The Great Lakes Entomologist

Volume 54
Numbers 1 & 2 - Spring/Summer 2021 *Numbers 1 & 2 - Spring/Summer 2021*

Article 7

November 2021

Agricultural natural enemies benefit predominantly from broader scales of environmental heterogeneity: A quantitative review

Aaron Iverson
St. Lawrence University, aiverson@stlawu.edu

Robyn Burnham
University of Michigan, rburnham@umich.edu

John Vandermeer
University of Michign, jvander@umich.edu

Recommended Citation

Iverson, Aaron; Burnham, Robyn; and Vandermeer, John 2021. "Agricultural natural enemies benefit predominantly from broader scales of environmental heterogeneity: A quantitative review," *The Great Lakes Entomologist*, vol 54 (1)
DOI: https://doi.org/10.22543/0090-0222.2391
Available at: https://scholar.valpo.edu/tgle/vol54/iss1/7

Agricultural natural enemies benefit predominantly from broader scales of environmental heterogeneity: A quantitative review

Cover Page Footnote

We thank Louis Iverson for providing useful comments on this paper and the University of Michigan Department of Ecology and Evolutionary Biology for funding.

Agricultural Natural Enemies Benefit Predominantly from Broader Scales of Environmental Heterogeneity: A Quantitative Review

Aaron L. Iverson[1,*], Robyn J. Burnham[2], John H. Vandermeer[2]

[1] Environmental Studies Department, St. Lawrence University, Canton, NY, USA
[2] Department of Ecology and Evolutionary Biology, University of Michigan, USA
* Corresponding author: (e-mail: aiverson@stlawu.edu; phone: (315) 229-5970).

Abstract

Naturally occurring predator and parasitoid communities are well known to respond to multiple scales of environmental heterogeneity within and around agroecoystems, yet our understanding of which scales are most influential on different functional guilds of enemies is limited. Using vote-counting methodology, we synthesized the results from 40 empirical studies that observed how natural enemy richness, diversity, or parasitism rate is affected by environmental heterogeneity at a local scale (e.g. a focal field), an intermediate scale (e.g. habitat in immediate proximity of a focal field), and landscape scale (e.g. habitat within >200 m radius around focal field). Heterogeneity at all scales was more commonly beneficial than antagonistic to natural enemies as a whole, where positive responses were always significantly larger than negative responses. However, when using a conservative approach of comparing the positive and 'non-positive' (combined neutral and negative responses), landscape heterogeneity was the only scale where positive responses significantly outweighed non-positive responses. The same trend held for natural enemy guilds; though all guilds had more positive than negative responses to all scales of heterogeneity, intermediate and landscape scales were the only scales where any guild had significantly more positive than non-positive responses. These results suggest the importance of incorporating geographically large-scale strategies when seeking to conserve natural enemies and enhance or sustain conservation biological control services.

Keywords: agroecosystem, biological control, landscape, parasitoid, predator

---

The push towards agricultural intensification over the past several decades has resulted in simplified cropping systems and landscapes, as is highlighted by an increase in monocultures and a decrease in natural and semi-natural habitats in surrounding areas. This environmental simplification is generally found to result in compromised ecosystem services, such as decreased pollination, eroded soil nutrient and water supplies, and diminished pest control (Millennium Ecosystem Assessment 2005, Tscharntke et al. 2005, Foley et al. 2011). In terms of pest control, environmental simplification can decrease the abundance, diversity, or effectiveness of natural enemies of crop pests (Root 1973, Andow 1991, Perfecto et al. 2003, Bianchi et al. 2006, Vandermeer and Perfecto 2007, Letourneau et al. 2011), which may, in turn, push farmers to be more reliant on synthetic pesticides. In addition to causing environmental harm, this chemical-based pest control is vulnerable to losing its effectiveness through the development of pesticide resistance. These limitations, coupled with a growing demand for organic produce and increasing costs of synthetic inputs, have generated a large interest in controlling pests through biological control (Lewis et al. 1997, Landis et al. 2000, Simon et al. 2010).

Understanding how natural enemies are influenced by their environment is critical for developing strategies to augment the effectiveness of biological control services. To date, much research has shown that heterogeneity at both a local and landscape scale in agricultural areas commonly correlates with higher densities of natural enemies (for syntheses, see: Andow 1991, Bengtsson et al. 2005, Bianchi et al. 2006, Letourneau et al. 2011, Chaplin-Kramer et al. 2011), though a recent synthesis reveals the role of landscape heterogeneity to be mixed (Karp et al. 2018). Despite these advances, the relative importance of local vs. landscape environmental heterogeneity on natural enemies is not well understood. In the current review, we address this research gap.

The importance of landscape heterogeneity on biological control is evident in the literature, as the home range of many arthropod individuals extends far beyond the scale of a crop field (Tscharntke et al. 2007, Rusch et al. 2010), and may reach up to several kilometers (Roschewitz et al. 2005). Studies investigating the role of landscape heterogeneity often focus on the habitat composition extending from a couple hundred meters to several kilometers beyond a focal field (e.g., percent of non-crop area within a given radius of a field). Many studies highlight the importance of providing natural, semi-natural, or perennial habitat that natural enemies can inhabit when conditions in the agricultural area make survival difficult (Thies and Tscharntke 1999, Clough et al. 2005, Attwood et al. 2008, Rusch et al. 2010). These refuges—forests, hedgerows, field margins, fallows, meadows, or wetlands—may function as source habitats for predator or parasitoid populations and provide alternative resources (e.g. prey, pollen, nectar), permanent vegetation for reproduction and overwintering, or protection during disturbances (Rusch et al. 2010, Morandin and Kremen 2013). Landscapes with more natural/semi-natural areas may also provide benefits in terms of connectivity, allowing organisms a conduit for migration (Benton et al. 2003).

Similarly, local (within-field) heterogeneity has repeatedly been shown to positively influence the natural enemy community in agroecosystems (Andow 1991, Simon et al. 2010, Letourneau et al. 2011, Iverson et al. 2014). Studies of local heterogeneity usually compare fields of different planned (e.g., crop species) or sometimes associated diversity (e.g. weeds). Many studies compare monocultural to polycultural cropping systems. Two dominant theories are postulated to help explain why pest regulation in agroecosystems often results from higher local floristic diversity: the resource concentration hypothesis and the natural enemies hypothesis (Root 1973). The resource concentration hypothesis proposes that specialized herbivores will be better able to persist in areas where their food source is concentrated (e.g., monocultures) compared to polycultures, where they will be less efficient at locating acceptable food plants. This phenomenon results from one or more different mechanisms: (1) polycultures may cause chemical interference by collectively containing more plant volatiles which confuse or repel herbivores relying on olfactory cues in their search for host plant species; (2) herbivores may be visually confused when navigating through multiple plant species to reach their host; (3) a difference in host quality between polyculture and monoculture systems may result from changes in inter-plant competition; (4) the increased amount of non-host surface area in polycultures may inhibit herbivores through increasing search times for locating host plants; and (5) abiotic factors, such as differences in shade, humidity, wind, and mid-day temperatures between the two cultural practices (Andow 1991). Although these same mechanisms could also decrease the efficiency of natural enemies, evidence suggests natural enemies may not be as inhibited, and some even have enhanced search efficiencies in polycultures (Perfecto and Vet 2003).

The natural enemies hypothesis (Root 1973) proposes that natural enemies will be present in higher numbers in more complex habitats via at least two mechanisms. First, complex habitats will likely host a greater diversity of prey due to a greater diversity of host plants and microhabitats. Second, complex habitats offer other food resources, such as nectar and pollen, which are especially important for enemies (e.g., parasitoid wasps) whose different life stages require different foods. Both of these mechanisms result in increased temporal stability and availability of resources for the natural enemies.

The response of arthropods to environmental simplification at different scales can vary by organism, and often depends on the organism's trophic position and dispersal ability, which are often a function of body size (Tscharntke et al. 2005, Gabriel et al. 2010, Gonthier et al. 2014). Higher trophic-level organisms, and especially specialists (e.g., many parasitoids), are often more susceptible to habitat fragmentation than herbivorous pests (Kruess and Tscharntke 2000, Tscharntke et al. 2005, Klein et al. 2006). Many parasitoids may also be particularly sensitive to local heterogeneity due to their often limited dispersal abilities and narrow host ranges (van Nouhuys 2005, Shaw 2006), whereas natural enemy species that have high dispersal potential, such as ballooning spiders, might be less influenced by local habitat heterogeneity and more influenced by landscape heterogeneity (Clough et al. 2005, Schmidt and Tscharntke 2005). Furthermore, the influence of heterogeneity may be highly context-dependent, where the interaction between local and landscape heterogeneity is important. For example, local heterogeneity can be more influential for organisms in simplified (e.g., high proportion of cropped area) rather than in complex landscapes, as simple landscapes may not have as many natural enemies dispersing into farms from the surrounding landscape, and farms in these landscapes thus benefit relatively more from local management improvements (Thies and Tscharntke 1999, Tscharntke et al. 2005, Gabriel et al. 2010, Geiger et al. 2010, Batáry et al. 2011, Winqvist et al. 2011, Concepción et al. 2012, Tuck et al. 2014). Relatedly, local heterogeneity may be particularly important in landscapes of intermediate complexity where overly simplified landscapes are not able to support a pool of natural enemies from which to draw (Tscharntke et al. 2005).

It is well established that environmental heterogeneity at local and landscape scales is important for natural enemies, yet we do not have a clear understanding of which scale may be most commonly important among natural enemy guilds. Understanding the most influential scale for different organisms is critical for farmers, land managers, conservation practitioners, and policy makers in order to prioritize the scale of management that leads to the most effective and efficient biological control. In the present review, we provide a quantitative analysis based on a vote-counting methodology of 40 studies to determine which scale of environmental heterogeneity is most influential for natural enemy diversity, abundance, and parasitism rate. We also explore whether the response to scale varies depending on the natural enemy functional guild.

Methods

Literature search and study selection: To collect relevant studies, we reviewed the first 60 results from all cross-field combinations of the following two fields in addition to the term "agroecosystem OR agriculture": 1) local, landscape, management, intensification or scale, and 2) natural enemies, predator, parasitoid, parasitism, biodiversity, biocontrol or biological control. For example, one query included the terms "agroecosystem OR agriculture" plus one term from group 1 (e.g. "local") plus one term from group 2 (e.g. "natural enemies"). From these search results (N = 2100), we first eliminated studies that were clearly unrelated to the topic based on the title. We then read the abstracts and, if still deemed to be relevant, the full content of the remaining studies that were selected based on their title. From these, we included only studies that consisted of field experiments or surveys that investigated how natural enemy abundance, richness, diversity, size/condition, or parasitism rate differed between agricultural areas of differing management intensities at a local, intermediate, or landscape scale (for our categorization of scales, see below). We did not constrain by biogeographic region. Our search yielded a total of 40 studies (Kruess and Tscharntke 1994; Marino and Landis 1996; Murphy et al. 1996; Bommarco 1998; Elliott et al. 1998; Murphy et al. 1998; Carmona and Landis 1999; Menalled et al. 1999; Thies and Tscharntke 1999; Kruess and Tscharntke 2000; Nicholls et al. 2001; Östman et al. 2001; Elliott et al. 2002; Armbrecht and Perfecto 2003; Harmon et al. 2003; Kruess 2003; Menalled et al. 2003; Thies et al. 2003; Weibull et al. 2003; Costamagna et al. 2004; Pfiffner and Wyss 2004; Prasifka et al. 2004; Tylianakis et al. 2004; Bianchi et al. 2005; Clough et al. 2005; Purtauf et al. 2005a, 2005b; Roschewitz et al. 2005; Schmidt and Tscharntke 2005; Schmidt et al. 2005; Thies et al. 2005; Gianoli et al. 2006; Klein et al. 2006; Wilby et al. 2006; Aroga and Ambassa-Kiki 2007; Cai et al. 2007; Gardiner et al. 2009; Meyer et al. 2009; Thies and Tscharntke 2010). We conducted literature searches in Aug 2010.

Data compilation: We compiled the response of natural enemy diversity (including species richness and other diversity metrics), such as Simpson's and Shannon's diversity indices, abundance, and parasitism rate to three scales of environmental heterogeneity (local, intermediate, landscape; see below). Multiple observations were possible within a given study. If a study assessed multiple metrics (e.g., both richness and abundance) for a single species or a single group, each metric was considered as a separate observation. If a study considered multiple scales, one observation (and only one) was recorded for each of the three scales per natural enemy metric. For example, if a study calculated landscape diversity at 1 km, 2 km, and 3 km radii, all of which fit into our category of 'landscape diversity', we distilled the information into one observation. To do so, if the response to at least one scale was positive and there were no negative responses, we recorded the observation as positive (and did the same for a negative response). If all responses were neutral or if there were discordant responses (positive and negative), we recorded the observation as neutral. We did the same if there were multiple measures of environmental heterogeneity at the same scale (e.g. percent non-crop area and landscape habitat diversity at 1km). If studies reported natural enemy responses for individual species and for larger groupings (e.g., by guild or for all natural enemies), we used the most inclusive grouping that was presented.

We grouped observations into three distinct environmental heterogeneity scales: local, intermediate, and landscape. Local-scale heterogeneity was characterized by the within-field planned or associated diversity of plants. Most often, these studies compared monoculture to polyculture cropping systems, but some included within-field weed diversity (Clough et al. 2005, Purtauf et al. 2005b, Roschewitz et al. 2005). We categorized intermediate-scale heterogeneity as structural diversity located in the immediate surroundings of a field. This category included measures such as proximity to field edges, presence of refuge strips, or field perimeter-to-area ratios. For example, fields with higher perimeter-to-area ratios had relatively more field margins per unit area and were considered more complex. Landscape-scale heterogeneity pertained to regions incorporating multiple fields and/or habitat patches or beyond (minimum 200 m radius but up to 6 km radius from sampling location). More heterogeneous landscapes had a greater diversity of habitat types or a larger proportion of semi-natural, natural, or non-crop area.

We then categorized the observations according to the functional guild of the natural enemy, permitting comparisons of the relative importance of environmental heterogeneity to different functional guilds. In one analysis, we coarsely divided the observations into parasitoids or predators. In another analysis, we further divided the predators into either ground-foraging species or plant-foraging species (Table 1, Appendix 1). Although most species of natural enemies are capable of foraging on both the ground and on plants, we separated them by the habitat in which they spend the majority of their foraging time (if known), or by where they were captured in the study based on the capturing method, e.g. sweep netting vegetation vs. pitfall traps. Plant-foraging species included primarily enemies that are strong fliers (e.g., coccinellid beetles, pompilid and sphecid wasps, and most beneficial insects in the orders Neuroptera and Hemiptera) or species that are almost exclusively plant-dwelling (e.g., syrphid fly larvae). Ground-foraging species included primarily ground-foraging ants (Formicidae), ground-foraging beetles (Carabidae and Staphylinidae), and ground-dwelling spiders (Araneae). Although they are often plant-foragers too, spiders were grouped as ground-foraging because nearly all researchers in our included studies collected these using pitfall traps (Harmon et al. 2003, Weibull et al. 2003, Pfiffner and Wyss 2004, Clough et al. 2005, Schmidt and Tscharntke 2005). The category of parasitoids included several families of Hymenoptera and, to a lesser extent, Diptera.

Data analysis: Each observation was recorded as positive, negative, or neutral depending on whether natural enemy diversity, abundance, size, or parasitism rate significantly ($p < 0.05$) increased (positive), decreased (negative), or showed no significant effect (neutral) in the more heterogeneous environment. Using these tallies, we calculated the effect on the natural enemy community of 1) environmental heterogeneity (all three scales combined), 2) scale of heterogeneity (each scale considered separately), and 3) functional guild of natural enemy. Furthermore, we observed if the type of natural enemy metric (i.e., abundance, diversity, or parasitism rate) affected these outcomes. We grouped the metrics of species richness and diversity indices under the category 'diversity'. Only two studies compared the sizes or condition of the natural enemies (Bommarco 1998, Östman et al. 2001); these observations were included in the 'abundance' category. For all analyses, we determined whether the observed frequency of positive responses compared to the combined neutral and negative responses was significantly different ($p < 0.05$) from the expectation of a binomial distribution, where the probability of success was 0.5 for either outcome.

Results

Benefits of environmental heterogeneity: Overall effect and effect by scale: Our literature search yielded 40 pertinent studies and 130 observations. Overall, we found that the number of positive responses (54.6% of observations) by natural enemies to a heterogeneous environment with all scales combined far outweighed the number of negative responses (3.8% of observations; Table 1, Fig. 1). However, the number of neutral responses was also relatively large (41.5% of all observations). The extent of the benefit of heterogeneity on natural enemies depended on the scale at which the heterogeneity was observed, and only at the landscape scale were the positive responses (61.9%) of natural enemies significantly larger than the combined neutral (34.9%) and negative responses (3.2%; Table 1, Fig. 1). Intermediate-scale heterogeneity still had a majority (55.6%) of observations returning a positive response, while local-scale heterogeneity had the lowest percentage, with 38.7% of total responses being positive (and 58% neutral responses), though negative responses to local heterogeneity were still low (3%).

Effect by natural enemy guild: When we subdivided results by natural enemy guild, we found that positive outcomes from increased heterogeneity were also always much greater than negative outcomes for all guilds. However, the positive outcomes were only significantly greater than the combined neutral and negative effects for plant-foraging predators at intermediate and landscape scales and for parasitoids at a landscape scale (Table 1, Fig. 1). No guild showed a significantly positive response (compared to combined neutral and negative responses) at the local scale.

Effect by natural enemy metric: When the results were dissected according to the reporting metric (i.e., abundance, diversity, or parasitism rate), for all scales

Table 1. Proportion positive, neutral, and negative responses of natural enemies, including separate enemy guilds and metrics (diversity, abundance, parasitism rate), to increasing environmental heterogeneity.

	Positive	Neutral	Negative	p*	N
All scales combined					
All natural enemies combined	0.55	0.42	0.04	0.127	130
Parasitoids	0.58	0.40	0.02	0.084	53
Predators combined	0.52	0.43	0.05	0.324	77
Ground-foraging predators	0.38	0.55	0.08	0.923	40
Plant-foraging predators	0.67	0.30	0.03	**0.018**	33
Species diversity[a]	0.57	0.37	0.07	0.181	30
Species abundance	0.52	0.44	0.05	0.356	66
Parasitism rate	0.59	0.41	0.00	0.115	34
Landscape scale[b]					
All natural enemies combined	0.62	0.35	0.03	**0.021**	63
Parasitoids	0.66	0.34	0.00	**0.031**	29
Predators combined	0.59	0.35	0.06	0.115	34
Ground-foraging predators	0.47	0.47	0.07	0.500	15
Plant-foraging predators	0.72	0.22	0.06	**0.015**	18
Species diversity[a]	0.70	0.20	0.10	0.055	10
Species abundance	0.55	0.42	0.03	0.237	31
Parasitism rate	0.68	0.32	0.00	**0.026**	22
Intermediate scale					
All natural enemies combined	0.56	0.39	0.06	0.203	36
Parasitoids	0.50	0.43	0.07	0.395	14
Predators combined	0.59	0.36	0.05	0.143	22
Ground-foraging predators	0.42	0.50	0.08	0.613	12
Plant-foraging predators	0.80	0.20	0.00	**0.011**	10
Species diversity[a]	0.60	0.30	0.10	0.172	10
Species abundance	0.58	0.37	0.05	0.180	19
Parasitism rate	0.43	0.57	0.00	0.500	7
Local scale					
All natural enemies combined	0.39	0.58	0.03	0.859	31
Parasitoids	0.50	0.50	0.00	0.377	10
Predators combined	0.33	0.62	0.05	0.905	21
Ground-foraging predators	0.23	0.69	0.08	0.954	13
Plant-foraging predators	0.20	0.80	0.00	0.813	5
Species diversity[a]	0.40	0.60	0.00	0.623	10
Species abundance	0.38	0.56	0.06	0.773	16
Parasitism rate	0.40	0.60	0.00	0.500	5

* Bold numbers indicate values where the frequency of positive responses compared to the combined neutral and negative responses was significantly different from a binomial distribution ($p < 0.05$).
[a]Diversity metric includes species richness and other diversity measures (e.g., Simpson's and Shannon's diversity indices).
[b]For a definition of scales (landscape, intermediate, local), see 'Methods'.

combined and at each individual scale, again positive outcomes far outweighed negative outcomes. However, parasitism rate at a landscape scale was the only metric where positive outcomes (68.2%) were significantly higher than the combined neutral and negative outcomes, although species diversity was marginally significant ($p = 0.055$) at a landscape scale (Table 1).

Discussion

Overall response to environmental heterogeneity: We show that the natural enemy community consistently benefits from environmental heterogeneity, both within and around agroecosystems. In all scale and natural enemy functional guild categories, we observed a much greater number

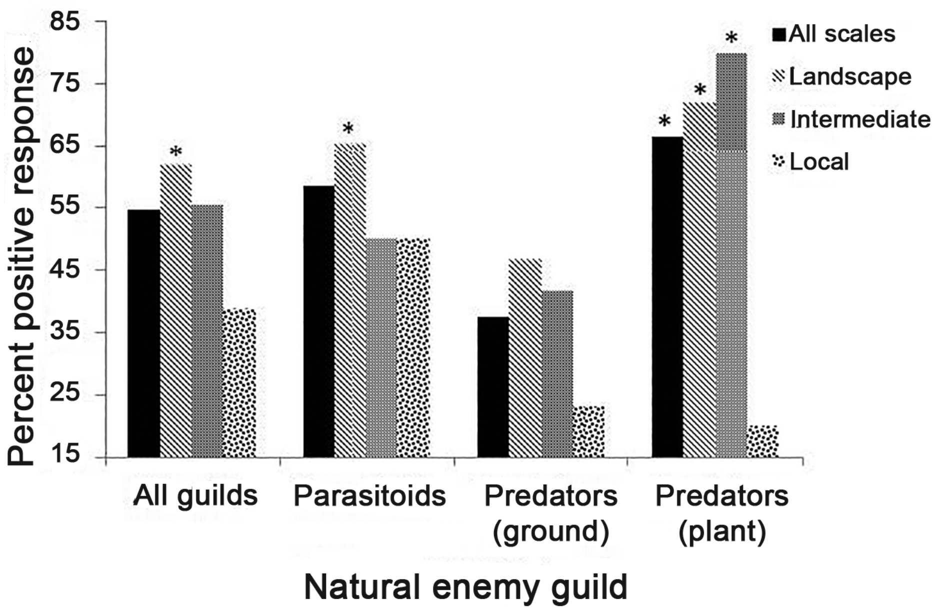

Figure 1. Percent of all observations returning a positive response of natural enemy abundance or diversity as a result of environmental heterogeneity at local, intermediate, and landscape scales, as well as at all scales combined. *Indicates cases where the frequency of positive responses compared to the combined neutral and negative responses was significantly different from a binomial distribution ($P < 0.05$).

of positive than negative responses, where positive responses on average outweighed negative responses by a factor of 14. These results corroborate the growing body of evidence showing beneficial responses of natural enemy communities to environmental heterogeneity at local or landscape scales (Andow 1991, Langellotto and Denno 2004, Bianchi et al. 2006, Poveda et al. 2008, Simon et al. 2010 Chaplin-Kramer et al. 2011, Letourneau et al. 2011, Gonthier et al. 2014). Despite a clear pattern of positive responses outweighing negative responses, we also observed many neutral impacts of heterogeneity on the natural enemy community, corroborating other studies which show mixed results and highlighting the ecological complexities associated with assessing impacts of heterogeneity (Karp et al. 2018). Our results help to disentangle the varied responses of environmental heterogeneity by separately assessing the impact of three different scales of heterogeneity on different guilds of natural enemies.

Scales of heterogeneity: Although positive responses outweighed negative responses at all scales, beneficial effects were especially pronounced at landscape scales. These results suggest that broad-scale heterogeneity is extremely valuable in maintaining natural enemy populations, supporting the idea that many arthropod species interact with their environment at a larger-than-local level (Thies and Tscharntke 1999), with important implications regarding regional planning and management processes. These results also provide support for a density-mediated mechanism (the enemies hypothesis), i.e., a top-down mechanism of herbivore control (Hairston et al. 1960). Here, natural enemies likely benefit from increased food and habitat resources in non-crop areas surrounding farm fields. However, trait-mediated effects (the resource concentration hypothesis) often function simultaneously and complementarily to the enemies hypothesis, and may still be an important factor in many of these studies.

Although the effects of local heterogeneity can often be as important as, or more important than, effects of landscape heterogeneity in agroecosystems (Puech et al. 2014), our results are consistent with the findings of other vote-count studies that have focused on single scales, where higher positive responses of natural enemies to environmental heterogeneity appear to be found at landscape scales. For instance, Bianchi et al. (2006) found that 74% of their observations showed a positive response to landscape heterogeneity, whereas studies of local heterogeneity showed (surprisingly consistent) positive responses barely to exceed 50% of all responses for natural enemies (52.7% in Andow 1991; 52% in Poveda et al. 2008; 53.3% in Simon et al. 2010). Our results are also consistent with recently reported declines in arthropod biodiversity in natural areas, where intensified land use (agricultural cover) at a landscape-scale, more so than local-scale variables, was a primary driver of declines in species abundance and richness in grasslands (Seibold et al. 2019).

Arthropod guilds and environmental heterogeneity: The positive responses to increased broad-scale heterogeneity observed in the parasitoid and especially plant-foraging predator communities may reflect their particular sensitivity to environmental disturbance at these scales. Parasitoids and many plant-foraging predators, such as syrphid flies, predatory wasps, and some predatory beetles, are reliant on alternative food sources, such as pollen and nectar, at some point in their life cycles (Langellotto and Denno 2004). Although some crops or weeds within crops may provide these resources, they are often most abundant in non-crop areas. Furthermore, the small size and high prevalence of prey specialization in parasitoids may also contribute to lower dispersal abilities and increased sensitivity to a simplified environment (Roland and Taylor 1997).

On the other hand, ground-foraging predators, such as ground spiders and carabid beetles, may be relatively less reliant on resources in non-crop habitat and more sensitive to soil management practices, such as tilling (Sharley et al. 2008), which could mask any differences in vegetation diversity or structure. Many of these species rely on stable soil habitats for protection (e.g., overwintering) or for oviposition (Rusch et al. 2010). For instance, Langellotto and Denno (2004) observed a large impact, especially on spiders, from enhancing the structural complexity of soil detritus. Other studies have shown that structural diversity, rather than plant species diversity, in the landscape physically inhibits carabid movement between fields (Frampton et al. 1995, Mauremooto et al. 1995). Additionally, some spiders are able to avoid size-dispersal limitations through long-distance windborne dispersal (ballooning), which may allow them to be less affected by intensively managed landscapes (Weyman et al. 2002).

When the metrics of parasitism rate, abundance, and diversity were considered independently, parasitism rate at a landscape scale was the only category where observations of enemies benefitting from heterogeneity were significantly more frequent than the combined neutral and negative observations. These results may again reflect how the often small and specialized parasitoids may be particularly sensitive to environmental disturbance (see above).

Management implications: Our findings support the value of increasing environmental heterogeneity for promoting natural enemy presence in agroecosystems. Our results suggest that farmers can enhance their local natural enemy community through increases in within-field diversity (e.g., polycultures), but especially through improvements in broader-scale, and especially landscape-scale, heterogeneity. Although landscape-scale heterogeneity will often, but not always, apply beyond the scope of an individual farm, intermediate-scale enhancement may be provided, for example, by increasing the size of vegetated (not bare) field margins, decreasing the size of fields, or including vegetation strips (e.g., floral strips, beetle banks) within fields. These vegetation strips may be especially effective if specific plants that provide resources for natural enemies, but do not simultaneously attract pests, are included (Pfiffner and Wyss 2004). Intentional set-aside conservation areas around crop fields need not trade-off with crop productivity, where benefits to yield from biocontrol may outweigh small losses in cultivated area (Pywell et al. 2015). Furthermore, vegetation strips or weedy field margins offer additional benefits, such as habitat for biodiversity, including pollinators, and erosion control (Wratten et al. 2012, Morandin and Kremen 2013).

The benefit of landscape-scale heterogeneity emphasizes the importance of region-wide land management or collective, community-scale initiatives. Currently, many management suggestions that seek to enhance biological control have focused solely on increasing local diversity (Gurr et al. 2000). We suggest, therefore, that government agencies and organizations should not only encourage farmers to make local-scale changes for biodiversity enhancement but should provide incentives for individual landholders and communities to make landscape-level management decisions that will positively impact biodiversity. Government-supported or certification-based (*sensu* Tscharntke et al. 2014) economic incentives could play an important role in promoting landscape heterogeneity. Although planning at large geographic scales is challenging, additive effects are common, where the land-use changes of individual farmers scale up to landscape-level effects (Holzschuh et al. 2008, Gabriel et al. 2010).

Our results suggest the importance of focusing management strategies on a particular pest or group of pests, as we show that the scale of management can have differential effects based on the natural enemy guild. For example, if the dominant pest spends all or part of its life cycle in the soil, ground-foraging predators, such as ground spiders and carabid beetles, may be the most effective biocontrol agents. As we show that these predators generally respond less to environmental heterogeneity and likely more to direct soil management, it may be important to vary a farm's cultural techniques to optimize the survival and growth of the predators. However, caution must be exercised to avoid a "one-problem, one-species" approach, as it is clear that the consortium of natural enemies is important for biological control given the inherent complexities of food webs even in simplified agroecosystems (Altieri 1999, Tscharntke et al. 2007, Vandermeer et al. 2010).

Limitations and further research: Enhancements in the natural enemy community may not necessarily translate into enhanced crop health (Symondson et al. 2002). However, although we did not include the effect of environmental heterogeneity on direct biocontrol, crop yield, or pest abundance, other studies have shown that natural enemy species often respond more strongly to heterogeneity than do pest species (Langellotto and Denno 2004, Chaplin-Kramer et al. 2011). Similarly, Risch et al. (1983) showed in a review of 150 studies that herbivores respond in an opposite manner to local heterogeneity, where 53% of herbivore species were significantly less abundant on more diverse farms. These studies suggest that an improved natural enemy community often translates into improved crop health.

Further research is needed to clarify the complex ecological interactions that underpin effective biocontrol and the influence of spatial scale on these interactions. A growing number of studies highlight indirect effects, both density- and trait-mediated (Werner and Peacor 2003), and the potential effects of land management, as well as intrinsic (self-organized) factors, in structuring them (Vandermeer and Perfecto 2008, Hsieh et al. 2012, Liere et al. 2014). Furthermore, the high proportion of neutral responses of natural enemies to heterogeneity may reflect the large variance in response, indicating that we may not be considering the appropriate metrics for understanding natural enemy distributions. The relatively high occurrence of neutral responses may also be reflective of the vote-counting method we employed, which is not sensitive to subtle effects.

Although mechanisms of local-level influences on natural enemies are better understood, mechanisms at a landscape scale are less clear, undoubtedly due to the difficulty of landscape-scale manipulation or comparison. To address this gap, we encourage research that characterizes the landscape in terms of traits or resources, rather than relying solely on coarse landscape metrics (e.g., non-crop area) (*sensu* Schellhorn et al. 2015). Additionally, research on biocontrol should report the dispersal abilities, if known, of each of the organisms studied, allowing for a clearer consensus on the role of dispersal in an organism's sensitivity to environmental heterogeneity.

Conclusions

The simplification of agricultural lands threatens the health of many ecosystems worldwide, impacting both humans and the biodiversity on which we depend (IAASTD 2008, IPBES 2019). It is therefore critical to understand how we can implement agroecosystems that provide important services, such as pest control, with an eye on reducing reliance on pesticides and other practices that simplify rather than diversify agriculture. Boosting natural enemy populations through habitat enhancement is one way to achieve this goal. Our results suggest that environmental heterogeneity, especially at broader (i.e., intermediate and particularly landscape) scales, is important for increasing the diversity and abundance of natural enemies. These findings highlight the importance of not only individual landowners, but also collective land management practices, in maximizing potential biocontrol services from natural enemies.

Acknowledments

We thank Louis Iverson for providing useful comments on this paper and the University of Michigan Department of Ecology and Evolutionary Biology for funding.

Literature Cited

Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems & Environment. 74: 19–31.

Andow, D. A. 1991. Vegetational diversity and arthropod population response. Annual Review of Entomology. 36: 561–86.

Armbrecht, I., and I. Perfecto. 2003. Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. Agriculture Ecosystems and Environment. 97: 107–115.

Aroga, R., and R. Ambassa-Kiki. **2007**. Effects of maize–cowpea intercropping on maize stem borers and their natural enemies, pp. 314–328. *In* Badu-Apraku, B., Fakorede, M., Lum, A., Menkir, A., Ouedraogo, M. (eds.), Demand-Driven Technol. Sustain. Maize Prod. West Cent. Africa. International Institute of Tropical Agriculture, Ibadan, Nigeria.

Attwood, S. J., M. Maron, A. P. N. House, and C. Zammit. **2008**. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Global Ecology and Biogeography. 17: 585–599.

Batáry, P., A. Báldi, D. Kleijn, and T. Tscharntke. **2011**. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proceedings of the Royal Society B. 278: 1894–902.

Bengtsson, J., J. Ahnstrom, and A.-C. Weibull. **2005**. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. Journal of Applied Ecology. 42: 261–269.

Benton, T. G., J. A. Vickery, and J. D. Wilson. **2003**. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution. 18: 182–188.

Bianchi F.J., W.K.R.E. van Wingerden, A.J. Griffioen, M. van der Veen, M.J.J. van der Straten, R.M.A. Wegman, and H.A.M. Meeuwsen. 2005. Landscape factors affecting the control of *Mamestra brassicae* by natural enemies in Brussels sprout. Agriculture Ecosystems and Environment. 107:145–150.

Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. **2006**. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B. 273: 1715–27.

Bommarco, R. 1998. Reproduction and energy reserves of a predatory carabid beetle relative to agroecosystem complexity. Ecological Applications. 8: 846–853.

Cai, H.-J., Z.-S. Li, and M.-S. You. **2007**. Impact of habitat diversification on arthropod communities: A study in the fields of Chinese cabbage, *Brassica chinensis*. Insect Science. 14: 241–249.

Carmona, D. M., and D. A. Landis. **1999**. Influence of refuge habitats and cover crops on seasonal activity- density of ground beetles (Coleoptera : Carabidae) in field crops. Biological Control. 28: 1145–1153.

Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. **2011**. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecology Letters. 922–932.

Clough, Y., A. Kruess, D. Kleijn, and T. Tscharntke. **2005**. Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. Journal of Biogeography. 32: 2007–2014.

Concepción, E. D., M. Díaz, D. Kleijn, A. Báldi, P. Batáry, Y. Clough, D. Gabriel, F. Herzog, A. Holzschuh, E. Knop, E. J. P. Marshall, T. Tscharntke, and J. Verhulst. **2012**. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. Journal of Applied Ecology. 695–705.

Costamagna, A. C., F. D. Menalled, and D. A. Landis. **2004**. Host density influences parasitism of the armyworm *Pseudaletia unipuncta* in agricultural landscapes. Basic and Applied Ecology. 5: 347–355.

Elliott, N. C., R. W. Kieckhefer, J. Lee, and B. W. French. **1998**. Influence of within-field and landscape factors on aphid predator populations in wheat. Landscape Ecology. 14: 239–252.

Elliott, N. C., R. W. Kieckhefer, and G. J. Michels. **2002**. Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. Environmental Entomology. 31: 253–260.

Foley, J. A., N. Ramankutty, K. A. Brauman, E. S. Cassidy, J. S. Gerber, M. Johnston, N. D. Mueller, C. O'Connell, D. K. Ray, P. C. West, C. Balzer, E. M. Bennett, S. R. Carpenter, J. Hill, C. Monfreda, S. Polasky, J. Rockstrom, J. Sheehan, S. Siebert, D. Tilman, and D. P. M. Zaks. **2011**. Solutions for a cultivated planet. Nature. 478: 337–342.

Frampton, G., T. Cilgi, G. Fry, and S. D. Wratten. **1995**. Effects of grassy banks on the dispersal of some carabid beetles (Coleoptera: Carabidae) on farmland. Biological Conservation. 71: 347–355.

Gabriel, D., S. M. Sait, J. a Hodgson, U. Schmutz, W. E. Kunin, and T. G. Benton. **2010**. Scale matters: the impact of organic farming on biodiversity at different spatial scales. Ecology Letters. 13: 858–69.

Gardiner, M., D. Landis, C. Gratton, C. DiFonzo, M. O'Neal, J. Chacon, M. Wayo, N. Schmidt, E. Mueller, and G. Heimpel. **2009**. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. Ecological Applications. 19: 143–154.

Geiger, F., G. R. de Snoo, F. Berendse, I. Guerrero, M. B. Morales, J. J. Oñate, S. Eggers, T. Pärt, R. Bommarco, and J. Bengtsson. **2010**. Landscape composition influences farm management effects on farmland birds in winter: A pan-European approach. Agriculture, Ecosystems & Environment. 139: 571–577.

Gianoli, E., I. Ramos, A. Alfaro-Tapia, Y. Valdéz, E. R. Echegaray, and E. Yábar. 2006. Benefits of a maize–bean–weeds mixed cropping system in Urubamba Valley, Peruvian Andes. International Journal of Pest Management. 52: 283–289.

Gonthier, D. J., K. K. Ennis, S. Farinas, H.-Y. Hsieh, A. L. Iverson, P. Batáry, J. Rudolphi, T. Tscharntke, B. J. Cardinale, and I. Perfecto. 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proceedings of the Royal Society B. 281: 20141358.

Gurr, G. M., S. D. Wratten, and P. Barbosa. 2000. Success in conservation biological control of arthropods, pp. 105–132. *In* Gurr, G.M., Wratten, S.D. (eds.), Biological Control Measures of Success. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist. 94: 421–425.

Harmon, J. P., E. E. Hladilek, J. L. Hinton, T. J. Stodola, and D. a. Andow. 2003. Herbivore response to vegetational diversity: spatial interaction of resources and natural enemies. Population Ecology. 45: 75–81.

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2008. Agricultural landscapes with organic crops support higher pollinator diversity. Oikos. 117: 354–361.

Hsieh, H.-Y., H. Liere, E. J. Soto, and I. Perfecto. 2012. Cascading trait-mediated interactions induced by ant pheromones. Ecology and Evolution. 2: 2181–91.

IAASTD. 2008. Agriculture at a Crossroads. Island Press, Washington, D.C.

IPBES. 2019. Global assessment report on biodiversity and ecosystem services of the Interngovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn, Germany.

Iverson, A. L., L. E. Marín, K. K. Ennis, D. J. Gonthier, B. T. Connor-Barrie, J. L. Remfert, B. J. Cardinale, and I. Perfecto. 2014. Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. Journal of Applied Ecology. 51: 1593–1602.

Karp, D. S., R. Chaplin-Kramer, T. D. Meehan, E. A. Martin, F. DeClerck, H. Grab, C. Gratton, L. Hunt, A. E. Larsen, A. Martínez-Salinas, M. E. O'Rourke, A. Rusch, K. Poveda, M. Jonsson, J. A. Rosenheim, N. A. Schellhorn, T. Tscharntke, S. D. Wratten, W. Zhang, A. L. Iverson, L. S. Adler, M. Albrecht, A. Alignier, G. M. Angelella, M. Zubair Anjum, J. Avelino, P. Batáry, J. M. Baveco, F. J. J. A. Bianchi, K. Birkhofer, E. W. Bohnenblust, R. Bommarco, M. J. Brewer, B. Caballero-López, Y. Carrière, L. G. Carvalheiro, L. Cayuela, M. Centrella, A. Ćetković, D. C. Henri, A. Chabert, A. C. Costamagna, A. De la Mora, J. de Kraker, N. Desneux, E. Diehl, T. Diekötter, C. F. Dormann, J. O. Eckberg, M. H. Entling, D. Fiedler, P. Franck, F. J. Frank van Veen, T. Frank, V. Gagic, M. P. D. Garratt, A. Getachew, D. J. Gonthier, P. B. Goodell, I. Graziosi, R. L. Groves, G. M. Gurr, Z. Hajian-Forooshani, G. E. Heimpel, J. D. Herrmann, A. S. Huseth, D. J. Inclán, A. J. Ingrao, P. Iv, K. Jacot, G. A. Johnson, L. Jones, M. Kaiser, J. M. Kaser, T. Keasar, T. N. Kim, M. Kishinevsky, D. A. Landis, B. Lavandero, C. Lavigne, A. Le Ralec, D. Lemessa, D. K. Letourneau, H. Liere, Y. Lu, Y. Lubin, T. Luttermoser, B. Maas, K. Mace, F. Madeira, V. Mader, A. M. Cortesero, L. Marini, E. Martinez, H. M. Martinson, P. Menozzi, M. G. E. Mitchell, T. Miyashita, G. A. R. Molina, M. A. Molina-Montenegro, M. E. O'Neal, I. Opatovsky, S. Ortiz-Martinez, M. Nash, Ö. Östman, A. Ouin, D. Pak, D. Paredes, S. Parsa, H. Parry, R. Perez-Alvarez, D. J. Perović, J. A. Peterson, S. Petit, S. M. Philpott, M. Plantegenest, M. Plećaš, T. Pluess, X. Pons, S. G. Potts, R. F. Pywell, D. W. Ragsdale, T. A. Rand, L. Raymond, B. Ricci, C. Sargent, J.-P. Sarthou, J. Saulais, J. Schäckermann, N. P. Schmidt, G. Schneider, C. Schüepp, F. S. Sivakoff, H. G. Smith, K. Stack Whitney, S. Stutz, Z. Szendrei, M. B. Takada, H. Taki, G. Tamburini, L. J. Thomson, Y. Tricault, N. Tsafack, M. Tschumi, M. Valantin-Morison, M. Van Trinh, W. van der Werf, K. T. Vierling, B. P. Werling, J. B. Wickens, V. J. Wickens, B. A. Woodcock, K. Wyckhuys, H. Xiao, M. Yasuda, A. Yoshioka, and Y. Zou. 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proceedings of the National Academy of Sciences. 115: E7863–E7870.

Klein, A. M., I. Steffan-Dewenter, and T. Tscharntke. 2006. Rain forest promotes trophic interactions and diversity of trap-nesting hymenoptera in adjacent agroforestry. Journal of Animal Ecology. 75: 315–323.

Kruess, A. 2003. Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. Ecography. 26: 283–290.

Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. Science (80-.). 264: 1581–4.

Kruess, A. and T. Tscharntke. 2000. Species richness and parasitism in a fragmented landscape : Experiments and field studies with insects on *Vicia sepium*. Oecologia 122: 129–37.

Landis, D. A., S. D. Wratten, and G. M. Gurr. **2000**. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology. 45: 175–201.

Langellotto, G. A., and R. F. Denno. **2004**. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia. 139: 1–10.

Letourneau, D. K., I. Armbrecht, B. S. Rivera, J. M. Lerma, E. J. Carmona, M. C. Daza, S. Escobar, V. Galindo, C. Gutiérrez, S. D. López, J. L. Mejía, A. M. A. Rangel, J. H. Rangel, L. Rivera, C. A. Saavedra, A. M. Torres, and A. R. Trujillo. **2011**. Does plant diversity benefit agroecosystems? A synthetic review. Ecological Applications. 21: 9–21.

Lewis, W. J., J. C. Van Lenteren, S. C. Phatak, and J. H. Tumlinson. **1997**. A total system approach to sustainable pest management. Proceedings of the National Academy of Sciences. 94: 12243–12248.

Liere, H., I. Perfecto, and J. Vandermeer. **2014**. Stage-dependent responses to emergent habitat heterogeneity: consequences for a predatory insect population in a coffee agroecosystem. Ecology and Evolution. 4: 3201–3209.

Lundgren, J.G., K. Wyckhuys, and N. Desneux. 2009. Population responses by *Orius insidiosus* to vegetational diversity. BioControl. 54(1): 135-142.

Marino, P. C., and D. A. Landis. **1996**. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. Ecological Applications. 6: 276–284.

Mauremooto, J. R., S. D. Wratten, S. P. Worner, and G. L. A. Fry. **1995**. Permeability of hedgerows to predatory carabid beetles. Agriculture, Ecosystems & Environment. 52: 141–148.

Menalled, F. D., A. C. Costamagna, P. C. Marino, and D. A. Landis. **2003**. Temporal variation in the response of parasitoids to agricultural landscape structure. Agriculture, Ecosystems & Environment. 96: 29–35.

Menalled, F. D., P. C. Marino, S. H. Gage, and D. A. Landis. **1999**. Does agricultural landscape structure affect parasitism and parasitoid diversity? Ecological Applications. 9: 634–641.

Meyer, B., F. Jauker, and I. Steffan-Dewenter. **2009**. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. Basic and Applied Ecology. 10: 178–186.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-Being: Health Synthesis. Washington, D.C.: Island Press.

Morandin, L. and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecological Applications 23(4): 829–39.

Murphy, B. C., J. A. Rosenheim, and J. Granett. **1996**. Habitat diversification for improving biological control: abundance of *Anagrus epos* (Hymenoptera: Mymaridae) in grape vineyards. Environmental Entomology. 25: 495–504.

Murphy, B., Rosenheim, J., Dowell, R., and J. Granett. 1998. Habitat diversification tactic for improving biological control: Parasitism of the western grape leafhopper. Entomologia Experimentalis et Applicata 87(3): 225–35.

Nicholls, C. I., M. Parrella, and M. A. Altieri. **2001**. The effects of a vegetational corridor on the abundance and dispersal of insect biodiversity within a northern California organic vineyard. Landscape Ecology. 16: 133–146.

Östman Ö, B. Ekbom, J. Bengtsson, and A. Weibull. 2001. Landscape complexity and farming practice influence the condition of polyphagous carabid beetles. Ecological Applications. 11: 480–488.

Perfecto, I., A. Mas, T. Dietsch, and J. Vandermeer. **2003**. Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodiversity and Conservation. 12: 1239–1252.

Perfecto, I., and L. E. M. Vet. **2003**. Effect of a nonhost plant on the location behavior of two parasitoids: The tritrophic system of Cotesia spp. (Hymenoptera: Braconidae), *Pieris rapae* (Lepidoptera: Pieridae), and *Brassica oleraceae*. Environmental Entomology. 32: 163–174.

Pfiffner, L., and E. Wyss. **2004**. Use of sown wildflower strips to enhance natural enemies of agriculture pests, pp. 165–186. *In* Gurr, G.M., Wratten, S.D., Altieri, M.A. (eds.), Ecological Engineering for Pest Management. CSIRO Publishing, Collingwood, Austrailia.

Poveda, K., M. I. Gomez, and E. Martinez. **2008**. Diversification practices: their effect on pest regulation and production. Revista Colombiana de Entomologia. 34: 131–144.

Prasifka, J. R., K. M. Heinz, and R. R. Minzenmayer. **2004**. Relationships of landscape, prey and agronomic variables to the abundance of generalist predators in cotton (*Gossypium hirsutum*) fields. Landscape Ecology. 19: 709–717.

Puech, C., S. Poggi, J. Baudry, and S. Aviron. **2014**. Do farming practices affect natural enemies at the landscape scale? Landscape Ecology. 125–140.

Purtauf, T., J. Dauber, and V. Wolters. **2005a**. The response of carabids to landscape simplification differs between trophic groups. Oecologia. 142: 458–464.

Purtauf, T., I. Roschewitz, J. Dauber, C. Thies, T. Tscharntke, and V. Wolters. **2005b**. Landscape context of organic and conventional farms: Influences on carabid beetle diversity. Agriculture, Ecosystems & Environment. 108: 165–174.

Pywell, R. F., M. S. Heard, B. A. Woodcock, S. Hinsley, L. Ridding, M. Nowakowski, and J. M. Bullock. **2015**. Wildlife-friendly farming increases crop yield: Evidence for ecological intensification. Proceedings of the Royal Society B. 282.

Risch, S. J., D. A. Andow, and M. A. Altieri. **1983**. Agroecosystem diversity and pest control: Data, tentative conclusions, and new research directions. Environmental Entomology. 12: 625–629.

Roland, J., and P. D. Taylor. **1997**. Insect parasitoid species respond to forest structure at different spatial scales. Nature. 386: 710–713.

Root, R. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). Ecological Monographs. 43: 95–124.

Roschewitz, I., M. Hücker, T. Tscharntke, and C. Thies. **2005**. The influence of landscape context and farming practices on parasitism of cereal aphids. Agriculture, Ecosystems & Environment. 108: 218–227.

Rusch, A., M. Valantin-Morison, J. P. Sarthou, and J. Roger-estrade. **2010**. Biocontrol-based integrated management of oilseed rape pests. Springer Netherlands, Dordrecht.

Schellhorn, N. A., V. Gagic, and R. Bommarco. **2015**. Time will tell: Resource continuity bolsters ecosystem services. Trends in Ecology and Evolution. 30: 524–530.

Schmidt, M. H., I. Roschewitz, C. Thies, and T. Tscharntke. **2005**. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. Journal of Applied Ecology. 42: 281–287.

Schmidt, M. H., and T. Tscharntke. **2005**. Landscape context of sheetweb spider (Araneae: Linyphiidae) abundance in cereal fields. Journal of Biogeography. 32: 467–473.

Seibold, S., M. M. Gossner, N. K. Simons, N. Blüthgen, J. Müller, D. Ambarlı, C. Ammer, J. Bauhus, M. Fischer, J. C. Habel, K. E. Linsenmair, T. Nauss, C. Penone, D. Prati, P. Schall, E. D. Schulze, J. Vogt, S. Wöllauer, and W. W. Weisser. **2019**. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature. 574: 671–674.

Sharley, D. J., A. A. Hoffmann, and L. J. Thomson. **2008**. The effects of soil tillage on beneficial invertebrates within the vineyard. Agricultural and Forest Entomology. 10: 233–243.

Shaw, M. R. 2006. Habitat considerations for parasitic wasps (Hymenoptera). Journal of Insect Conservation. 10: 117–127.

Simon, S., Bouvier, J., Debras, J., and B. Sauphanor. 2010. Biodiversity and pest management in orchard systems: A review. Agronomy for Sustainable Development. 30(1): 139–52.

Symondson, W. O. C., K. D. Sunderland, and M. H. Greenstone. **2002**. Can generalist predators be effective biocontrol agents? Annual Review of Entomology. 47: 561–594.

Thies, C., I. Roschewitz, and T. Tscharntke. **2005**. The landscape context of cereal aphid-parasitoid interactions. Proceedings of the Royal Society B. 272: 203–10.

Thies, C., I. Steffan-dewenter, and T. Tscharntke. **2003**. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos. 101: 18–25.

Thies, C., and T. Tscharntke. **1999**. Landscape structure and biological control in agroecosystems. Science (80). 285: 893–895.

Thies, C., and T. Tscharntke. **2010**. Biological Rape Pest Control in Spatio-Temporally Changing Landscapes, pp. 273–284. *In* Williams, I.H. (ed.), Biocontrol-Based Integrated Management of Oilseed Rape Pests. Springer Netherlands, Dordrecht.

Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. a. Rand, J. M. Tylianakis, S. Van Nouhuys, and S. Vidal. **2007**. Conservation biological control and enemy diversity on a landscape scale. Biol. Control. 43: 294–309.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. **2005**. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecology Letters. 8: 857–874.

Tscharntke, T., J. C. Milder, G. Schroth, Y. Clough, F. DeClerck, A. Waldron, R. Rice, and J. Ghazoul. **2014**. Conserving biodiversity through certification of tropical agroforestry crops at local and landscape scales. Conservation Letters. 1–10.

Tuck, S. L., C. Winqvist, F. Mota, J. Ahnström, L. a. Turnbull, and J. Bengtsson. **2014**. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. Journal of Applied Ecology. 51: 746–755.

Tylianakis, J. M., R. K. Didham, and S. D. Wratten. **2004**. Improved fitness of aphid parasitoids receiving resource subsidies. Ecology. 85: 658–666.

Vandermeer, J., and I. Perfecto. **2007**. The agricultural matrix and a future paradigm for conservation. Conservation Biology. 21: 274–277.

Vandermeer, J., and I. Perfecto. **2008**. Spatial pattern and ecological process in the coffee agroforestry system. Ecology. 89: 915–920.

Vandermeer, J., I. Perfecto, and S. Philpott. **2010**. Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service. Bioscience. 60: 527–537.

van Nouhuys, S. 2005. Effects of habitat fragmentation at different trophic levels in insect communities. Annales Zoologici Fennici. 42: 433–447.

Weibull, A.-C., Ö. Östman, and A. Granqvist. **2003**. Species richness in agroecosystems: the effect of landscape, habitat and farm management. Biodivers. Conserv. 12: 1335–1355.

Werner, E. E., and S. D. Peacor. **2003**. A review of trait-mediated indirect interactions in ecological communities. Ecology. 84: 1083–1100.

Weyman, G., K. Sunderland, and P. Jepson. **2002**. A review of the evolution and mechanisms of ballooning by spiders inhabiting arable farmland. Ethology, Ecology & Evolution. 14: 306–326.

Wilby, A., L. P. Lan, K. L. Heong, N. P. D. Huyen, N. H. Quang, N. V. Minh, and M. B. Thomas. **2006**. Arthropod diversity and community structure in relation to land use in the Mekong Delta, Vietnam. Ecosystems. 9: 538–549.

Winqvist, C., J. Bengtsson, T. Aavik, F. Berendse, L. W. Clement, S. Eggers, C. Fischer, A. Flohre, F. Geiger, J. Liira, T. Pärt, C. Thies, T. Tscharntke, W. W. Weisser, and R. Bommarco. **2011**. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. Journal of Applied Ecology. 48: 570–579.

Wratten, S. D., M. Gillespie, A. Decourtye, E. Mader, and N. Desneux. **2012**. Pollinator habitat enhancement: Benefits to other ecosystem services. Agriculture, Ecosystems & Environment. 159: 112–122.

Appendix 1. Summary of articles included in analysis, showing categories of natural enemy guild, natural enemy classification, number of observations showing a positive, neutral, or negative response to environmental heterogeneity (at landscape, local, and intermediate scales), and type of metric assessed.

			Landscape			Local			Intermediate			
Author	**Guild***	**Natural enemies**	**Pos**	**Neu**	**Neg**	**Pos**	**Neu**	**Neg**	**Pos**	**Neu**	**Neg**	**Metric#**
Armbrecht & Perfecto 2003	Ground-foraging	Hymenoptera: Formicidae				1			1		1	D
Aroga & Ambassa-Kiki 2007	Plant-foraging	Dermaptera: Forficulidae; Coleoptera: Coccinellidae; Blattodea: Blattellidae; Araneae: Araneidae; Hypmenoptera: Formicidae; Hemiptera: various					1					A
Bianchi et al. 2005	Plant-foraging, Parasitoids	Coleoptera: Staphylinidae, Carabidae; Hymenoptera: Braconidae, Trichogramma; Neuroptera: Chrysopidae	3	3								A, P
Bommarco 1998	Ground-foraging	Coleoptera: Carabidae	1									A (Condition)
Cai et al. 2007	All	Various				3	1					A, D
Carmona & Landis 1999	Ground-foraging	Coleoptera: Carabidae								1		A
Clough et al. 2005	Ground-foraging	Araneae: various	1	1			2		2			A, D
Costamagna et al. 2004	Parasitoids	Hymenoptera: Braconidae		1								A
Elliot et al. 1998	Plant-foraging	Coleoptera: Coccinellidae; Neuroptera: Chrysopidae; Hemiptera: Nabidae	6									A
Elliot et al. 2002	Plant-foraging	Coleoptera: Coccinellidae; Neuroptera: Chrysopidae; Hemiptera: Nabidae	2	3								A
Gardiner et al. 2009	All	Various	1									A
Gianoli et al. 2006	All	Various					1					A

Continued on next page

Appendix 1. Continued.

			Landscape			Local			Intermediate			
Author	**Guild***	**Natural enemies**	**Pos**	**Neu**	**Neg**	**Pos**	**Neu**	**Neg**	**Pos**	**Neu**	**Neg**	**Metric#**
Harmon et al. 2003	Ground-foraging	Coleoptera: Carabidae, Staphylinidae; Araneae					2	1				A
Klein et al. 2006	Plant-foraging	Hymenoptera: Eumenidae, Pompilidae, Sphecidae					2		1	1		A, D
Kruess & Tscharntke 1994	Parasitoids	Hymenoptera: Braconidae, Eulophidae, Eupelmidae, Pteromalidae, Torymidae	2						3			A,D,P
Kruess & Tscharntke 2000	Parasitoids	Hymenoptera: Pteromalidae, Eupelmidae, Braconidae, Ichneumonidae	2						1	1		A,D,P
Kruess 2003	Parasitoids	Hymenoptera: Braconidae, Pteromalidae, Eucoilidae	2	2		3	1					A, D, P
Lundgren et al. 2009	Plant-foraging	Hemiptera: Anthocoridae				1						A
Marino & Landis 1996	Parasitoids	Diptera: Tachinidae; Hymenoptera: Braconidae, Ichneumonidae	1							1		A
Menalled et al. 2003	Parasitoids	Hymenoptera: Braconidae	3	2								P
Menalled et al. 1999	Parasitoids	Hymenoptera: Braconidae, Eulophidae, Ichneumonidae	1	2								P
Meyer et al. 2009	Plant-foraging	Diptera: Syrphidae	1		1							D, A
Murphy et al. 1996	Parasitoids	Hymenoptera:Mymaridae							1			A
Murphy et al. 1998	Parasitoids	Hymenoptera:Mymaridae				1						P
Nicholls et al. 2001	Plant-foraging, Parasitoids	Coleoptera: Coccinellidae; Neuroptera: Chrysopidae; Hemiptera: Nabidae; Diptera: Syrphidae; Hymenoptera: Mymaridae							4	4	1	A, P

Appendix 1. Continued.

Author	Guild*	Natural enemies	Landscape			Local			Intermediate			Metric#
			Pos	Neu	Neg	Pos	Neu	Neg	Pos	Neu	Neg	
Östman et al. 2001	Ground-foraging	Coleoptera: Carabidae		1		1			1			A (Condition)
Pfiffner & Wyss 2004	Ground/ plant-foraging	Coleoptera: Carabidae; Araneae; various other predators							2	4		A, D
Prasifka et al. 2004	Ground/ plant-foraging	Araneae; Coleoptera: Coccinellidae; Hemiptera: Anthocoridae, Nabidae, Lygaeidae (subfamily Geocorinae)	1						1			A
Purtauf et al. 2005a	Ground-foraging	Coleoptera: Carabidae	1	1								A, D
Purtauf et al. 2005b	Ground-foraging	Coleoptera: Carabidae	1	1			2					A, D
Roschewitz et al. 2005	Parasitoids	Hymenoptera: various	1				1					P
Schmidt et al. 2005	Ground-foraging	Araneae: various	1	1		1	1					A, D
Schmidt & Tscharntke 2005	Ground-foraging	Araneae: Linyphiidae	2	1								A
Thies & Tscharntke 1999	Parasitoids	Hymenoptera: Ichneumonidae	1				1		1			P
Thies et al. 2003	Parasitoids	Hymenoptera: Ichneumonidae	1									P
Thies et al. 2005	Parasitoids	Hymenoptera: Aphidiidae	3									P
Thies and Tscharntke 2010	Parasitoids	Hymenoptera: Ichneumonidae	1									P
Tylianakis et al. 2004	Parasitoids	Hymenoptera: Aphidiidae							1	1		P
Weibull et al. 2003	Ground-foraging	Araneae; Coleoptera: Carabidae, Staphylinidae		1	1		2		1	1		D
Wilby et al. 2006	All	Various		2		1	1					A, D

* "All" refers to studies containing all mentioned guilds (parasitoids, ground foragers, and plant foragers)
#A=abundance, D=diversity (species richness or diversity index), P=parasitism rate. Two studies (indicated by the designation 'Condition') assessed the condition of natural enemies as an indicator of natural enemy status; due to a low sample size, these observations were grouped with the A (abundance) studies.