use across different plant or insect species?' Admittedly, these surveys historically focused predominantly on the weed target, but now routinely include closely related species that co-occur at survey locations, because host species used routinely by the focal herbivorous insects were in danger of being overlooked. These field-sampling exercises are termed 'field host range surveys' or 'native range surveys of host use' (e.g. Rafter and Walter, 2012; Rafter et al., 2022; Sutton et al., 2021; Hinz et al., 2024).

During this initial cataloguing and prioritisation of potential agents, the research question that should be confronted next is:

'What is the species status of the various host-associated insect populations?' These would be the ones initially identified to a single species and recorded from multiple plant species in the native range surveys. This issue also needs to be confronted when a *prima facie* 'generalist' insect is recorded on the target weed species in native range surveys, but for which the weed target is not a listed host for the insect in the scientific literature (Rafter et al., 2013; Rafter and Raghu, 2020). At other times this question may also need to be addressed, for example when unanticipated issues are encountered with culturing the insect under quarantine conditions (e.g. Hausmann et al., 2016; Rafter et al., 2022). This may arise, for instance, when geographically separated populations of the host plant (target weed) and a herbivore species of interest are found and some sort of ecological disjunction across the populations (e.g. in behaviour, feeding or life cycle) suggests that the species status requires further investigation (Havill et al., 2018; McCulloch et al., 2018; Rafter and Walter, 2020; Rafter and Raghu, 2020; Nawaz et al., 2022). 'The key question here is whether individuals present on one host plant species recognise and mate with individuals present on an alternative host plant species' (Rafter and Walter, 2020). This question stems from the 'Recognition Concept of Species' as it is the most realistic concept in dealing with species from the population genetics perspective. And it is entirely mechanistic through its focus on how individual organisms meet and mate in the field within their usual environmental context (e.g., Paterson, 1991; Walter, 2003; Rafter and Walter, 2013; Hereward et al., 2017). It thus provides the most realistic conceptual framework for testing for the possibility of cryptic species among host-associated populations.

Several technical approaches are available for investigating the possibility of cryptic species. They include observational analyses of mate recognition behaviour (and the signals involved) or characterisation of the Specific-Mate Recognition System (SMRS) (Milne et al., 2002; Rafter and Walter, 2013; Rungrojwanich and Walter, 2000; Walter, 2003), reciprocal cross-mating tests on the recognition process (Fernando and Walter, 1997; Milne et al., 2007; Rafter and Walter, 2013; Wongnikong et al., 2020) (both of which allow allopatric populations to be tested), and analyses of gene flow between host-associated populations in sympatry (Hereward et al., 2013, 2017; Rafter and Walter, 2013; McKendrick et al., 2017). Asexual populations should also be investigated for host-associated cryptic species, although it is their behaviour relative to host plants that provides the focus for investigation (Najar-Rodriguez et al., 2009). A crucial aspect in analyses of gene flow is the design of the ecological sampling of the host-associated populations to be tested (Rafter et al., 2013). Multiple lines of inquiry (i.e. behavioural, molecular and chemical) are important as accurate delineation of species boundaries is more likely with this approach than in pursuing a single research angle (Rafter et al., 2013).

Native range surveys are sometimes structured in such a way that it is possible to repeat surveys at various assigned locations over a period of two to five years (depending on funding availability) (Goolsby et al., 2006; McCulloch et al., 2022). This then enables researchers to determine the spatio-temporal patterns of insect host use, although such data are rarely used in a way that reveals 'the statistically consistent pattern of relative host use in the field', which is the third question in the research framework proposed (above) for species that use multiple host species. This in part is because by this stage the biocontrol research programme is focused on insects that are likely to be host-specific, and it is at this point that prospective herbivores are introduced into quarantine or laboratories in the native range for intensive host specificity testing.

Quarantine testing commences with the most conservative method for determining the fundamental host repertoire [see Braga and Janz (2021)] of prospective herbivorous biocontrol agents. Screening typically begins with no-choice experiments and is followed by choice tests and multi-generation assays (Sheppard et al., 2005; van Klinken, 2000). These tests are conservative with respect to the biocontrol goal of avoiding non-target environmental impacts. Caution is necessary, of course, but we believe an argument can be made that the approach is over-cautious, with this temerity traceable to the host-finding mechanism of the candidate biological control insects being short-circuited by the confined environment in which the tests are conducted (Walter, 2003; van Klinken, 2000; Sheppard et al., 2005; Hinz et al., 2014). Nevertheless, the relative rates of mating, oviposition, feeding and survival across plant species, as derived from no-choice tests, do provide some indication of which plant taxa have the features required for sustaining populations, so it is referred to as the 'fundamental host repertoire' (Sheppard et al., 2005; Rafter et al., 2021).

Host testing results derived from quarantine conditions should be interpreted within a framework of what is known about insect-host-plant interactions (e.g. Manners et al., 2010). Host localisation and recognition is underpinned by a catenary behavioural process and can include many different sensory inputs, including chemoreception, vision and touch (Finch and Collier, 2000; Walter, 2003; Jones et al., 2022), each of which has a particular intermediary function within a particular environmental context (Walter and Hengeveld, 2014). The primary host plant (which must be established to be the target weed in the case of a candidate biological control agent) will have the entire range of sensory stimuli that result in herbivores ultimately being present on the plant regularly and in relatively consistent numbers (Rajapakse et al., 2006; Rafter and Walter, 2020) and will be nutritionally suited to the herbivore in question (Manners et al., 2010; Jones et al., 2020b). They are adapted, in other words, to localise these plants and to survive on them and reproduce (Schoonhoven et al., 1998; Walter, 2003; Jones et al., 2020b, 2022).

The relative rates of survival, feeding, mating and oviposition across test plants from quarantine no-choice tests provide a conservative indication of which plant taxa have features required for sustaining populations of the candidate biological control agent and the taxa identified through this experimental process are classified as part of the fundamental host repertoire (Sheppard et al., 2005; van Klinken, 2000). These plant species then need to be tested further, in open field host range tests where possible to allow the host-finding mechanism of the insects to operate unconfined and under the usual environmental conditions inhabited by the organisms. This will help to determine which test plants are within the realised host repertoire (Briese, 2005; Rafter et al., 2021; Le Falchier et al., 2025).

Once the realised host repertoire of a candidate biocontrol agent is determined through the quantification of host plant associations in the native range and the host specificity testing described above, the candidate is either discarded or, if deemed sufficiently host-specific when reviewed by regulatory authorities, will be released in the field on the infestations of the weed. Investigation at this point does not routinely expand from determining the pattern of fundamental and realised host repertoire to confronting the final question in the research framework, namely: 'How are hosts recognised and localised before oviposition takes place in the field?', although there has been urging within the discipline for the mechanisms that underpin host recognition to be explicitly investigated (e.g. Park et al., 2018; Park and Thompson, 2021; Wheeler et al., 2021; Pessina et al., 2024). The point is particularly well made by Park et al. (2018): "In weed biological control programs, pre-release host-specificity testing relies traditionally on no-choice and choice feeding, oviposition, and development tests. Rarely have they included detailed examination of behavioural responses to olfactory and visual cues of biological control candidates, although a better understanding of the mechanisms underlying host recognition may explain potential discrepancies between choice and no-choice tests, and/or between tests conducted in the lab versus field conditions."

We note, also, that molecular techniques are under development in attempts to enhance the effectiveness and efficiency of the initial screening of potential biological control agents. Kumaran and Raghu (2024), for example, provide a start in seeking correlations between 'generalists' and 'specialists' in terms of chemosensory receptors and enzymes. The correlation would allow generalists to be screened out even before host-testing began. The mechanistic model we advocate suggests at least two lines that will need consideration in these efforts and in those research programs in which genetical manipulation is envisaged for the host-searching mechanism of biological control agents and pest species. Firstly, the role of thresholds in the interaction of insects with different host species indicates that all receptors involved in the interaction with host plants by a particular herbivorous species should not necessarily be treated as strict equivalents, for the behaviour associated with them may vary with respect to environmental circumstances or the immediate history of the insects involved, for example. The second consideration involves the thresholds themselves. Are they determined genetically in any straightforward fashion? This aspect (and others undoubtedly are relevant to the issue) need to be understood before the behaviour of the insects could be subject to genetic manipulation in the laboratory.

Improving our mechanistic understanding of the host-interaction mechanism of herbivorous insects in the risk assessment process, by incorporating the focused questions from the research framework proposed for insects deemed to be generalist, will further reduce risk of unanticipated non-target impacts and will help to streamline timeframes for what can be a long testing process (5–10 years). We acknowledge that no method of ecological investigation can be prescriptive or linear, as each species presents its own broad suite of problems to be investigated (Rafter and Walter, 2020). The various questions relevant to understanding the host relationships of particular herbivorous insects, in general, are likely to be addressed in parallel. For example, knowledge of the host recognition mechanism of a focal insect being investigated for its biocontrol potential is likely to inform which plant species should be included in test lists for risk assessment through laboratory screening and to validate interpretation of host specificity testing.

Integrating the mechanistic research framework into weed biocontrol investigations more explicitly may also reduce the likelihood of potential agents being discarded prematurely, especially if they are perceived *prima facie* to be generalist in their host relationships. Should a cryptic species complex be "hidden" under the name of that single species (Rafter and Raghu, 2020; Rafter et al., 2022; Loxdale and Balog, 2025, this issue), a potentially good candidate species for biocontrol may be masked by inadequate taxonomy and may therefore be inadvertently discarded from further consideration. Also, the threshold-based host recognition and localisation system that leads these insects to hosts in the field may well justify the further consideration of a species for biocontrol release on the basis that the secondary host plant species (or phylogenetic equivalents) are not present in the adventive range of the weed. A better understanding of the host-interaction mechanism of prospective biocontrol agents should also allow the more effective and accurate anticipation of how the insect will 'perform' in the area of introduction in terms of establishment and impact (as also advocated by Hinz et al., 2024). The research framework proposed for generalist herbivores (Rafter and Walter, 2020) and the host-interaction model developed subsequently (Jones et al., 2020a) thus has direct applicability to applied entomology, and the questions and opportunities it opens for consideration clearly support their validity in the terms advocated by Andrewartha (1984) (see above).

Further consideration of the host recognition model – implications for weed biocontrol

The mechanistic model of host searching by herbivorous insects that use multiple host plants is, we note, the only mechanistic model developed for the host interactions of these insects (Jones et al., 2020a, 2022). The only alternative behavioural model available, that of host choice, seems never to have been developed beyond a verbal statement. Whereas Cunningham (2012) used the term 'host choice' in his title, his paper goes on to describe the mechanism of insect olfaction in the host recognition process and demonstrates how complex neural processing involved in real choice is not open to insects. Their behaviour is governed by simpler neural processing of the recognition cues of various modalities, which explains the behaviour of these insects more realistically (Bisch-Knaden et al., 2022; Bandyopadhyay and Sachse, 2023). Jones et al. (2020a) further demonstrate how threshold and feedback effects also play a role in insect host recognition when there is overlap in recognition cues from different host plant species.

These developments in our understanding of insect host-recognition process suggest a change in terminology with respects to 'no-choice' and 'choice' and 'preference tests', as these terms invoke the perception that the insect can evaluate and decide among options that are presented to them. The presentation of two plant species, simultaneously, to an insect in a cage helps sustain the view that the insect makes an active choice when ovipositing. But even if the insect is attracted strongly to one of the plant species and receives no sensory information from the other, the resultant pattern of oviposition would seem to represent the result of choice, despite the behaviour of the insect patently not being influenced in this way. Despite the important consequences of these neurological and behavioural considerations, the two (or more) species assay methodology is crucial to biological control as it provides an indication of relative rates of survival, feeding, mating and oviposition across tested plants (Sheppard et al., 2005; van Klinken, 2000), and thus an indication of risk that needs to be evaluated further with testing methods that allow more of the host recognition mechanism to be expressed (i.e. open field testing, targeted native range surveys or common garden experiments). Suggested alternative terminology for 'no-choice' tests include 'confinement tests' or 'recognition tests', and 'choice tests' could be 'weed target + test plant', 'multiple plant species exposure tests' or 'multiple recognition tests'.

Weed biocontrol – feedback into the development of ecological and evolutionary theory

Of 457 agents intentionally released globally between the years 1902 and 2008, 60 (13.1%) have been recorded attacking non-target species in the field, with such non-target attack acknowledged to occur in one of three different ways (Hinz et al., 2019, 2020):

1. 'Collateral damage' occurs when non-target feeding follows outbreaks of released biocontrol agents and the associated depletion of the weed target. This occurs on plant species unrelated to the weed and on which the agent cannot complete development, thus this damage lacks persistence.
2. 'Spillover', which also occurs at high agent densities, but the non-target feeding is observed on closely related plants. Again, the agents do not sustain populations on these species.
3. 'Sustained' damage is inflicted when the agent can develop completely and effectively on a non-target plant species and sustain populations on it, regardless of the presence or absence of the weed target in the nearby vicinity. This indicates the non-target plant is within the realised host repertoire of the biocontrol agent and represents a failure of the host-specificity testing process to identify this risk *a priori.*

The proportion of records of non-target attack relative to agent releases continues to decline, through a combination of tighter regulation and higher thresholds for risk assessments. More critical to such improvements in risk assessment methods, however, is that they are now underpinned by developments in ecological and evolutionary theory (Briese, 2005; Sheppard et al., 2005; Cullen et al., 2023). In one half of the cases of non-target attack, almost all in the early days of biocontrol, these outcomes were either predicted or were predictable, but in most cases the affected species had not been tested pre-release, when in the past 20 years or so they would certainly have been included. This improvement in risk assessment results from the adoption of Wapshere's (1974) 'centrifugal phylogenetic testing' approach, which was rooted in plant taxonomy. Also, continual refinements of this approach to host test list development have been made by including genetic approaches to infer plant evolutionary relationships (Briese, 2005; Chen et al., 2024, 2025).

What has not been detected when historical weed biocontrol agent releases and non-target attacks have been reviewed is any evidence of evolutionary changes or shifts in the host repertoire of the biocontrol agent species through fundamental changes to the mechanism by which hosts are recognised and located (Van Klinken and Edwards 2002; Hinz et al., 2019; 2020). This demonstrates that both the fundamental and realised host use repertoire of herbivores can be accurately delimited, especially if the questions that make up the research framework for so-called generalist insect herbivores are addressed during investigation. These research outcomes have implications for ecological and evolutionary interpretations.

Firstly, Braga and Janz (2021) state that the mapping of the fundamental host repertoire of herbivores is not an easy task, in part due to the need for methods to map repertoire in a systematic way. It seems that the applied discipline of weed biocontrol has been routinely confronting the question of fundamental *vs.* recognised host repertoire when screening for host-specific weed biocontrol agents using multiple complementary methodological approaches in both the field and laboratory.

Secondly, the long-term practice of weed biocontrol demonstrates that the host-interaction mechanism, and thus the realised host repertoire of herbivores, is stable through time as demonstrated by the mass release of 457 herbivores introduced into novel environments as weed biocontrol agents. We note that such stability in the complex adaptations that constitute the host-interaction of herbivorous insects is predicted by the Recognition Concept of species and the associated autecological approach to understanding the spatio-temporal dynamics of species. This contributes to our growing understanding of species and their origins (Walter and Hengeveld, 2014).

Discussion

In the present article, we strongly suggest that practical outcomes that are sought for various pest management systems involving insects are likely to be strengthened if the relevant underlying theoretical models and premises (which are often tacit) are taken into serious consideration. Even small shifts in one's underlying perspective can have profound practical implications, for such adjustments are likely to refocus the underlying research questions and resulting practical outcomes. The prevailing theory surrounding generalist insects is based on concepts of resource use and host choice, whereas the theory we advocate here (and also Rafter and Walter, 2020 and Jones et al., 2022), is centred on host-recognition and behavioural thresholds in the localisation and exploitation of their host species in the field. The shift in terminology may appear small but it is significant in understanding insect behaviour and how we may manipulate this to promote desirable practical outcome(s).

This same argument would hold for other areas in applied ecology in which the host-recognition mechanism and its associated behavioural thresholds are central to the success of management approach(es), for example the deployment of trap crops, landscape scale management and biosecurity eradication programmes. The genetic control of pests has been invigorated with the advent of gene editing tools such as CRISPR (Jinek et al., 2012; Raban et al., 2023) and an enhanced understanding of genetic drives (Champer et al., 2016; Raban et al., 2020). The potential for incorporating these advancements into the management of so-called generalist insect pests or for augmenting existing control tools is being explored in the theoretical or social context at least (Webber et al., 2015). The urge to incorporate these technologies into the management of pest insects by changing the behaviour of ovipositing females exists, but which aspects of the host interaction mechanism one should target for 'engineering' is not yet clear. If all host species are seen as rough equivalents to one another, a sensory component might be targeted that is activated by a key chemical compound in one host species and not another. If the recognition and threshold model is used to focus research, this should rather be on a mechanistic understanding of host recognition and the mode of operation of thresholds, for the effective alteration of their underlying genetics. The choice of the underlying theory on which to base such investigations is clear.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

MR: Conceptualization, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing. GW: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing.

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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.

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