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Review

Predicting Landscape Configuration Effects on Agricultural Pest Suppression

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Arthropod predators and parasitoids attack crop pests, providing a valuable ecosystem service. The amount of noncrop habitat surrounding crop fields influences pest suppression, but synthesis of new studies suggests that the spatial configuration of crops and other habitats is similarly important. Natural enemies are often more abundant in fine-grained agricultural landscapes comprising smaller patches and can increase or decrease with the connectivity of crop fields to other habitats. Partitioning organisms by traits has emerged as a promising way to predict the strength and direction of these effects. Furthermore, our ability to predict configurational effects will depend on understanding the potential for indirect effects among trophic levels and the relationship between arthropod dispersal capability and the spatial scale of underlying landscape structure.

Highlights

Understanding how landscape structure influences pest suppression in crop fields is critical for the design of sustainable agricultural landscapes.

New research shows that landscape configuration (spatial arrangement), in addition to composition, strongly affects natural enemy and pest populations, ultimately affecting crop yield.

Natural enemies tend to be more abundant in fine-grained landscapes (comprising smaller fields and habitat patches) and are influenced by the connectivity of crop fields to other habitat types.

Configuration effects on pest suppression depend on organismal traits and the relationships between spatial scales at which arthropods disperse and those of underlying landscape structure.

Landscape configuration can affect pest suppression through multiple indirect effect pathways, which need more investigation.

Landscape Structure Influences Pest Suppression in Crop Fields

In agricultural landscapes, predatory and parasitic arthropods suppress herbivorous arthropod populations, providing an essential ecosystem service valued at billions of dollars annually [1]. In recent decades researchers have begun to identify factors driving the abundance of **natural enemies** (see Glossary), pests, and the effectiveness of **pest suppression** in crop fields, with the aim of designing and managing agricultural landscapes to maximize this and other services [2–5]. Positive outcomes from enhanced pest suppression could include greater crop yields, reduced pesticide use, and increased arthropod diversity in agricultural landscapes. Arthropod communities in crop fields are influenced by the landscape that surrounds them: on their own, crop fields are unsuitable for some beneficial insects because they are usually monocultures and undergo frequent disturbance. This means that other nearby habitats may be especially important for determining which arthropods colonize farm fields. Most research on how landscape structure influences pest suppression has focused on effects of **landscape composition** (i.e., amounts of habitat). In general, seminatural habitats can provide natural enemies with resources including food, overwintering habitat, nest sites, and refuge from agricultural disturbance, allowing them to survive and then colonize crop fields to exploit the herbivores that accumulate there [3]. Pest suppression is generally thought to increase when crop fields are surrounded by more noncrop or seminatural habitat. However, while this occurs in some circumstances, the effects of landscape composition on pest suppression overall are inconsistent, varying among systems and organisms [4].

Beyond composition, there is also variation in **landscape configuration** [6]. Multiple lines of reasoning suggest that configurational aspects of landscape structure should affect pest suppression. First, since there is **spillover** of beneficial organisms along interfaces between habitat **patches** [7], configurational variables such as patch size, shape, amount of shared edge, and **connectivity** should influence the amount of spillover that occurs and how far into fields natural enemies can penetrate. Second, some organisms require resources from multiple **land-cover types** and are thought to benefit from **landscape complementation** [8]. Evidence now strongly suggests that landscape configuration is an important predictor of pest suppression [5,9], and the rate of publication on this topic has been accelerating. Therefore, here we highlight recent advances in knowledge of how landscape configuration affects natural enemy abundance and pest suppression, identifying gaps in our understanding and suggesting frameworks for future configuration studies.

Mounting Evidence That Landscape Configuration Affects Pest Suppression

Thirty-three recent studies, 70% of which were published since 2014, provide evidence as to how landscape configuration affects pest suppression (Figure 1). All but two of these reported significant

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effects of landscape configuration on at least one variable related to pest suppression, but the strength and direction of these effects were highly context dependent (see Supplements S1 and S2 in the supplemental information online for details of each study). Configuration is multifaceted, describing spatial characteristics (i.e., size, shape, and spatial arrangement) of habitat patches in a landscape. Therefore, it is difficult to encapsulate succinctly and can be quantified using dozens of intercorrelated and sometimes redundant **landscape metrics** [10–12]. The range of metrics researchers use can obscure broader patterns; therefore, to generalize, we group configurational metrics into three families: (i) **grain size**; (ii) shape complexity; and (iii) connectivity.

Grain Size

Landscapes fall along a spectrum of complexity from coarse-grained with large patches and a low density of edges to fine-grained with small patches and relatively more edges. Pest suppression is generally expected to be greater in fine-grained agricultural landscapes because, in smaller fields, enemies that emerge from field margins or nearby seminatural habitats can reach crop field edges and interiors more easily. The potential for complementation should also be higher in fine-grained landscapes since more cover types are likely to be within the foraging range of generalist natural enemies. Some studies focus on edge density (i.e., length of patch edges per unit area) as a useful index of configurational complexity; although edge density can relate to shape complexity, in general it is used to describe grain size rather than shape [13–16]. Others focus on field size; in landscapes where crop fields are the dominant cover type, field size is the main factor determining landscape grain.

There is now strong evidence that fine-grained agricultural landscapes can enhance natural enemies, although the effects are not always consistent. In one of the most comprehensive studies to date, Martin *et al.* [13] found that natural enemy abundance varied strongly with edge density of landscapes surrounding 35 South Korean crop fields of various types. Syrphids, parasitoids, predatory wasps, and staphylinids were more abundant in fields surrounded by landscapes with higher edge densities, and these configurational effects dwarfed the effects of the amount of seminatural habitat. The same has been found for insectivorous wasps in wheat [17], parasitoids in cucumber [18], and coccinellids in rice [19]. In North America, edge density appears to have similar effects on aphid predators in cereal crops, with more chrysomelids, nabids, and overall higher aphid enemy richness in fine-grained landscapes [15,16]. However, results are inconsistent for some taxa, including coccinellids in soybeans and cereal grains [15,16,20–22] and spiders [23–26] and carabids [13,22,24,27] in wheat and other crops.

Compelling trends emerge when natural enemies are partitioned according to their traits, particularly overwintering habitat use and dispersal mode. Recently, data from over 1500 European landscapes (49 studies) were analyzed together, revealing that predators overwintering in habitats outside crop fields were more abundant in fine-grained landscapes with higher edge density. This pattern held true for flying and ground-dispersing enemies, but not for wind-dispersers. For taxa that overwinter in crop fields, the effect was opposite: they tended to be more abundant when edge density was low and/or when surrounded by crops rather than by seminatural habitat. Importantly, these effects of configuration were masked when natural enemies were considered as a group; the pattern only emerged when they were partitioned by traits related to habitat use and dispersal mode [14].

We need more information on how grain size affects herbivores, rates of suppression, crop damage, and yield. Evidence on herbivores is biased toward aphids (Figure 1), and variously suggests that finer-grained landscapes can have more [18,19,23] or fewer [27] herbivores, or the results were inconsistent [28] or showed no effects [29,30]. The recent synthesis of data from Europe provides more clarity; pests overwintering outside of fields decreased with edge density, whereas pests overwintering in crop fields were mostly unaffected [14]. Only a few studies have tested for effects of grain size on actual rates of pest suppression, crop damage, or yield. Tests of predation or parasitism rates have again focused on aphids, with mixed [29] or no effect detected [28,30,31]. There have been two notable developments linking grain size to yield. First, in South Korean crop fields [13] yields were higher in finer-grained landscapes when fields were managed conventionally (although crop damage also increased), but there was no significant pattern when fields were managed organically. Second,

Glossary

Connectivity: 'The degree to which the landscape facilitates or impedes movement among resource patches' [71]. This can be quantified in several ways, such as distances between or among patches, or characteristics of the landscape between patches that influence how easily organisms can disperse.
Grain size: average size (diameter or area) of habitat patches on a landscape [72]. Grain size is described on a spectrum from fine (small patches) to coarse (large patches). This term has other meanings in different contexts, even within landscape ecology [73]. Fine-grained landscapes have a higher density of edges (boundaries between patches) and, thus, grain size is often quantified in terms of edge density. Similarly, in landscapes dominated by crop fields, grain is determined largely by field size.
Hyperparasitoid: parasitoid that exploits other parasitoids, eventually killing them.
Intraguild predation: when organisms in higher trophic levels attack or feed on one another, often with the result of complicating or dampening trophic cascades. For example, some birds eat both herbivorous and predatory arthropods.
Land cover type: a category of habitat comprising a given vegetation type (e.g., grassland, forest, annual crop).
Landscape complementation: when two or more habitat types occur in proximity such that organisms can move between them to access resources they require. Species that require resources distributed across multiple habitat types (e.g., food, breeding sites, structures used for overwintering) are expected to be more abundant in landscapes with more complementation [8].
Landscape composition: amount or diversity of different land-cover types occurring within a landscape.
Landscape configuration: size, shape, and/or spatial arrangement of patches in a landscape.
Landscape metric: quantitative variable describing landscape structure (composition and/or configuration) based on maps in

the recent synthesis of data from Europe [14] showed that edge density had mixed effects on yield, with results depending on the amount of seminatural habitat present.

Shape Complexity

Habitat patches range in shape from simple to complex. In some contexts, elements are mostly rectangular, while in others, cover-type boundaries follow tortuous paths, resulting in irregular or convoluted shapes. Shape complexity could feasibly affect pest suppression: fields with more edge per unit area should have more interface with other habitats, allowing natural enemies to reach field interiors more easily.

Firm evidence for how patch shape complexity affects pest suppression has yet to emerge. Models suggest that the shape of seminatural areas and hedgerows would influence the control of aphids by coccinellids in adjacent fields [32], and indeed one recent study found not only the abundance of aphids, but also their parasitism rate increased with the fractal dimension of focal fields [29]. However, in an experimental study with broccoli planted in either square or I-shaped fields in Chile, there was no strong effect of shape on either aphids or their coccinellid predators [33]. Similarly, a recent study in the Midwest USA found no difference in natural enemy abundance between linear tallgrass prairie elements and blocks with equivalent area [34]. In rice agroecosystems in the Philippines, natural enemies, including coccinellids and linyphiid spiders, decreased with the fractal dimension of rice fields, the abundance of trichogrammatid wasps increased, but herbivores and several other taxa showed no response and, overall, neither predator nor parasitoid abundance was affected [19]. More research will be needed to determine whether there are predictable effects of patch shape complexity on pest suppression.

Connectivity

The ways in which landscape connectivity shapes the movement of organisms have been the subject of keen interest and debate for some time [35,36]. The simplest form of connectivity, as it relates to pest suppression, is the distance from a crop field to specific habitats in its surroundings. There is clear evidence that this type of connectivity influences natural enemy abundance, and that the direction of the effect depends on the type of habitat and its utility to the organism in question. Natural enemies on woody crops appear to benefit from proximity to forest: in apple orchards, spider richness and, in some cases, abundance increased with proximity to woody vegetation [37]; similarly, ants that prey on coffee pests were more abundant when they were close to forest, although, in some contexts, the opposite was true for spiders [38]. Finally, cherry trees harbored more spiders and greater predator richness when connected to forests, although other taxa were unaffected [39].

For natural enemies that rely only on resources within farm fields, proximity to seminatural habitats can be irrelevant [40] or even detrimental. For example, pests in sun-grown Brazilian coffee were suppressed by ants adapted to open habitats and, in this case, pest suppression increased at greater distances from forest fragments [41]. Similarly, some parasitoids overwinter in oilseed rape fields, and were more abundant and effective when fields were isolated from forests [42]. We know less about how distance to seminatural habitat affects herbivores. In apple orchards, herbivorous beetle richness, but not abundance, decreased with distance to forest [37]. Effects in coffee systems were mixed, with aphids increasing with distance to forest but coccid and pseudococcid bugs decreasing [38]. On cherry trees, herbivorous beetles increased with distance to forest, but aphids were unaffected [39].

Pest suppression in crop fields can also change with the spatial arrangement of other habitats without regard to their proximity to the focal field. For example, if seminatural habitat provides natural enemies to nearby crop fields, it is possible that, when patches of that habitat are more interconnected to one another, they sustain larger populations of natural enemies overall. In one study, syrphid flies in oilseed rape fields were more abundant when adjacent hedgerows were connected to forest [43]. In irrigated rice agroecosystems, fields are flooded and impounded by vegetated embankments (bunds) harboring natural enemies. In a recent study, parasitoids in rice fields increased with the physical connectivity of the network of bunds [19]. Similarly, predatory mirid bugs that attack tomato pests were enhanced when fallow areas in their surroundings were more connected; however, their

which habitats are classified categorically as different land-cover types .
Natural enemy: naturally occurring predators and parasitoids of crop pests.
Patch: contiguous area comprising a single land cover type (e.g., a forest or crop field).
Pest suppression: ecosystem service rendered by natural enemies that reduces insect pest densities and their damage to crops.
Spatial scale: spatial extent of an ecological process, pattern, or measurement. For example, organisms may be affected by surrounding landscape structure within a particular radius, and landscape ecologists often test effects of landscape structure within a predetermined radius around a focal patch. Similarly, organisms have different dispersal abilities, meaning that their movement occurs at varying spatial scales. This term is also related to landscape grain size, because patterns in fine-grained landscapes are expressed on smaller spatial scales than those in coarse-grained landscapes.
Spillover: provisioning of natural enemies from one cover type to another, most often from seminatural habitats into crops.
Trophic cascade: suppression of intermediate trophic levels, usually herbivores, by predators such that lower trophic levels are released. For example, predators reduce the numbers or feeding activities of herbivores, relieving pressure on plants.

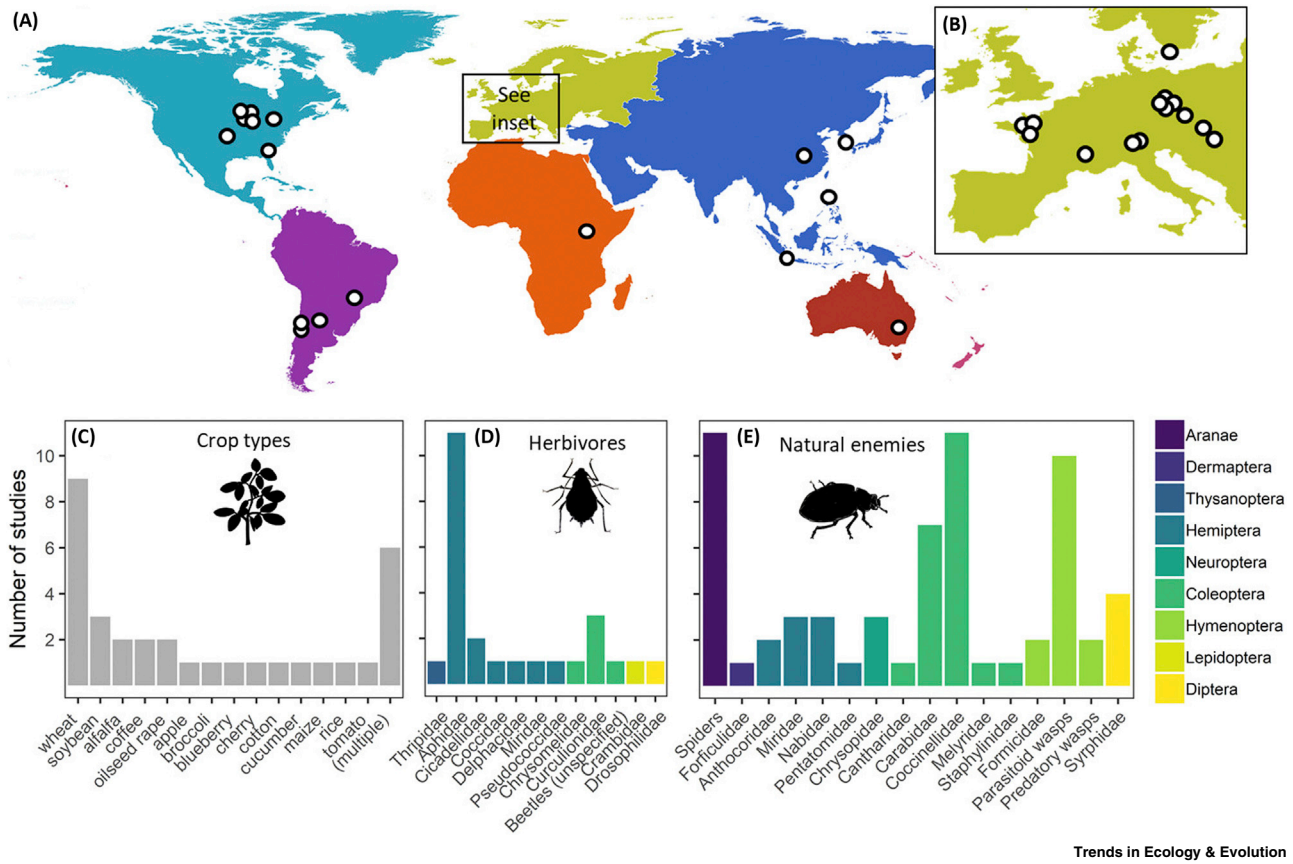

Figure 1. Overview of 33 Studies, 70% of Which Were Published since 2014, Testing Effects of Landscape Configuration on Agricultural Pest Suppression.

(A) Studies we reviewed occurred on six continents and in17 countries, but were biased toward Europe (B). Two studies are not depicted on the map; one of these was *in silico* [32] and the other was a pan-European synthesis [14]. (C) Configuration effects on pest suppression have been explored in an array of crop types, although more studies have taken place in wheat. (D) Most tests of how configuration affects pest densities have focused on aphids, while (E) effects on a wider range of natural enemies have been tested. In (D) and (E), bars represent insect families or functional groups, and are color coded by taxonomic order. See supplementary information online for additional details.

response to orchard connectivity was opposite, perhaps related to insecticide use in these crops [44]. Finally, carabids in cereal grains and maize responded positively to the connectivity of grasslands and winter crops, but not forests or maize [45].

Relative Strength of Compositional and Configurational Metrics

Landscape configuration is constrained by, and often correlated with, landscape composition. Therefore, the two types of variable are confounded with one another in many landscapes, and their respective effects are difficult to disentangle [6]. Likely, some patterns in pest suppression that were previously attributed to landscape composition were more accurately products of configuration and vice versa. However, some studies have utilized landscapes where composition and configuration are uncorrelated to test their relative strengths. In these cases, results are mixed, with some studies finding configuration effects to be stronger than those of composition [13,37,39], and others the opposite [25,30,31]. Clearly both components of landscape heterogeneity need to be accounted for, and it appears likely that in many landscapes composition and configuration contribute additively or interactively to pest suppression. For example, Martin *et al.* found that effects of edge density depended on whether there were large or small amounts of noncrop habitat surrounding fields [14].

Making Sense of Variability

Organismal Traits Underlie Context Dependencies

We now have clear evidence that multiple aspects of landscape configuration influence natural enemies and pests in crop fields. However, the mechanisms underlying these patterns are context specific. Consequently, asking how pest suppression is affected by configuration 'overall' can mask important details because the direction and magnitude of effects depend on the organisms and landscapes in question. We believe that one of the most important advances on this front has been to partition organisms based on traits such as dispersal mode and habitat use. With this approach, context specificities cease to be a liability and instead reveal biologically important patterns, such as the tendency of fine-grained landscapes to enhance natural enemies that overwinter outside of crop fields and disperse actively [14]. A recent analysis of data from 132 landscape composition studies found that the proportion of noncrop habitat affects pests and natural enemies inconsistently [4]. The authors noted that this could be due to either unmeasured landscape configuration effects or species-specific differences; it appears that both are likely.

When Configuration and Pest Suppression Appear Unrelated

In some contexts, pest suppression appears unaffected by landscape configuration. Several hypotheses have already been developed to account for when landscape composition does not affect pest suppression [46,47]; many of these also apply to landscape configuration. For example, the intermediate landscape complexity hypothesis [46] suggests that changes to landscape composition should matter more when there is an intermediate amount of seminatural habitat present. The same principle could easily apply to landscape configuration: if the landscape is extremely simplified, there may be too few natural enemies present for the spatial arrangement of their habitats to matter. Similarly, when seminatural habitats are abundant, changes in configuration could become trivial. Other hypotheses, for example, that seminatural areas sometimes promote pests more than natural enemies, that there may be no effective natural enemies for a given pest, or that farm management precludes effects of natural enemies [47], could also apply equally to landscape configuration.

Another important consideration is that pest suppression involves a complex set of multitrophic interactions (Box 1). For example, while we often focus on natural enemy responses to landscape characteristics, natural enemies also responded numerically to prey abundance in several studies reviewed here [15,16,21,33,38,44]. Similarly, prey densities reflect combined effects of landscape structure, susceptibility of crops to infestation, and the suppressing effects of natural enemies. Disentangling these effects is one of the most daunting challenges limiting our understanding of how landscape structure affects pest suppression (Box 1 and Figure 2).

Spatial scale is another critical consideration for understanding how pests and natural enemies interact with landscapes. Many configuration metrics are calculated based on areas of land within circles surrounding focal fields. Sometimes, the radius of the circle is chosen by the investigators, either arbitrarily or based on dispersal habits of the organisms in question. In other cases, models are run at multiple spatial scales with results interpreted for all of them or for the scale with the best model fit. Depending on the approach taken, studies may test patterns at spatial scales that do not match biological processes, with patterns going undetected or misinterpreted. We have developed a spatial scale-based framework for predicting when and how landscape configuration should affect natural enemy abundance (Box 2 and Figure 3). Key to this framework is the understanding that landscape patterns and organismal dispersal occur at varying spatial scales and that accounting for both should increase predictability.

There is also a temporal dimension to how configuration affects arthropods. Effects vary both within [29,30] and among [21] years, which is not surprising given that arthropod populations and plant phenology are in constant flux. Some organisms overwinter in one habitat but move to another in spring or summer and, in general, annual crop systems are temporally variable resource patchworks. Connecting crops grown in different seasons to create sequential habitat could benefit natural enemies with shorter dispersal ranges. For example, carabid beetles were better able to colonize maize

Box 1. Agricultural Pest Suppression as a Trophic Cascade

Viewing pest suppression through the lens of multitrophic interactions reveals causal pathways not accounted for by most study designs, which may change conclusions about how landscape configuration affects pest suppression. Although not always perceived this way, effective natural pest suppression is a **trophic cascade** in which predators or parasitoids suppress herbivores and release crops from damage. As such, it is important to consider whether the strength of this cascading effect changes with the configuration of surrounding landscapes (see arrows a, b, and c in Figure 2 in the main text).

Trophic cascades can be dampened or otherwise complicated by **intraguild predation**, in which members of higher trophic levels feed on one another, reducing pressure on herbivores. The strength of intraguild predation and, therefore, the effectiveness of pest suppression, can change with landscape composition. For example, when areas surrounding crop fields contain more seminatural habitat, birds can limit the effectiveness of arthropod natural enemies (arrow d) [65]. To our knowledge, there have been no tests of whether landscape configuration affects the strength of intraguild predation in agricultural landscapes (arrows d, e), although one recent study [30] found that **hyperparasitoids** were affected by landscape composition but not by configuration.

Currently, most studies test how landscape configuration affects natural enemy populations or predation rates on pests (arrows a and b). However, landscapes also directly influence pest abundance (arrow f). Furthermore, landscape composition and configuration can be confounded with other environmental variables, such as nutrient availability, which influences the susceptibility of crops to pests (arrows g and h). Finally, natural enemies often respond numerically to pest abundance (arrow i) and, therefore, pest abundance reflects the combined direct effects of crop susceptibility, landscape configuration, and natural enemy activity (arrows h, f, and b, respectively), plus all associated indirect effects. Taken together, this network of direct and indirect effects reveals several potential causal pathways of interest. For example, natural enemy abundance or predation rates are often used as a proxy for pest suppression potential, but high natural enemy density can occur precisely 'because' pests are abundant, and this numerical response of predators can outweigh their response to landscape factors. If herbivores are affected by landscape structure, but the predators are primarily responding to herbivore abundance, correlations between landscape characteristics and natural enemies could be spurious and misleading. Untangling these indirect effects with experimental manipulation and statistical methods such as structural equation models [39,66] that tease out the direct and indirect effects will be essential for explaining how landscapes affect dynamics around pest suppression.

fields in spring when they shared more edges with cereal crops grown in winter [45]. Pests also move from crop to crop over the course of the year [48], so further research could examine how the spatial arrangement of crop fields facilitates flows of natural enemies from one to the other and/or hinders the flow of pests [49].

Finally, landscape ecologists typically compute configuration metrics based on circular areas surrounding focal fields. This gives equal weight to everything within a given radius, and none to areas beyond it. In a recent paper, Miguet and colleagues showed that distance-weighted models can capture relationships between landscapes and biological processes more accurately [50]. These were not specifically developed for measuring ecosystem services in crop fields, but could be applied to this context. Similarly, cost-based models assign different weights to cover types surrounding focal fields to identify spatial arrangements that facilitate or discourage the flow of organisms [51]. Overall, quantifying configuration in terms of not only structure, but also function could improve our understanding of how it affects ecological processes [11].

Applications: When, How, and Why Does Landscape Configuration Change?

Our goal in understanding configuration effects on arthropods is to inform the design of agricultural landscapes to maximize biodiversity and pest suppression [52]. Landscape configuration is determined at three nested levels. First, it expresses physical geography: the spatial layout of water, topography, and soil depends on bedrock geology and/or glacial history and usually does not change within a human lifetime. Second, configuration is subject to historical cultural constraints. For example, landscapes inherit the spatial distribution of historic land tenure patterns and infrastructure (e.g., hedgerows or roads). Some of these features have been in place for decades, centuries, or

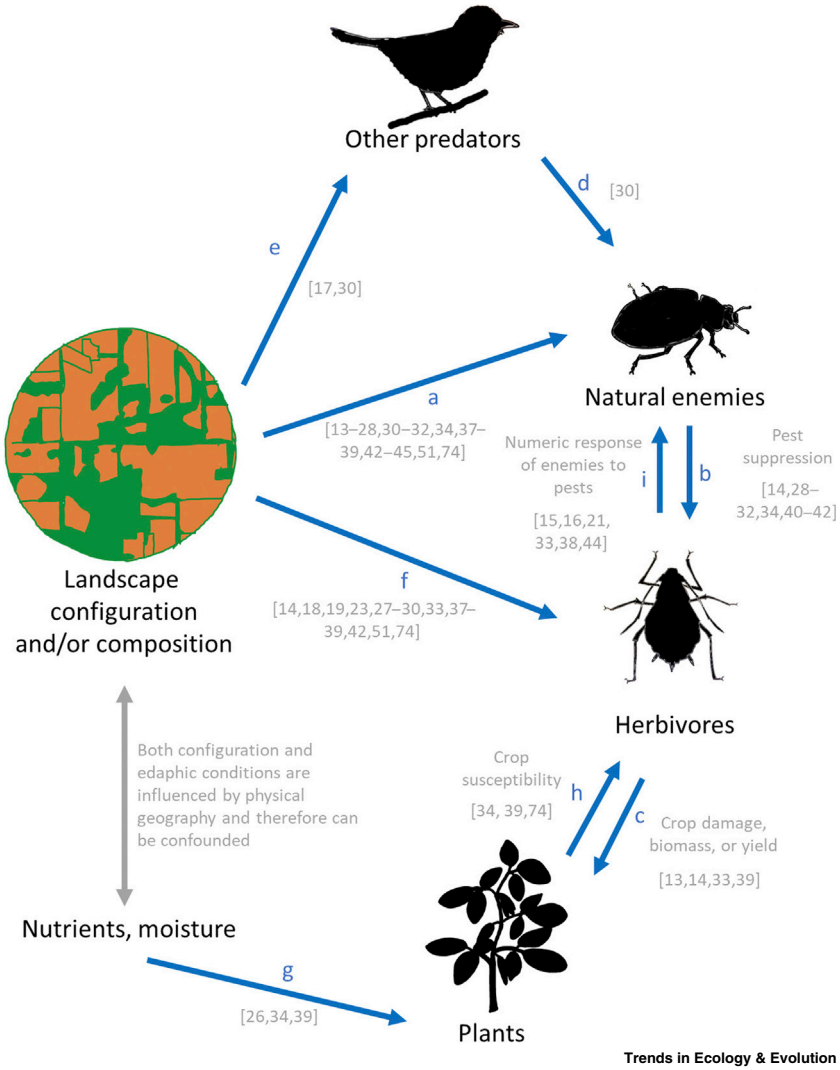

Figure 2. Viewing Pest Suppression through the Lens of Multitrophic Interactions Reveals Indirect Effect Pathways That Could Change Interpretation of Landscape Configuration Effects.

Configuration can affect crop yields by enhancing the strength of trophic cascades in which natural enemies suppress pests and release crops from damage (arrows a–c); however, configuration could also affect intraguild predation rates (arrows d, e). Pests, similar to their enemies, may respond directly to landscape configuration (f), and crop susceptibility could also correlate with configuration if they are both products of underlying physical geography (arrows g, h). Natural enemies may respond numerically to pest density in addition to, or instead of, landscape configuration (arrow i). We mapped 33 studies testing configuration effects on pest suppression onto the interaction web (bracketed numbers indicate citation numbers). The median and mode number of interactions tested per study was 2 (range: 1–5). Most studies test for correlations between landscape configuration and natural enemies, herbivores, and/or suppression rates (26, 13, and ten studies respectively). While a few studies have tested for effects along several interaction pathways simultaneously [13,30,34,39], these studies usually documented correlations rather than changes due to experimental manipulations and, therefore, some of the relationships could be spurious and their relative strengths hard to evaluate. For example, we note that, while six studies documented correlations between natural enemy and pest density (arrow i), without an experimental approach, the relative strengths of landscape predictors and numeric responses between enemies and prey are unknown. Based on [13–34,37–45,51,74].

Box 2. Landscapes from an Arthropod Perspective: Paired Spatial Scales Predict Configuration Effects on Pest Suppression

To understand how arthropods interact with landscape structure, we need to consider multiple types of spatial scale simultaneously [67]. Landscape grain size is variable, with spatial patterns expressed at different spatial scales depending on the size of crop fields and seminatural habitat patches (see Figure 3 in the main text). Similarly, organisms perceive their environment and disperse at varying spatial scales [68]. For example, coccinellid beetles readily disperse ~2 km [69], while some mirid bugs appear to disperse within 300-m ranges [44], and some carabid beetles range only 100 m or less during their lifespan [70] (see Figure 3B in the main text).

The relationship between these two spatial scales should bear upon how landscape structure affects organisms [67] and, therefore, influence the potential for pest control in agricultural landscapes. To consider the ratio between the two scales, we developed a framework for predicting when and how landscape configuration affects pest suppression (see Figure 3C in the main text). First, when the two spatial scales are strongly mismatched, configuration should be irrelevant. For example, if a pest or natural enemy with a large dispersal range lives in a fine-grained landscape, it can easily disperse from patch to patch, thus the details of their spatial arrangement and shape are likely to be irrelevant, as will be small changes in grain size. Similarly, if an organism with a very limited dispersal ability lives in a coarse-grained landscape, it will be limited to a single patch and, again, the shape and spatial arrangement of surrounding habitats may be irrelevant.

By contrast, when organismal and landscape spatial scales are more closely matched, the shape and spatial arrangement of patches is expected to be more important, and small changes in landscape grain size should have greater impact (see Figure 3C,D in the main text). We hypothesize that this relationship should take on a hump-shaped curve that peaks when the ratio of landscape to organismal scales is slightly greater than one. If an organism is able to reach only some cover types in a landscape, then changes in patch size, shape, or arrangement should strongly impact its ability to, for example, access resources in seminatural areas or to spill over into crop fields. However, once the dispersal of the organism overtakes the scale of landscape grain, changes to configuration may quickly become less relevant.

millennia, and change relatively slowly. Finally, configuration is influenced by contemporary drivers, such as crop prices and government policy [53].

Agricultural landscape configuration will continue to change with shifting economic conditions, technologies, and values. For example, farmers increasingly have spatially-explicit yield data that reveals marginal subsets of farm fields (i.e., sections that are consistently not profitable) [54], meaning that it may become practical to convert unproductive portions to seminatural habitat to avoid profit loss, enhance hunting or conservation value, or for bioenergy crops. This would result in both more seminatural habitat and reduced grain size. Similarly, the STRIPS (Science-Based Trials of Rowcrops Integrated with Prairie Strips) project in Iowa, USA [55] has shown that subdividing crop fields with small linear plantings of native grassland produced a diverse and disproportionately large payback in enhanced biodiversity and ecosystem services. Successful examples of agricultural landscape redesign incorporate transdisciplinary approaches that engage stakeholders and institutions as well as researchers [56].

Concluding Remarks and Future Perspectives

There is now clear evidence that landscape configuration affects agricultural pest suppression. Natural enemies are often more abundant in crop fields occurring in fine-grained landscapes and can benefit from the spatial connectivity of habitats. However, responses to configuration are rife with underexplored indirect effects, trait-based differences, and patterns occurring at spatial scales that are difficult to discern. Future research should explore these context specificities and use them to learn when and how we should expect configuration to affect pest suppression (see Outstanding Questions).

Maximizing pest suppression in agroecosystems should be complementary to the goal of biodiversity conservation in general. There is recent evidence that, similar to pest suppression, cropland biodiversity is enhanced in landscapes with smaller fields [57,58]. There is also increasing evidence for the positive impact of biodiversity in maintaining crop yields globally [59] and, given evidence of precipitous insect decline [60,61], we need new approaches to maintain biodiversity and ecosystem services in agricultural landscapes [52,62]. However, we also note that, while ecosystem services are a

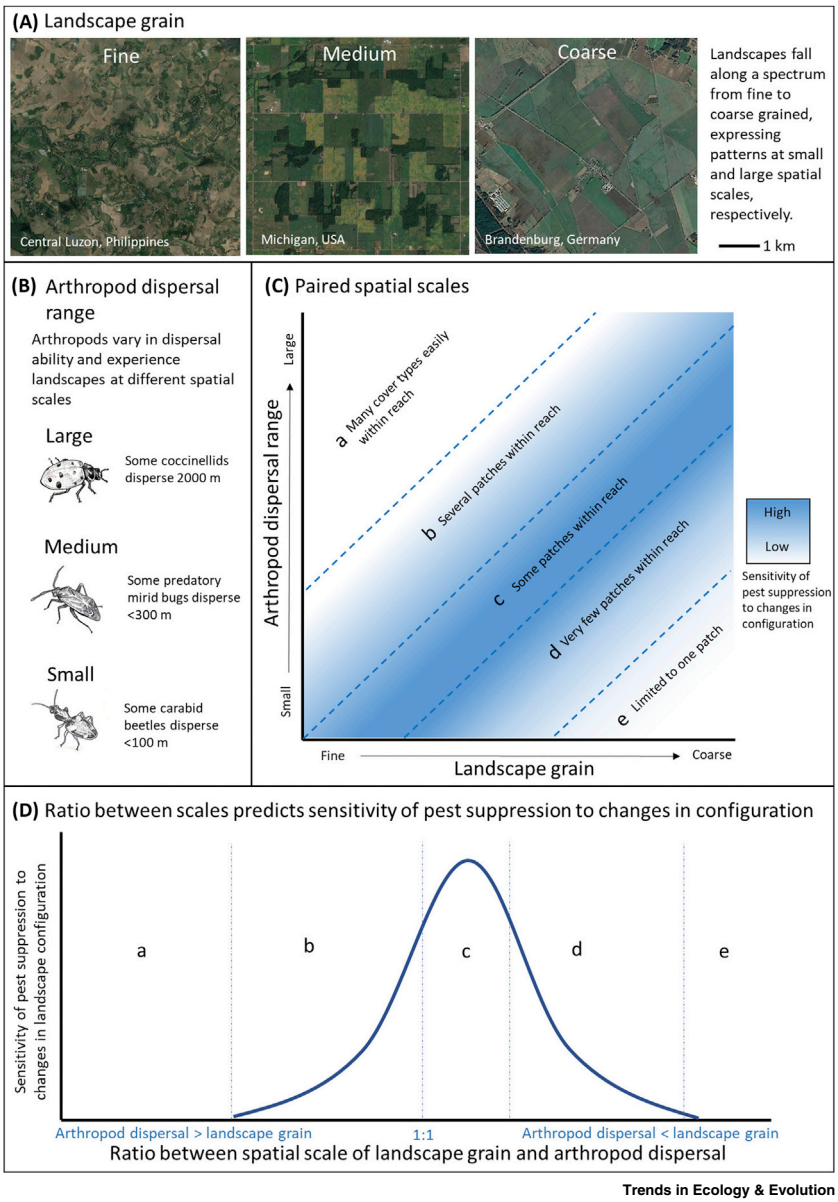

Figure 3. A Framework That Uses Spatial Scale to Predict Sensitivity of Pest Suppression to Landscape Configuration.

(A) Landscape grain ranges from fine (small patches) to coarse (large patches), thus expressing patterns at varying spatial scales. (B) Similarly, arthropods have different dispersal distances and, thus, experience landscapes at different spatial scales. (C) Pairing these two scales (landscape grain and arthropod dispersal) and examining them simultaneously reveals a framework for predicting the sensitivity of these organisms to changes in landscape configuration. When the two spatial scales are strongly mismatched, configuration is likely to be irrelevant either because the organism can access a wide variety of patches already or because it is restricted to a single patch. For example, if a predator with a 100-m dispersal radius occurs in a landscape with crop fields averaging 50 m in diameter, we expect their configuration will be irrelevant because it can easily access several fields; similarly, if fields were 1 km in diameter, configuration may be irrelevant because the predator cannot access other patches regardless of their spatial arrangement. However, if fields averaged 200 m in diameter, field and dispersal diameters would be equal and configuration more relevant. (D) The relationship in (C) can be re-expressed as the ratio between spatial scales on the *x*-axis, resulting in a hump-shaped curve predicting that

(Figure legend continued at the bottom of the next page.)

compelling justification for some types of biodiversity conservation, services often involve common species rather than rare ones [63] and many organisms reside exclusively in nonagricultural habitats. Configurations that optimize ecosystem services may not be beneficial for rare species and habitat specialists, and, in these cases, strategies that focus on preserving, restoring, or optimally configuring natural or seminatural habitats are needed.

Finally, we perceive the need for more experimental manipulation. With few exceptions [33,34,39], nearly all studies of the effect of landscape configuration on pest suppression are observational or semiexperimental. This is understandable given the logistics of manipulating landscapes, but it limits our inference to what we can glean from extant patterns. Landscape-scale manipulative experiments clarified our understanding of the efficacy of landscape corridors [35], and a similar effort manipulating configuration in agricultural landscapes would help us reach general conclusions about effects on pest suppression as well as other ecosystem services and biodiversity in general. Studies using extant landscapes can only test the range of configurations that currently exist, but future landscapes will likely include novel configurations outside these limits. Large-scale and long-term experiments would also provide a setting to isolate various species interactions and evaluate indirect effect strengths (Box 2), and to identify trends that emerge over longer time periods [64].

Outstanding Questions

How does landscape configuration affect the strength of intraguild predation? Intraguild predation can dampen pest suppression and is likely to be more prevalent in some types of landscape than others.

When do natural enemies respond more strongly to landscape structure (composition and configuration) than to prey densities, and vice versa? These two factors are often confounded and disentangling them will clarify how landscape structure affects pest suppression.

Which traits predict natural enemy and pest responses to landscape configuration? Recent work highlights how traits can resolve inconsistencies in arthropod responses.

Will we continue to find more general trends by considering the foraging strategy, dispersal distance, alternate food needs, or nesting resource use of organisms?

Logistically, what is the best way to characterize landscape configuration and use it as a predictor variable? Compared with composition, it is hard to characterize; given the range of available metrics, ecologists can test a small number of these *a priori* but, in so doing, risk picking an irrelevant metric. Alternatively, one can cast a wider net and test many metrics; however, this risks model overfitting, spurious correlations, or significant effects from obscure metrics with dubious biological meaning.

More broadly, how will landscape configuration change in response to evolving technologies, values, and economic conditions? As our understanding of configuration effects on pest suppression improves, can we collectively design optimally configured landscapes to conserve biodiversity and maximize ecosystem services?

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configuration effects on organisms involved in pest suppression will be strongest when landscape grain is spatially similar to arthropod dispersal abilities. The curve is offset from a 1:1 ratio because we predict sensitivity to configurational changes should peak when arthropod dispersal ability is slightly smaller than landscape grain size (i.e., once multiple cover types are comfortably within dispersal distance, their configuration will be less important).

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