Managing biological control services through multi-trophic trait interactions: review and guidelines for implementation at local and landscape scales

David J. Perović [a] *, Sagrario Gámez-Virués [a] *, Douglas A. Landis [b], Felix Wäckers [cd], Geoff M. Gurr [ae], Stephen D. Wratten [f], Min-Sheng You [a], Nicolas Desneux [g],

[a] State Key Laboratory of Ecological Pest Control for Fujian & Taiwan Crops and Institute of Applied Ecology, Fujian Agriculture and Forestry University, Fuzhou, China

[b] Department of Entomology, Michigan State University, East Lansing, USA

[c] BioBest Sustainable Crop Management, Westerlo, Belgium

[d] Centre for Sustainable Agriculture, Lancaster University, Lancaster, UK

[e] Graham Centre, Charles Sturt University, Orange, Australia

[f] Bio-Protection Research Centre, Lincoln University, Lincoln, New Zealand

[g] INRA (French National Institute for Agricultural Research), Univ. Nice Sophia Antipolis, CNRS, UMR, Sophia Antipolis, France

* Authors contributed equally

Correspondence: Sagrario Gámez-Virués: sagrariogamez@gmail.com

Geoff M. Gurr: ggurr@csu.edu.au

Running headline: *multi-trophic traits & multi-scale filters*

Abstract

Ecological studies are increasingly moving towards trait-based approaches, as the evidence mounts that functions, as opposed to taxonomy, drive ecosystem service delivery. Among ecosystem services, biological control has been somewhat overlooked in functional ecological studies. This is surprising given that, over the past several decades, much of biological control research has been focused on identifying the multiple characteristics (traits) of species that influence trophic interactions. These traits are especially well-developed to describe interactions between arthropods and flowers – important for biological control, as floral resources can provide natural enemies with nutritional supplements, which can dramatically increase biological control efficiency. Traits that underpin the biological control potential of a community and that drive the response of arthropods to environmental filters, from local to landscape-level conditions, are also emerging from recent empirical studies. We present here, an overview of the traits that have been identified to 1) drive trophic interactions, especially between plants and biological control agents through determining access to floral resources, and enhancing longevity and fecundity of natural enemies, 2) effect the biological control services provided by arthropods, and 3) limit the response of arthropods to environmental filters, ranging from local management practices to landscape-level simplification. We use this review as a platform to outline opportunities and guidelines for future trait-based studies focused on the enhancement of biological control services.

Key-words ecosystem services, environmental filters, functional ecology, arthropods, traits

Contents

I. INTRODUCTION

Biotic processes underpin the ecosystem services on which humans rely (Díaz, Lavorel, de Bello *et al.*, 2007). The combined scenarios of climate change, increased human population pressure, and severe declines in biodiversity, present a looming threat to future food security. Conventional agriculture presently relies on high-input management practices to maximise yields, which has been widely identified as unsustainable (Matson, Parton, Power *et al.*, 1997; Potts, Biesmeijer, Kremen *et al.*, 2010). Promoting the biotic processes which underpin ecosystem service delivery can help fill yield gaps while allowing agriculture to remain sustainable into the future (Bommarco, Kleijn & Potts, 2013). Understanding the biotic processes that govern ecosystem services is beginning to take a prime position in research and more importantly to draw the attention of policy-makers (Secretariat of the Convention on Biological Diversity, 2014, Dicks, Viana, Bommarco, *et al.*, 2016). Parallel to the growing focus on ecosystem service delivery, ecological research has begun to move away from a taxonomic-level resolution to a trait-based and community-level, functional ecological focus (*e.g.,* Díaz, Kattge, Cornelissen *et al.*, 2016; Kunstler, Falster, Coomes *et al.*, 2016), as traits within the community have been demonstrated to govern the biotic processes that drive ecosystem service delivery (Díaz *et al.*, 2007).

(1) The response–effect model

The delivery of ecosystem services is linked to species-traits that determine responses to environmental filters, as posited by the response–effect model (Lavorel & Garnier, 2002). These so-called *response traits* represent pre-adaptations to the environment. Species are filtered along environmental gradients depending on these pre-adaptations (Figure 1). The implications for ecosystem service delivery depend on response-diversity in the community and how strongly response traits are linked with the traits that determine ecosystem service delivery, which are known as *effect traits* (Figure 1). Environmental filters can therefore strongly limit ecosystem service delivery of a community through filtering of species with particular traits. The response–effect model has been well established for the effects of management practices on ecosystem service delivery by the first trophic level (*e.g.,* Laliberté & Tylianakis, 2012; Minden & Kleyer, 2011). Extending the trait-based approach to multi-trophic-level processes, and predicting ecosystem services delivery, has been identified as the next frontier in functional ecology (Reiss, Bridle, Montoya *et al.*, 2009), and particularly important for agriculture (Wood, Karp, DeClerck *et al.*, 2015). Understanding the functional significance of different traits is, thus, an essential aspect of trait-based approaches (Rosado, Dias & Mattos, 2013; Shipley, de Bello, Cornelissen, *et al.*, 2016). Progress has been hampered, however, by the disproportionate level of readily-available traits for plants compared with other organisms (Levine, 2015). Trait databases for arthropods, for example, are just developing. In order to advance this field, emphasis needs to be placed on testing the importance of arthropod traits on target processes as these databases develop (Moretti, de Bello, Ibanez *et al.,* 2013; Moretti, Dias, de Bello *et al.*, 2017). As a result of the current imbalance in functional trait information, most multi-trophic-level efforts have been limited to a mix of plant (effect) traits with other functional metrics for higher trophic levels (*e.g.,* abundance of functional groups, Storkey, Brooks, Haughton *et al.*, 2013; Storkey, Döring, Baddeley *et al.*, 2015*ab*), or more traditional taxonomic-level measures (*e.g.*, de Bello, Lavergne, Meynard *et al.*, 2010). To date, only a limited number of ecosystem services have been addressed, in traits studies, across multiple trophic levels (*e.g.*, biomass production, Moretti *et al.*, 2013; and cultural ecosystem services, Storkey *et al.*, 2013; Storkey *et al.*, 2015*a*).

(2) Identifying the functional significance of traits

The relationship between biodiversity and ecosystem functioning is thought to be driven by two, not necessarily independent components. The first can be summarised by the mass ratio hypothesis (Grime, 1998), which posits that contribution to ecosystem function is proportional to the relative abundance of a species or functional group within the community, so that ecosystem function is dominated by the dominant species. The second is that diversity within the community can maximise the functional output due to niche complementary (Tilman, Reich, Knops *et al.* 2001). The predominance of either of these components may depend on the traits in question and on their functional role. Shifts in trait distribution in the community, and their relationship with environmental filters and ecosystem functioning, will describe this functional relationship, and can be monitored with appropriate functional diversity indices (*e.g.,* Ricotta & Moretti, 2011). For example, community-weighted mean (CWM) and functional diversity (FD*var*) can identify relationships between single traits and environmental filters, and also to ecosystem functioning, related to dominant and complementarity processes, respectively; but care should be taken in avoiding correlation between these separate although related indices (see Dias, Berg, de Bello, *et al.,* 2013).

(3) The multi-trophic response–effect framework

Lavorel, Storkey, Bardgett *et al.* (2013) propose an extension of the response–effect model to incorporate trophic interactions between plants and higher trophic levels, and outline a framework (both conceptually and mathematically) for following multi-trophic level communities, shaped by management effects, and further filtered through trophic interactions, to the resultant ecosystem service delivery. At the core of this framework is the differentiation of two types of response and effect traits: *environmental* response and effect traits; and *trophic* response and effect traits (Figure 2a-e). Each of these types of traits need to be considered to understand the prediction of ecosystem services, especially those directly related to trophic interactions, such as biological control. In proposing this *multi-trophic response–effect framework*, Lavorel *et al.* (2013) identify two main challenges to its application, (1) consideration of more than two trophic levels, and (2) extending environmental filters beyond the local scale to incorporate landscape-level effects. In their subsequent proof-of-concept, Moretti *et al.* (2013) further identify the limitation that functional links between trophic levels (and mechanisms that guide them) are often simply unknown, therefore, severely limiting our potential to predict ecosystem services and to understand how they may be optimised by management practices.

(4) Biological Control.

Among ecosystem services delivered by arthropods, biological control has received virtually no attention in functional-ecological literature. Even seminal reviews have referred to biological control only in passing (*e.g.*, Lavorel *et al.*, 2013), and exemplary practical studies have dealt with biological control somewhat incidentally in describing food sources for birds, which themselves provide cultural ecosystem services (*e.g.*, Lavorel *et al.*, 2013; Storkey *et al.*, 2013; Storkey *et al.*, 2015*ab*). This lack of attention is surprising given the significant value of biological control services for agriculture (Losey & Vaughan, 2006) and the potential that biological control offers in closing the yield gap (*e.g.*, Gurr, Lu, Zheng *et al.*, 2016), plus the availability of a range of response and effect traits for natural enemies, including trophic linkages with plants, which have been identified in the biological control literature over several decades (*e.g.*, Wäckers & van Rijn, 2012) (Figure 2c).

While studies that represent specific steps in the multi-trophic response–effect model (Figure 3) are not unknown in the biological control context (Table 1), particularly for trophic-linkages, these studies have generally been limited in that they do not extend from environmental filters through to biological control services. While these studies have generally not self-identified as being trait-based (a more-recent development in ecology), they have nevertheless often recorded characteristics that can be synthesized under a trait-based framework to reveal the mechanisms that drive species interactions and ecosystem-service delivery. Biological control studies are typically limited by their highly specific taxonomic focus, meaning that results are not easily transferable to different species interactions or environmental settings. The advantage of the trait-based approach, in this regard, is to consolidate such disparate studies and to reveal the mechanisms driving species patterns (McGill, Enquist, Weiher & Westoby, 2006), which, under a taxonomic perspective, are often dismissed as being idiosyncratic (Straub, Finke & Snyder, 2008).

(5) Review structure

Here, we review response and effect traits across multiple trophic levels that may underpin the ecosystem service delivery of biological control provided by arthropods in managed agroecosystems. In order to facilitate future empirical efforts, we present our review within a multi-trophic trait-based perspective. We focus on functional traits that have been identified in the literature that appear to link arthropod response traits to management drivers (*i.e..,* in-field management intensity, management of local plant diversity and landscape-level simplification), and establish arthropod and plant trophic-response linkages, and finally identify traits describing the biological control potential of natural enemies. We structure the overview of these traits into three sections: response traits related to environmental filters; traits that underpin interactions between trophic levels; and, effect traits related to the ecosystem service delivery of biological control. The section on response traits to environmental filters is further divided into three sub-sections to address the three *environmental filters* (management drivers) that we perceive can drive arthropod communities and biological control services in agroecosystems, (1) agricultural management practices that have direct or indirect effects on arthropod natural enemies; (2) management of local plant diversity and the availability of resources that may benefit biological control agents; and (3) landscape-level filters for arthropods, and how these filters may affect trophic interactions. We conclude with a summary of how these traits may be used to inform management decisions to enhance biological control agents, and the direction that future empirical studies should take to extend the application of these efforts. The traits identified throughout all sections are summarized in Table 2, along with their expected role in ecosystem functioning (through dominant or complementary processes), and any related traits that should be studied in parallel or controlled for when testing their functional role. To facilitate future work, our terminology is kept consistent with that of the recent handbook for arthropod traits development by Moretti *et al*. (2017).

II. RESPONSE TRAITS RELATED TO ENVIRONMENTAL FILTERS

(1) Response to agricultural management practices

Although trait-based studies are still limited in agroecosystems (Wood *et al.*, 2015), an understanding of responses is beginning to emerge for community filtering related to management intensity for arthropods. In-field management intensity has shown consistent effects within individual functional groups, such as for flower-visitors (including both herbivores, *e.g.,* Lepidoptera, and biological control agents, *i.e.,* Syrphidae), and ground-dwelling predators (spiders and beetles), and also across the arthropod community as a whole (comprising herbivores, pollinators, predators and detritivores); species traits strongly determining the responses. Accordingly, species can be divided into two broad categories: 1) those favoured by management intensification, which have relatively small body size and reduced feeding specialization, and, 2) those disfavoured with relatively large body size and increased feeding specialization (flower-visitors, Rader, Bartomeus, Tylianakis *et al.*, 2014; ground-dwelling predators, Hanson, Birkhofer, Smith, *et al.*, 2017; Hanson, Palmu, Birkhofer & Smith, 2016; arthropod community as a whole, Gámez-Virués, Perović, Gossner *et al.*, 2015) (Figures 1 & 2b). Traits such as limited dispersal tendency, clutch size (reproductive potential), voltinism (generations per year) and annual rhythm (activity period) have been shown to be filtered out with increasing management intensity (*e.g.,* for butterflies, Börschig, Klein, von Wehrden *et al.*, 2013), reflecting strong responses to disturbance. Additionally, some of these traits can also be strongly correlated (Börschig *et al.*, 2013; Perović, Gámez-Virués, Börschig *et al.*, 2015), inferring low response diversity to management intensity. Correlations between dispersal tendency and life-history traits have also been noted, for example, for spiders; such *dispersal syndromes* may be explained by adaptations to ephemeral habitats, leading to trade-offs in investment in dispersal at the expense of maturity and reproduction (delayed age at maturity) (Bronte & Saastamoinen, 2012). In-field management intensity has been linked with increased dispersal in spiders and predatory beetles (Hanson *et al.*, 2017).

The filtering of traits related to disturbance strongly restricts response diversity across the entire arthropod community. Intensified agricultural landscapes tend, therefore, to be strongly dominated by communities of relatively small, generalist species with longer activity period (annual rhythm) (Gámez-Virués *et al.*, 2015) (Figure 2b). Reduced in-field management intensity and diversified management regimes have, in contrast, been linked with reduced biotic homogenization across all taxa (not just for arthropods, *e.g.*, Allan, Bosdoff, Dormann, *et al.* 2013); and in terms of biological control agents, with the conservation of both functionally similar groups of spiders (based on their body size, hunting mode and habitat preference) and also beetles (based on their body size and adult feeding specialization), thus, increasing functional redundancy (Rusch, Birkhofer, Bommarco, *et al*. 2014).

(2) Response to local plant diversity and resource availability

The impact of plant diversity on the second and third trophic levels has long been recognized; Root (1973), for example, identified that plant communities with reduced taxonomic diversity encourage arthropod communities dominated by feeding specialist herbivores and associated specialist parasitoids, while more-generalist predators were less strongly affected. Local plant diversity may provide benefits for natural enemies through different mechanisms, for example, by providing shelter, increased structural complexity, and alternate food resources (both alternate prey and floral resources: nectar and pollen) (see Landis, Wratten & Gurr, 2000; Gurr, Wratten, Landis & You, 2017, for a review). Habitat utilization and hunting mode, are arthropod traits that respond to shelter and structure: web-building spider richness, for example, increases with plant diversity and vegetation coverage (along with prey richness) (Diehl, Mader, Wolter & Birkhofer 2013). Spiders that utilize shelters such as rocks and holes are sensitive to agricultural practices but conserved in less disturbed grassy margins (Birkhofer, Wolters & Diekötter, 2014). In terms of provisioning alternate prey, flower strips have been shown to alter the dominant taxa found in spider webs, but not prey abundance or diversity, and may therefore, benefit feeding generalists (Mader, Birkhofer, Fiedler, *et al*., 2016).

While some natural enemies are more commonly associated with floral resources (*e.g.*, Syrphidae, and Hymenopteran and Dipteran parasitoids), many other species have been shown to also benefit, including spiders (see Nyffeler, Olson & Symondson, 2016). More specific details of the plant traits that managers can consider for enhancing biological control are given in detail in Section III, under trophic linkages.

(3) Response to landscape-level filters

The effects of reduced landscape heterogeneity associated with agricultural intensification are well established for arthropods in agricultural systems (Tscharntke, Klein, Kruess *et al.*, 2005). The underlying mechanisms driving this relationship are reviewed in Tscharntke, Tylianakis, Rand *et al.* (2012). In terms of response traits, feeding specialists are most strongly affected by reduced habitat diversity (Figure 2b), and such effects appear to be compounded for species with low reproductive rate (Holland, Fahrig & Cappuccino, 2005; Ryall & Fahrig, 2006; Rytwinski & Fahrig, 2011; Vance, Fahrig & Flather, 2003) and with limited dispersal tendency (Batáry, Báldi, Szél *et al.*, 2007; Rand & Tscharntke, 2007; Tscharntke *et al.*, 2005). Natural enemies are generally observed to be more sensitive to reduced habitat diversity than their prey (Kruess & Tscharntke, 1994; Kruess & Tscharntke, 2000; Rand *et al.*, 2007; Tscharntke & Kruess, 1999). This may be a result of an interaction between trophic level and feeding specialisation (Holt, 2010; Holt, Lawton, Polis *et al.*, 1999; Ryall & Fahrig, 2006; Steffan-Dewenter & Tscharntke, 2000), but may be further compounded by differences in dispersal ability, found for example, in parasitic wasps and their hosts, as the impact of habitat fragmentation is strongly contingent on dispersal (Keitt, Urban & Milne, 1997).

The importance of landscape configurational heterogeneity (the size, shape, and even arrangement of patches within the landscape) has only been explored in more-recent studies (Fahrig, Baudry, Brotons *et al.*, 2011; Gámez-Virués *et al.*, 2015; Holzschuh, Steffan-Dewenter & Tscharntke, 2010; Perović, Gurr, Raman, *et al.,* 2010; Perović *et al.*, 2015; Plećaš, Gagic, Janković *et al.*, 2014; Woltz & Landis, 2014). Landscape configurational heterogeneity has been shown to be a strong filter for body size, leading to dominance by species with relatively large individuals in landscapes characterised by larger patches, but may interact with filtering of body size associated with management intensity and land use diversity (*i.e.,* compositional heterogeneity) (Gámez-Virués *et al.*, 2015). The relative importance of these two components of landscape heterogeneity, composition and configuration; however, varies between taxa. For butterflies, where habitat edges are known to be important for dispersal (Settele, Feldmann & Reinhardt, 1999), stronger filtering is evident along configurational heterogeneity gradients for traits associated with feeding specialization, wing length, and migration tendency (Perović *et al.*, 2015). Dispersal mode can also interact with spatial patterns of suitable habitat in colony success within the landscape for spiders (Birkhofer, Bird, Bilde & Lubin, 2014). This highlights the need for consideration of traits that describe species habitat usage and assessment of landscape in terms of functional land-use (see Fahrig *et al.*, 2011; Perović *et al.*, 2015).

(4) Interaction between environmental filters

The effects of landscape heterogeneity also interact with in-field management intensity and local plant diversity. Increased landscape heterogeneity in the surrounding landscape (even within 250 m of managed fields) can strongly buffer against the negative effects of in-field management intensity on species filtering (Gámez-Virués *et al.*, 2015; Perović *et al.*, 2015). The extent to which resources are limited (*i.e.,* level of landscape heterogeneity) within a landscape will dramatically affect the impact of local plant diversity on biological control agents (Jonsson, Straub, Didham *et al.*, 2015), and is expected to interact strongly with species dispersal ability (Tscharntke *et al.*, 2012). Local plant diversity describes the availability of resources proximate to cropping areas, and therefore represents resources available for species with limited dispersal ability. The dispersal ability of species is, therefore, expected to be a trait of primary importance in the variation of arthropod response to landscape level patterns and in-field management intensity and local plant diversity (Table 2). Potentially interacting with this is the degree to which species must separate their activities, for example, parasitic wasps may need to switch between host-location, within the crop, and nectar-location outside the crop (Wäckers, 2008). These resources need to be more or less co-located for parasitic wasps, given their dispersal limitations.

(5) Future directions

(a) Response Traits

Trait research for arthropods is in its early stages, and available traits are not always tested for functional importance, nor based on standardized measurements. Rather, functions are often inferred from easily measured characteristics (*i.e.* soft traits *sensu* Nock *et al*., 2016). Body size, for example, is a presently ambiguous arthropod trait. Body size is readily available from taxonomic descriptions of species and often used as a proxy for dispersal ability, but may also be reflective of other functions, including dietary requirements (Chown & Terblanche 2007).This is reflected in the apparent interaction between the response of body size to in-field management intensity and landscape heterogeneity (Gámez-Virués *et al.*, 2015). Additional traits should be considered in concert with body size in its role as a response trait, for example, wing length (or wing length to body size ratio) and dispersal mode, or (standardized) metabolic rate, depending on the process of interest.

The traits outlined above (and summarized in Table 2) represent expected functional links with biological control, and offer a starting point for testing these relationships, along with interacting and confounding traits. Consideration should be given to the expected relationship between trait distribution and ecosystem function. CWM of feeding specialization, for example, is expected to decrease (representing greater proportions of feeding generalists) with increasing in-field management intensity, representing a shift in the dominant state in this trait. A parallel shift (decrease) in functional diversity (FD*var*) would also describe homogenization and decreased response diversity in the community. Similarly, in-field management intensity is expected to lead to increases in CWM for life-history traits, such as voltinism and annual rhythms, as species with more generations per year and longer activity periods have more opportunities to avoid or recover from disturbances (see Table 2 for details on other traits).

Presently, a number of arthropod natural enemy taxa have burgeoning trait databases dedicated specifically to them (hoverflies, Speight, Castella, Obrdlik, *et al*., 2011; carabids, Homberg, Homberg, Schäfer, *et al.,* 2013; ants, Bertelsmier, Luque, Confais & Courchamp, 2013; Parr, Dunn, Sanders, *et al*., 2016; soil invertebrates, including spiders, Pey, Laporte & Hedde, 2014), these offer opportunities for empirical studies to test the functional importance of available traits. Currently available traits for arthropods, however, tend to be based on generalizations for species, which may miss the individual level variation: *intra-specific variation,* responsible for functional differences (Bolnick, Amarasekare, Araújo, *et al*., 2011; Violle, Enquist, McGill, *et al*., 2007). As trait research moves forward, it has been advocated that such variation be accounted for, by directly measuring collected specimens following standardized protocols (Moretti *et al*., 2017). Moretti *et al*., (2017) identify morphological, feeding, life history, physiological and behavioural traits thought to be functionally important for, and generalizable across, all terrestrial invertebrates, and offer standardized guidelines for measuring these; this handbook should act as a guide to unite future trait research for arthropods. It should be noted that a major advantage offered by a trait-based approach is the transferability and escaping context-dependence for studies within specific regions or localities (McGill, *et al*., 2006; Hortal, de Bello, Alexandre, *et al*., 2015); as trait measures are not presently based on standardized protocols, this currently limits applicability in this regard (Moretti *et al*., 2017).

Additional traits that explain more-specific physiological mechanisms responsible for different environmental tolerances in arthropods have also been identified in the literature (in addition to those listed in Moretti *et al*., 2017). Leonhardt, Wallace, Blüthgen *et al*., (2015), for example, measured cuticular characteristics to explain desiccation resistance (and predation resistance). Molecular characteristics, such as sensitivity and adaptability to agro-chemicals represent an interesting opportunity for future trait categorization (*e.g.*, Liess, Schäfer & Schriever 2008; and see Van den Brink, Baird Baveco & Focks, 2013, for approaches to aquatic systems), as do holobiont-associated traits that consider microbial symbionts of insects in identifying environmental responses, such as heat resistance (and trophic interactions with plants and parasites) (*e.g.*, Feldhaar, 2011).

(b) Environmental Filters

We suggest that the interpolative power of landscape level environmental filters could be advanced in a number of ways. Firstly, landscape compositional and configurational heterogeneity may also drive the diversity of the plant community, although the scale of landscape effects on plants is perhaps reduced compared with arthropods (Nathan, 2006). As arthropod diversity and community structure are highly dependent on plant communities, this should be considered an important mechanism to explain arthropod patterns as well. Defining changes in plant diversity across the landscape is challenging both statistically (but see Matthiopoulos, Hebbelewhite, Aarts *et al*., 2011) and logistically (but see Moretti *et al*., 2013), especially given the emphasis on avoiding spatial-autocorrelation. Secondly, defining landscapes from an anthropocentric point of view (in terms of heterogeneity) may miss the dominant features or specific resources essential to certain taxa. Even within the same taxon, there may be very distinct differences in habitat requirements, such is the case for hoverflies, where some species have aquatic larvae, and so water bodies are highly important, but not so for those species with predacious larvae. Species, thus, may be grouped according to their habitat requirements, as those with similar habitat requirements can be expected to respond to the landscape, and landscape-change, in similar ways (Fahrig *et al.*, 2011; Perović *et al.*, 2015). Detailed habitat requirement data are readily available in trait databases for hoverflies (syrphthenet.net, Speight, Castella, Obrdlik *et al.*, 2011) and carabids (carabids.org, Homburg, Homburg, Schäfer *et al.*, 2013), among natural enemies these taxa offer a starting point for developing functional land-use maps that reflect habitat usage to better understand the role of landscape level filters.

Furthermore, the interaction between environmental filters operating at different spatial scales, lends itself neatly to community assembly models (*sensu* Leibold, Holyoak, Mouquet, *et al.,* 2004). The role of in-field management intensity and local plant diversity, representing a patch dynamics view (niche theory), can be investigated using traits related to disturbance adaptations (*e.g.*, body size, feeding specialization, age at maturity, dispersal tendency, annual rhythm) and habitat-requirements. Species sorting (colonist–competitor trade-offs) can be addressed by monitoring dominance by colonist (*e.g.*, via age at maturity, dispersal mode) versus competitor type traits (*e.g.*, relative growth rate, clutch size, parity, life-span, reproductive mode, voltinism). Mass-flow effects can be addressed by incorporating functional land cover maps and assessing the degree of functional connectivity (based on habitat requirement data for species expected to respond to the landscape in a similar way, *e.g.*, see Fahrig *et al.*, 2011), and with reference to traits related to dispersal (*e.g.*, body size and dispersal mode). In this regard, spatial connectivity networks (*e.g.*, graph theory), can elegantly model meta-population dynamics by incorporating patch quality and connectivity based on functional landscape arrangement (*e.g.*, cost-distance) and species specific dispersal ability (Urban & Keitt, 2001). To date only single community-assembly processes have been assessed in such a fashion (Martín-Queller & Saura, 2013), but graph models could be adapted to incorporate all competing processes. Furthermore, with or without graph models, understanding species sorting processes can be complemented by studying interaction networks (*e.g.*, Schleuning, Fründ & García, 2015; Ibañez, Aràne & Lavergne, 2016).

III. TRAITS UNDERPINNING INTERACTIONS BETWEEN TROPHIC LEVELS

(1) Response to plant defence

Plant characteristics associated with defence against herbivores have direct effects on natural enemies (Bottrell & Barbosa, 1998; Parolin, Bresch, Poncet *et al.*, 2012). Characteristics that translate into easily measured traits include the presence of physical defences such as trichomes and cuticular waxes; trichomes, for example, have been shown to negatively affect natural enemies (Simmons & Gurr, 2004).

Plant volatiles are often cited in plant–natural enemy interactions (*e.g.*, Turlings & Wäckers, 2004), especially for their role in herbivore-induced defence signalling (herbivore-induced plant volatiles, HIPV) (*e.g.*, Simpson, Gurr, Simmons *et al.*, 2011). The plant volatiles produced vary depending on the type of pest-damage experienced, suggesting that specific natural enemy responses may be prompted (and have therefore co-evolved) (McCormick, Unsiker & Gershenzon, 2012). More evidence, however, is needed to generalize these relationships in terms of traits, which cannot already be inferred through parasitoid host-specificity (McCormick *et al.*, 2012; Vet, Wäckers & Dicke, 1991). Potential exists for future work in categorizing and generalizing natural enemy responses to chemical signals produced by different plants (and plants by their chemicals signatures), and identifying natural enemy traits that may predict responses to chemical signals, for example, antennal responses (see below for flower volatiles).

(2) Response to plant structure

Although the provision of floral resources is the benefit most-generally emphasised for natural enemies (Ramsden, Menéndez, Leather *et al.*, 2014), structural complexity of plants may be an important plant trait for future focus for biological control studies. Plant structure has been linked with predation efficiency and reduced intra-guild predation (*e.g.*, Desneux & O'Neil, 2008; Finke & Denno, 2006). Spiders, for example, are often highly abundant in agricultural systems and, given their partitioning of niche space and hunting modes, represent the textbook example of complementarity in biological control (Schmitz, 2008), the structural complexity of local plant communities could, therefore, be expected to be highly influential in inter- and intra-guild interactions involving such taxa (Figure 2c).

(3) Response to floral resources

Exploitation of floral-resources by natural enemies represents the area in which trait linkages have been best established for biological control (Wäckers & van Rijn, 2012). Traits driving links between flowers and flower-visitors are also well established in the pollinator literature, offering future insights for flower-visiting biological control agents. Links between flowers and flower-visitors can be summarised under three mechanisms: attraction to flowers, access to floral resources, and nutritional suitability of the reward provided. It should be noted here, that while trait linkages are better established for certain natural enemies, utilization of flowers and flower resources have been recorded for most groups of natural enemies, including spiders (see Nyffeler, *et al.,* 2016).

(a) Attraction

Much of the literature dealing with the benefits of floral resources for natural enemies has been concerned, primarily, with attraction to flowers in the field and under laboratory conditions – and focused generally on singular traits. Attraction to colour has often been tested for natural enemies; yellow has generally been found to be favoured over other colours (Figure 2c). Care should be taken when interpreting results from the literature, however, as attraction to trap colour is generally tested, rather than to flower colour, and responses vary depending on the physiological state of the insect (Maredia, Gage, Landis *et al.*, 1992; Mitsunaga, Shimoda, Mukawa *et al.*, 2012; Wäckers, 1994; Wäckers, Björnsen & Dorn, 1996).

Floral olfactory cues have also received a substantial level of attention in laboratory trials (Wäckers, 2004; Wäckers & van Rijn, 2012). These efforts, however, have not focused on developing chemical signatures to define attraction for particular species or functional groups of natural enemies. As with plant defence chemicals, we see potential for pursuing a trait-based approach to generalize natural enemy responses (at the community level) to plant volatiles and flower odour, rather than continuing in cataloguing specific pairs of plants–arthropod species interactions.

Much of the work at the field level has attempted to establish attraction to flowers by demonstrating changes in abundance of natural enemies in the proximity of resource plants. Abundance of insects on flowers (or in the proximity to flowers), however, is a result of attraction plus retention; the influence of each of these aspects needs to be carefully controlled (Wäckers & van Rijn, 2012). In one of the few studies to explicitly assess the plant traits when monitoring natural enemy attraction and retention, Fiedler and Landis (2007*b*) showed that abundance of natural enemies, at the community level (across various taxa), is strongly linked with blooming, total area in bloom, peak bloom timing, and maximum height of flowers and, also, decreased (average) corolla width; the latter is linked with nectar access (as described below) (Figure 2c). We suggest that this approach should act as a model for future trait-based field studies in assessing the benefits of local plant diversity for biological control agents. Linking plant traits in this way to arthropod traits (rather than species abundance), would be the logical next step. Ultimately, this should also include a measure of biological control efficiency within and adjacent to floral resources, and the extent to which these effects are landscape-context dependent.

(b) Access

Flower–pollinator co-evolution has seen the development of various mechanisms to limit exploitation of floral rewards by ‘non-target’ flower-visitors, and access to floral resources may be denied to some visitors due to flower morphology (Wäckers & van Rijn, 2012), temporal availability, competition with other flower-visitors (Wäckers, 2005), and even due to the chemical properties of the nectar and pollen (Winkler, Wäckers, Kaufman *et al.*, 2009) (Figure 2c).

(i) Traits linking floral and arthropod morphology

Matching head capsule width of natural enemies with corolla width of flowers, is a well-established factor in limiting nectar access (*e.g.,* Baggen, Gurr & Meats*,* 1999) (Figure 2c). Corolla depth also appears to be of critical importance. Van Rijn and Wäckers, (2016) identified a critical value (1.6 mm), above which hoverflies appear not to be able to access nectar sources (for Asteraceae, this threshold was even smaller). Critical values of a width-to-depth ratio may also be worth investigating, in concert with behavioural characteristics of flower-visitor species, including tendency to resist entering flowers with deep nectaries, even if not limited by corolla width (as observed by Vattala, Wratten, Phillips *et al.*, 2006, *c.f.* Baggen *et al.*, 1999). Hairs on the style and ovary may represent additional limitations to nectar access, despite matching mouthpart and nectary depth (Baggen *et al.*, 1999).

Tendency for nectar to spill onto the petals (*e.g.*, due to orientation Wäckers & van Rijn, 2012), or to rise up the stamen (Belevadi, Venkateshalu & Vivek, 1997) may be additional plant traits worth noting. Finally, some biological control agents with biting mouthparts are known to chew through petals to expose nectaries (Idris & Grafius, 1997; Inouye, 1983), which may benefit other nectar feeders (Inouye, 1983). Such traits may help to explain apparently idiosyncratic results of nectar benefits. Flowers, however, are not the only source of nectar for flower-visitors; plants with extra-floral nectaries are often advocated as nectar-resources (most notably *Centaurea cyanus*, certain *Vicia* species, and several Rosaceae), because nectar access is not limited by morphological features of these plants.

(ii) Activity period

An overlap in activity period (diurnal and annual rhythm) between biological control agents and plants is essential if floral resources are to benefit biological control delivery (Figure 2c). Several studies have demonstrated significant differences in natural enemy abundance before and after blooming (*e.g.*, Fiedler & Landis, 2007*a*; Stephens, France, Wratten *et al.*, 2005). Ensuring there is diversity in flowering time within the plant community (increased FD*var* for annual rhythm of blooming), has been advocated as a means of providing natural enemies with continuing exposure to floral resources (Rebek *et al.*, 2005; Vattala *et al.*, 2006). In this respect, Wäckers (2005), points out that honeydew and extra-floral nectar are often also available outside the limited flowering period, although generally honeydew is an inferior diet for natural enemies.

(iii)Competition

Access to floral resources may be further limited through competitive exclusion (Wäckers, 2005; Wäckers & van Rijn, 2012). Competition with larger pollinators may drive natural enemies away from generally accessible flowers (Campbell, Biesmeijer, Varma, *et al.*, 2012). Therefore, the broader assemblage of flower-visitors within the landscape may be an important variable in explaining the benefits of nectar rewards for biological control efforts. It is well established, for example, that bumblebees interfere with access to flowers for hoverflies (Wäckers & van Rijn, 2012), who in turn out-compete some butterflies for nectar sources (Wäckers, 2005). To some extent, evolutionary adaptations may have led to resource partitioning within the flower-visitor community, temporal partitioning (or temporal avoidance) can be observed in the activity time (diurnal) of hoverflies, when bumblebees are less active, and in lacewings, nocturnally, when hoverflies are inactive (Wäckers, 2005; Wäckers & van Rijn, 2012). Matching diurnal activity time of nectar production and animal foraging should therefore be considered for trait linkages between arthropod and plant communities (Figure 2c).

Competition for resources amongst the broader community asks which response traits will be favoured. If local plant-diversity is represented only by floral resources that are favourable to natural enemies (small accessible flowers, *e.g.,* low CWM for corolla depth), then natural enemies may be forced to compete amongst themselves for access to such flowers. Campbell *et al.*, (2012), observed that while hoverflies are not out-competed by bumblebees for access to preferred flowers (regardless of the mix of short and long corolla flowers), and that bumblebees did not visit short corolla flowers, parasitic wasps may be disadvantaged by competition with bumblebees and hoverflies when a mix of short and long corolla flowers are present.

There is much empirical evidence to suggest that diversity of floral resources strongly drives diversity of flower-visitors. Nectar-volume diversity among flowers, for example, best explains flower-visitor diversity (*e.g.*, hoverflies, tend to specialise on flowers with low volumes, Potts, Vulliamy, Roberts *et al.*, 2004). Pollinators, in general, tend to partition resource usage in the face of competition, when a choice of flowers is available (Fründ, Dormann, Holzschuh *et al.*, 2013). The functional diversity of floral resources and the functional diversity of the entire flower-visitor community, not just natural enemies, should therefore be considered when assessing the impact of local plant diversity on natural enemies under a trait-linkages perspective.

(c) Reward

Nectar composition has also been identified as a plant trait that is linked with trophic-response. Parasitoids, for example, are thought to prefer sucrose-dominant nectar (Baker & Baker, 1983). Sucrose-to-hexose ratio has been demonstrated to be linked with increasing longevity from nectar feeding in some parasitoids (Vattala *et al.*, 2006), while extremely low sucrose-to-hexose ratio nectars (so called hexose-dominant) may provide less benefit to longevity and this may outweigh, and negate, other trophic linkages (such as nectary width versus parasitoid head width). There is, perhaps, a continuum for the relationship between parasitoid longevity benefits and sugar ratios (Vattala *et al.*, 2006), and it has become clear that these responses may vary between species (Tompkins, Wratten & Wäckers, 2010; Lenaerts, Abid, Paulussen, *et al.*, 2016). While sucrose-rich nectar has also been identified as favourable for Lepidoptera (commonly the target of biological control initiatives), hexose-rich nectars have been identified as unfavourable (Rogers, 1985). Additionally, nectar concentrations may make some nectar sources selectively available to natural enemies only. Sucrose concentrations above 40% may only be available for feeding by natural enemies with mandibular mouthparts but not, for example, for adult Lepidoptera (Daniel, Kingsolver & Meyhofer, 1989). Finally, certain sugars such as, sucrose, fructose and melibiose show strong positive effects on parasitoid longevity (Wäckers, 2001), while others – rhamnose, lactose, galactose and raffinose – show no benefit. Additionally, some floral resources have also been reported to have negative impacts on parasitoid survival (Wäckers, 2001; Wäckers, 2004; Winkler *et al.*, 2009); mainly as a result of attraction without accessible reward, or potentially toxic effects (Adler, 2001). Future research should be focused towards more generalizable responses across a wider variety of natural enemy taxa. Incorporating the interaction of floral attraction and sugar chemistry should also be included in trait-linkage studies. Although open flowers tend to be hexose rich, the additional consideration of this trait may still more accurately explain natural enemy responses across the community.

(4) Future directions

We propose to focus future research towards more generalizable responses to plant traits across a wider variety of natural enemy taxa. Potential exists in categorizing and generalizing natural enemy responses to chemical signals and including plant defence chemicals and HIPVs, flower width-to-depth ratio, and interactions between floral attraction and nectar composition. These categories should ultimately be linked to natural enemy traits (physiological, morphological or behavioural) that can, also, be relatively easily measured (*e.g.*, antennal response, mouthparts, etc.).

Overall, we see great potential for biological control from focusing on plant traits, rather than simply identifying specific associations. Again, reference to the pollinator literature may offer potential to fill information gaps for traits. Intra-varietal variation in flower volatiles in strawberries, for example, has been shown to be closely linked with antennal response of bees, and to explain differences in flower visitation (Klatt, Burmeister, Westphal *et al.*, 2013). Further, Binkenstein, Renoult & Schaefer (2013) showed that in-field management intensity strongly interacts with expression of flower colour, which in turn significantly affects flower visitation. Additionally, pollinator syndromes have been identified (*e.g.*, as summarized in Rosas-Guerrero, Aguilar, Martén-Rodríguez *et al.*, 2014), which categorize associations between plants and flower-visitors. These syndromes identify detailed traits such as specific colours, odour types, diurnal pattern in opening times, shape, and orientation of flowers linked with dipteran, hymenopteran, coleopteran, and other pollinator taxa. Although many natural enemies may not necessarily be primary pollinators, secondary pollinators are also thought to be important for setting the limits (through evolutionary processes) of accessibility to nectar and pollen rewards provided by flowers (Rosas-Guerrero *et al.*, 2014), and their characteristics may be expected to be linked with those of the flowers they visit.

Studies that correlate representative traits of plant communities with arthropod communities under field conditions (such as Fiedler & Landis, 2007*b*) should act as a model for future trait-based field studies in assessing the benefits of local plant diversity for biological control agents. For example, decreased CWM of corolla depth (and also width), reflecting that the plant community is dominated by flowers accessible for natural enemies, is expected to be linked with visitation by natural enemies, and therefore conservation and delivery of biological control services. Increased FD*var* of corolla width is also important in avoiding competitive exclusion between natural enemies. Increased FD*var* of blooming period (annual rhythm) is also expected to favour natural enemies through increased temporal availability of floral resources, but complementary in annual rhythms (*e.g.*, CWM centred on the same Julian months) may be more influential. Shifts in CWM of body size across the entire flower-visitor community, which reflect dominance of bees, for example, should also be considered when investigating the functional role of flowers in terms of benefits to natural enemies and biological control (see Table 2 for details on other traits). Incorporating traits of the wider non-predator arthropod community for explaining interactions with biological control, may also be appropriate for ants. Traits that describe feeding guild (predators versus non-predators, *i.e.*, mandibular tooth length), are filtered by habitat, so too are traits related to aphid tending (*i.e.*, number of maxillary palp segments and scape length) (Yates, Andrew, Binns & Gibb, 2014), which may be antagonistic to biological control. Overall, additional attention should be given in such studies to identifying ecosystem service delivery associated with each community.

IV. EFFECT TRAITS RELATED TO ECOSYSTEM SERVICE DELIVERY OF BIOLOGICAL CONTROL

(1) Biological control potential

The ultimate goal of understanding trait-linkages is to improve ecosystem service delivery. Traits that define effective biological control agents have been suggested in the literature, and a trait-linkages perspective offers an opportunity to assess the relative importance of these. Balmer, Géneau, Belz *et al.*, (2014), suggest, for example, that predators and egg parasitoids offer more effective biological control as they immediately prevent further herbivory, in contrast to larval parasitoids that keep the host alive to prolong nutrient assimilation (it should be noted, however, that this is not the case for idiobionts, which paralyze the host). Beyond feeding guild, feeding specialization has been shown to have stronger effect, for example, on biological control of aphids, for both predators and parasitoids (Figure 2d). Diehl, Serada, Wolters & Birkhofer, (2013) show biological control to be most effective in specialist predator communities (and communities containing specialist, versus generalist only communities), and to have differing but additive effects depending on aphid host plant. The specialist advantage of parasitoids has also been shown to be linked to host traits (Gagic *et al.*, 2016; described in more detail below).

Body size diversity (FD*var*) of predators has been identified as a key factor in increasing pest suppression (Rudolf, 2012), suggesting the mechanism of 'interactive complementarity' (Fründ *et al.*, 2013) (Figure 2d). This may be driven by relative body sizes of predators and prey (allometry, see Schneider, Scheu & Brose, 2012; Brose 2010) in describing predator handling efficiency, or the relative body size of predators in encouraging complementarity and in avoiding intra-guild predation (Rusch, Birkhofer, Bommarco, *et al.*, 2015). Overlap in predator body size between taxa (*e.g.*, spiders and carabids) has been suggested to be key for avoiding intra-guild predation; a community dominated by larger members of one taxa, may have negative implications for the other predator taxa (Rusch et al. 2015). Schmitz (2008) reviewed the multi-predator literature and suggested two traits that determine predator complementarity: habitat domain (extent of usage of micro-habitat) and hunting mode (Figure 2d). At the landscape level, dispersal ability and density dependant response to prey have been predicted as key traits to drive pest suppression, as they are thought to be more stable across different landscape heterogeneity scenarios (Bianchi, Schellhorn, Buckley *et al.*, 2010) (Figure 2d).

Interactions within the natural enemy assemblage are known to strongly affect biological control services. Although increased natural enemy diversity has sometimes been described as idiosyncratic in its relationships with pest suppression, a trait-based perspective can reveal the mechanism that drive the otherwise indiscernible positive, negative and neutral interactions that may occur (reviewed in Straub *et al.*, 2008). Rough categorization of natural enemies, for example, as 'specialist parasitoids' may be uninformative, and traits such as prey preference, micro-habitat usage, preference to prey density, and phenology should be considered to better understand redundancy and complementary (Rosenheim & Corbett, 2003; Straub *et al.*, 2008) along with body size distribution in the community (Rusch *et al.,* 2015).

Further, prey body size and dispersal ability are thought to be related, and to interact with hunting mode in their impact on intra-guild predation and implications for herbivore suppression (Diehl, 1993). This is also true for parasitoids, but under a different mechanism (Rosenheim & Harmon, 2006), for example, egg parasitoids tend to be minute and pupal parasitoids relatively large. Gagic, *et al.*, (2016) identify aphid traits including feeding specialization, reproductive mode, body size, habitat specialization, host plant, aggregation, tendency to drop and ant tending (myrmecophily) influence parasitoid success, and interact with parasitoid host specialization. Further herbivore traits, such as 'hairiness' and colouration, related to defence (Moretti et al. 2017), are expected to link with natural enemy specialization, and cuticle thickness (Leonhardt, *et al.*, (2015) to link with 'biting force' and mouthpart morphology (Moretti et al. 2017) (Figure 2d).

(2) Future directions

While field studies tend to focus on assessing abundance of natural enemies, their conservation is not equal to biological control service delivery (MacFadyen, Davies & Zalucki, 2015). Although the impact of natural enemies on pest populations is often neglected in field studies, assessing biological control services is not an exceedingly challenging venture. This is becoming increasingly more feasible (see MacFadyen *et al.*, 2015, for techniques to quantify natural enemy impact), and it is a highly important step in predicting biological control services.

Overall, assessing biological control services and ultimately linking this to yield (Liere, Kim, Werling *et al.*, 2015) and financial cost–benefits (*e.g.*, Classen, Peters, Ferger *et al.*, 2014; Gurr *et al.*, 2016; Maas, Clough & Tscharntke, 2013) is a step that is sorely missing from most biological control studies (Bommarco *et al.*, 2013). Trait-linkages approaches offer a model for expanding our understanding of this whole-system process. FD*var* for hunting modes, across the natural enemy community, for example, is expected to reflect niche complementary and lead to increased biological control delivery, and decreased intra-guild predation (along with overlapping body size distribution within the predator community, *e.g.*, similar CWM across taxa). Increased FD*var* may be especially important in taxa with clear demarcations in hunting mode and habitat domain, such as spiders, and also parasitoids, which are often very much stage specific. Links between body size of herbivores and natural enemies are also expected to reflect biological control potential (Table 2).

V. MANAGEMENT IMPLICATIONS

Intensified local management practices, including local monoculture, are linked with dominance by generalist predators, and filtering-out of specialists and parasitoids, leading to decreased response diversity in natural enemy communities (Gámez-Virués *et al.*, 2015; Root 1973) (Figure 2b). This filtering does appear to be buffered, however, by increased landscape heterogeneity, especially compositional heterogeneity (the diversity of land uses) (Gámez-Virués *et al.*, 2015). The benefits of increased local plant diversity for encouraging biological control agents are also contingent on landscape heterogeneity (Jonsson *et al.*, 2015). Habitat management practices aimed at increasing local plant diversity (Landis *et al.*, 2000), should be guided by matching traits of the plant community with traits of targeted natural enemies, for example, plant communities with smaller, open flowers and covering a broad flowering period (Fiedler & Landis 2007*b*) (Figure 2c). Ultimately, however, environmental filtering of response traits determines the community of natural enemies available to deliver biological control services, and landscape compositional heterogeneity appears to be the environmental filter most strongly responsible for response diversity in the arthropod natural enemy community, as it moderates other filters (Figure 2b-d).

VI. CONCLUSIONS

(1) Conservation biological control studies can be adapted to the multi-trophic response–effect model, and stand to benefit from a deeper understanding of the underlying mechanisms that drive both natural enemy conservation and biological control delivery. Typically, such studies aim at conserving natural enemies by reducing mortality factors related to management, which can be best identified via environmental response traits (*e.g.*, following Gámez-Virués *et al.*, 2015; Perović *et al.*, 2015) (Table 1), but also by encouraging natural enemy activity, for example, through habitat management (Landis *et al.*, 2000).

(2) An important component of habitat management efforts is to identify *the right type of diversity* in the local plant community to encourage natural enemies (Landis *et al.*, 2000). Matching trophic response traits, of arthropods, with trophic effect traits, of plants, offers great opportunities to identify the types of flower mixes, for example, that offer the greatest benefit to biological control agents (Fiedler & Landis, 2007*b*). Environmental response traits of the plants considered for habitat manipulation should also be considered, to identify, for example, species that will tend to thrive under different local management practices (Moretti *et al.*, 2013), as this is likely a limiting factor in the success of any such flower mix (Fiedler & Landis, 2007*a*). Ultimately, conservation biological studies should include a final step of following natural enemies into crops and assessing biological control. Emphasis on functional diversity (*e.g.*, traits identified by Straub *et al.*, 2008) (Table 2) offers the most complete picture.

(3) Traits highlighted in Table 2 are suggested as a starting point for future studies; consideration should be given to the underlying ecological mechanism when identifying focal traits and the expected (statistical) responses. Consideration needs to be given to whether ecological interactions are expected to be related to the dominant state of a trait within the community (as measured with CWM) or by diversity in that trait (FD*var*). Traits may also interact or have confounding effects, such as body size, which may represent both dispersal ability and also nutritional requirements (among others things, Table 2), and may appear to give idiosyncratic responses unless considered in concert with other appropriate traits. Given, however, that body size is most easily measured, and therefore the most widely available trait for arthropods, it is likely to continue to be predominant in the literature.

(4) Finally, we suggest that functional diversity studies for arthropods stand to benefit from the development of readily available traits databases, as this has been key in the success of trait-based studies for plants (Levine, 2015; Moretti *et al.* 2017). Consolidation of existing traits, and communication of those emerging traits, should also become a priority in future biological control research.

VII. ACKNOWLEDGEMENTS

SGV conceived the review; DJP wrote the paper. DJP to FW order equals credit; GMG to ND equal contribution. We thank two anonymous reviewers for their invaluable comments and suggestions. SGV & DJP were supported by National Natural Science Foundation of China (No. 31230061 and No. 31320103922). GMG is supported by the National Thousand Talents Fellowship and the Advanced Talents of SAEFA in China. ND was supported by the project EUCLID (H2020-SFS-2014, grant number: 633999). Support for DAL was provided by the NSF

Long-term Ecological Research Program (DEB 1027253) at the Kellogg Biological Station and by Michigan State University AgBioResearch.

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Figures and Tables

Table 1. Examples of trait-based studies relevant to biological control and representing partial steps in the multi-trophic response–effect model.

Table 2. Arthropod traits identified to underpin response to environmental and trophic filters, and the ecological mechanisms that drive them.

Figure 1. Arthropod traits related to activity period, feeding specialisation, body size, and mobility (a) are known to be filtered by in-field management intensity (local) and landscape simplification (landscape) (b), creating distinct differences within the expression of traits related to ecosystem service delivery of biological control in the community (c).

Figure 2. Schematic of the multi-trophic response-effect trait model adapted to biological control, showing how ecosystem service delivery is mediated through a series of filters. Environmental filters, such as in-field management intensity and landscape simplification, filter environmental response traits of plants and arthropods. Trophic effect traits of the plant community in-turn filter arthropod trophic response traits. Ecosystem effect traits of the resultant arthropod natural enemy community will determine the delivery of biological control services, but these traits are firstly determined by the series of filters described above. Traits in smaller solid-bordered boxes are linked across filters and may limit response diversity; traits in broken-bordered boxes are linked across trophic levels and drive trophic interactions.

Figure 3. Schematic of trait linkage analysis (based on Moretti *et al.* 2013). Proportional abundance and traits of each taxa (plants and arthropods) used to relate responses to filters (via multiple tables multivariate approaches or via trait indices for regression analysis). Partial correspondence analysis is then used to link responses to environmental filters (Step 1), and to plant traits to arthropod traits (Steps 2), and biological control services (Steps 3). Full correspondence analysis is finally used to identify plant and arthropod traits that link with environmental filters and biocontrol services (Step 4).

Table 1. Examples of trait-based studies relevant to biological control and representing partial steps in the multi-trophic response–effect model

Reference	Study taxa	Environmental response traits	Trophic response traits	Effect
Gámez-Virués *et al*., 2015	arthropod community	arthropod response traits to local management intensity and landscape simplification – body size, feeding specialization		
Fiedler & Landis 2007*b*	plant and arthropod community		plant effect traits – peak bloom, floral area, maximum flower height, colour, hue, chroma, corolla size	
van Rijn & Wacker 2016	*Episyrphus balteatus* (Diptera: Syrphidae), 32 plant species		syrphid response traits – proboscis length, plant effect traits – critical flower depth	potential parasitism*
Winkler *et al*., 2007	*Diadegma semiclausum* (Hymenoptera: Ichneumonidae) and *Plutella. xylostella* (Lepidoptera: Plutellidae), *Fagopyrum esculentum*		head capsule width – corolla depth	parasitism

*indicated by adult longevity. Empty cells indicated that the information was not recorded.

Table 2. Arthropod traits identified to underpin responses to environmental and trophic filters, and the ecological mechanisms that drive them

Arthropod traits	Trait type	Other traits to consider in concert	Ecological mechanism	Driven by
Body size	Environmental response	*interacts with:* wing length, dispersal mode	Greater dispersal ability Higher nutritional requirements	Dominance Dominance
	Trophic response	*interacts with:* trophic level, mouthpart morphology, activity time (diurnal)	Access to nectar	Dominance
		links with: corolla depth and width, nectar volume, activity period (annual rhythm)	Competition/resource partitioning	Complementarity
	Ecosystem effect	*co-correlated with*: dispersal ability *interacts with:* phenology, hunting mode *links with:* body size of prey	Complementarity, intra-guild predation	Complementarity
Feeding specialization	Environmental response	*interacts with:* reproductive potential, dispersal ability, trophic level	Sampling effects (resource availability)	Dominance
	Ecosystem effect	*co-correlated with*: trophic level *interacts with:* phenology	Generalist predators	Dominance
Dispersal tendency	Environmental response	*co-correlated with*: activity period, reproductive potential (clutch size), generations per year (voltinism), age at maturity *interacts with:* feeding specialization	Resource locating, response to disturbance events	Dominance
Activity period (annual rhythm)	Environmental response	*co-correlated with*: reproductive potential (clutch size), generations per year (voltinism), dispersal ability	Greater opportunity to response to disturbances	Dominance
	Trophic response	*co-correlated with*: dispersal ability *links with:* blooming period	Activity period should match nectar availability	Dominance
		interacts with: body size, trophic level, extra-floral nectaries	Wider range in flowering time provides longer access Diurnal period and temporal avoidance	Complementarity
		links with: blooming period		

Activity time (diurnal)	Trophic response	*links with:* nectar production (diurnal), extra-floral nectaries	Activity time should match nectar production	Dominance
		co-correlated: body size, trophic level	Range of activity time in flower-visitors avoids competition	Complementarity
Hunting mode	Ecosystem effect	*interacts with:* body size, relative prey size *links with:* plant structure	Intra-guild predation	Complementarity
Colour preference	Trophic response	*links with:* flower colour	Sampling effect	Dominance

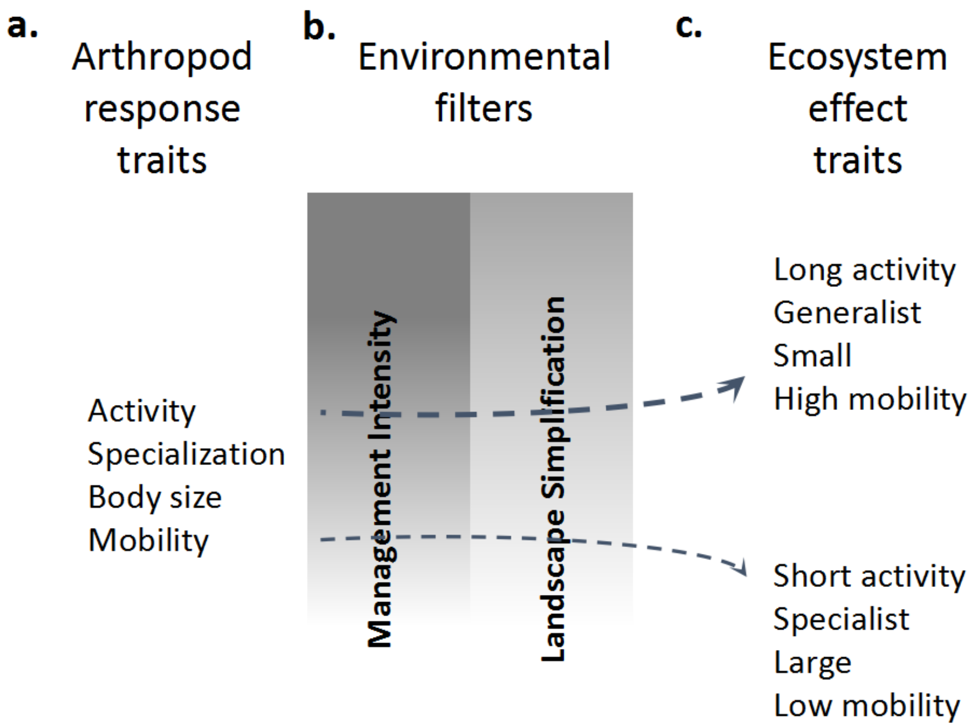

a.
Arthropod response traits
b.
Environmental filters
c.
Ecosystem effect traits
Activity
Specialization
Body size
Mobility
Management Intensity
Landscape Simplification
Long activity
Generalist
Small
High mobility
Short activity
Specialist
Large
Low mobility

Figure 1.

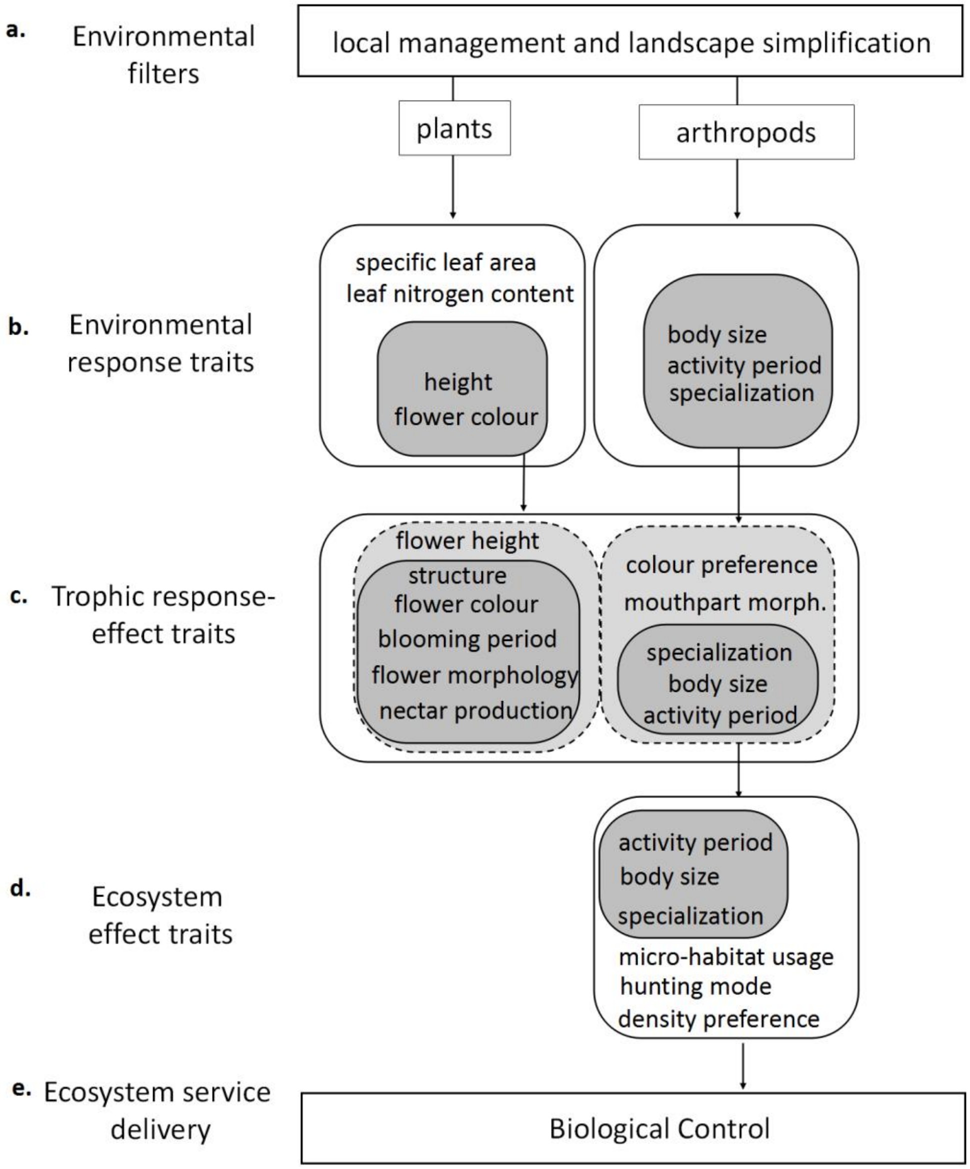
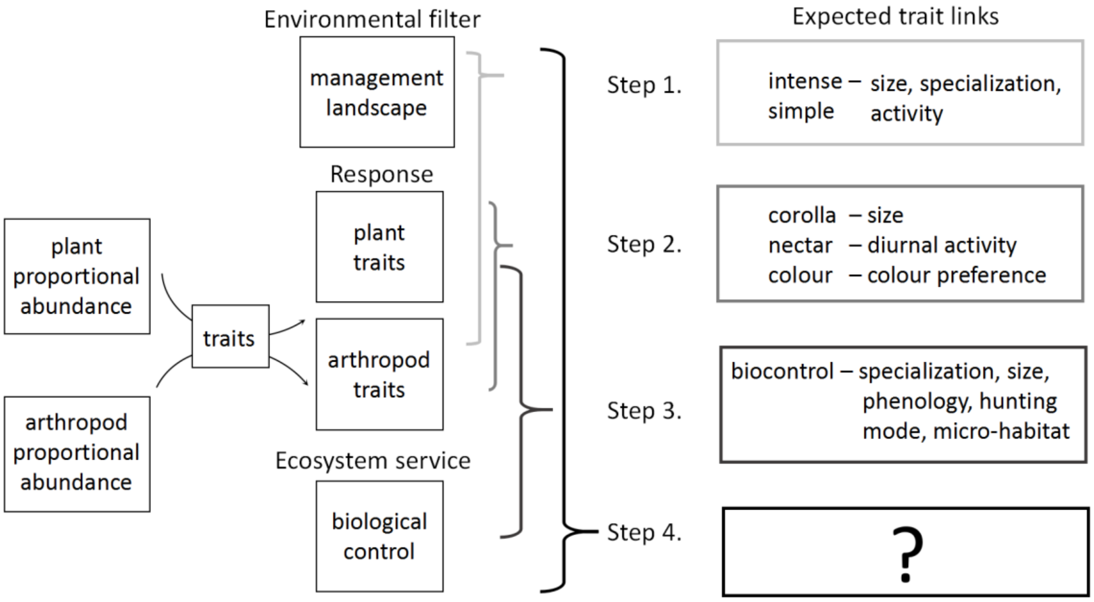

a.
Environmental filters
local management and landscape simplification
plants
arthropods
b.
Environmental response traits
specific leaf area
leaf nitrogen content
height
flower colour
body size
activity period
specialization
c.
Trophic response-effect traits
flower height
structure
flower colour
blooming period
flower morphology
nectar production
colour preference
mouthpart morph.
specialization
body size
activity period
d.
Ecosystem effect traits
activity period
body size
specialization
micro-habitat usage
hunting mode
density preference
e.
Ecosystem service delivery
Biological Control

Figure 2.


Environmental filter
management landscape
Response
plant traits
arthropod traits
Ecosystem service
biological control
plant proportional abundance
arthropod proportional abundance
traits
Step 1.
Step 2.
Step 3.
Step 4.
Expected trait links
intense – size, specialization,
simple activity
corolla – size
nectar – diurnal activity
colour – colour preference
biocontrol – specialization, size,
phenology, hunting
mode, micro-habitat
?