

# The impacts of spatial and temporal complexity across landscapes on biological control: a review

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Biological control is affected by the composition of landscapes surrounding agricultural fields. Natural enemy communities are typically more diverse, and effective at providing biological control services, in complex compared to simple landscapes. However, the use of simple metrics to characterize landscapes, such as the proportion of agricultural habitat, obscures the mechanisms by which landscapes affect biological control. Studies that evaluate the overall complexity of agricultural landscapes, and their temporal variability, allow for a greater mechanistic understanding of the impacts of landscape composition on biological control. From an applied perspective, decision support systems, which deliver real-time information about pest and natural enemy populations, are an effective tool for delivering recommendations to strengthen biological control across space and time.

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## Introduction

Biological control relies on diverse communities of natural enemies that disperse into crop fields to control pests [1,2<sup>\*\*</sup>]. As such, the composition of landscapes surrounding crop fields can strongly impact biological control [1]. More complex landscapes, where crop fields are surrounded by a high proportion of non-crop habitat, generally promote biodiversity of natural enemy populations and increased biological control [3–6], because diverse landscapes provide more resources required for survival and reproduction [4<sup>\*</sup>]. Conversely, simplified landscapes often have reduced biological control [2<sup>\*\*</sup>]. For example, a recent meta-analysis of 46 studies showed that natural enemy abundance and diversity increased significantly

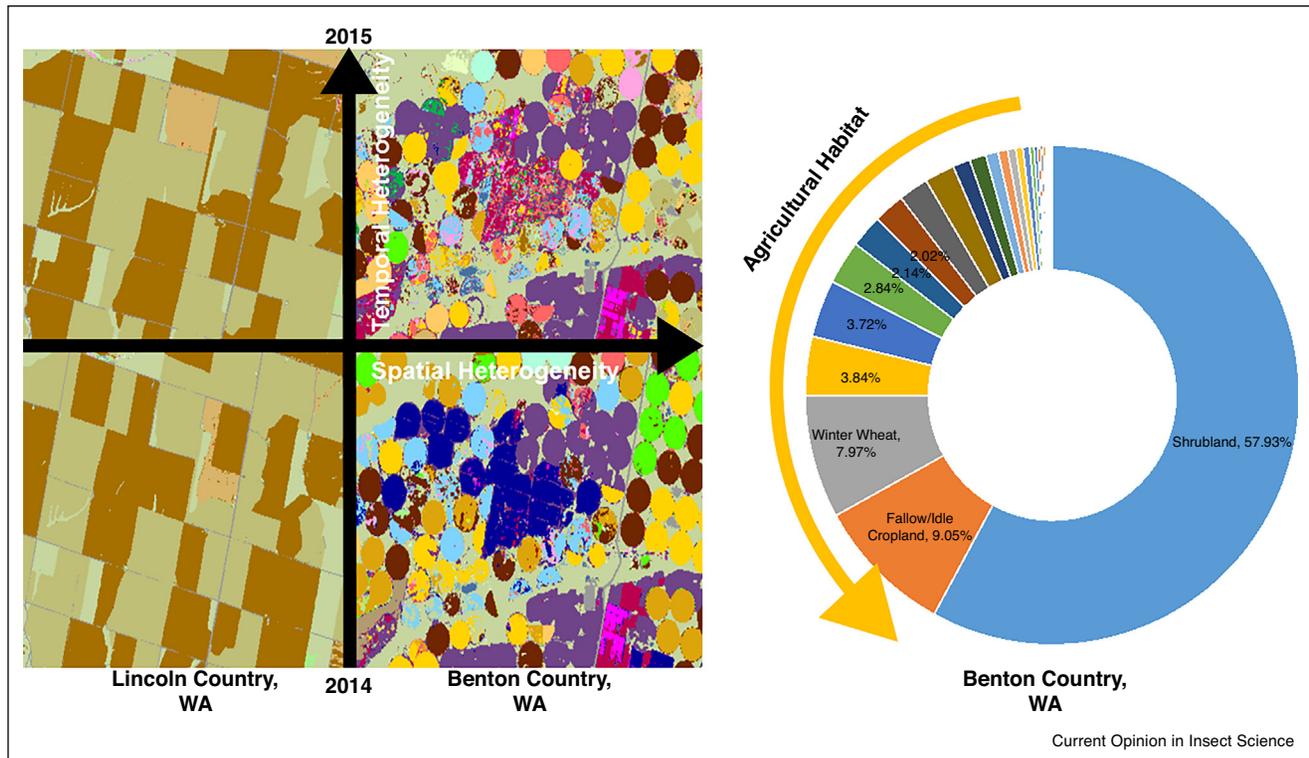
in complex compared to simple landscapes [6]. These results were consistent regardless of the methods used to characterize landscape complexity [6]. However, this study also found that pest abundance and plant damage did not differ significantly between simple and complex landscapes. This suggests that while complex landscapes generally promote robust natural enemy populations, they do not necessarily promote greater pest control, a result seen in other large-scale field studies [7].

The mechanisms by which landscape complexity affects natural enemy populations are often unclear. This is because many studies classify landscapes using simple metrics such as the proportion of ‘semi-natural’ habitat (*i.e.*, grasslands, forests, or non-crop vegetation) [2<sup>\*\*</sup>] (Figure 1). Semi-natural land helps sustain natural enemy populations [8–10], while agricultural intensification promotes homogeneous landscapes [11] (Figure 1) and often weakens biological control [12,13]. However, classifying landscapes based on binary systems, like semi-natural vs. agricultural land (Figure 1), ignores the fact that not all crops are equally detrimental for natural enemies (indeed, some crops promote natural enemies) and not all that natural habitats are equally beneficial [1,2<sup>\*\*</sup>,14<sup>\*</sup>], thereby obscuring the effects of particular habitat types.

Natural enemy population dynamics, and biological control, can also be impacted by the temporal heterogeneity of landscapes (Figure 1). Within seasons, landscapes change constantly due to plant growth and development [15<sup>\*\*</sup>,16], farm management practices [17], crop rotations [18], and human activity [19]. This variation mediates the suitability of landscapes for natural enemies, and their capacity to disperse into crop fields. Over longer scales, land-use change can affect natural enemy population dynamics and source/sink relationships between crop and non-crop habitats, while also impacting spatial overlap between natural enemies and pests [20]. Yet, many studies of biological control are conducted over relatively short time-scales, and thus fail to properly assess the role of temporal heterogeneity in landscapes both within and across seasons.

Here we discuss how biological control would benefit from comprehensive approaches to classifying landscapes over space and time. We explore how moving beyond binary metrics of landscape complexity can allow for greater evaluation of the source/sink potential of specific habitat types. Moreover, we discuss how landscape

Figure 1



A graphical illustration of spatial and temporal heterogeneity across landscapes (based on two counties in Washington State). The four-panel display depicts four landscapes, where different colors represent different habitat types. The two panels on the left illustrate simple landscapes with only two or three main habitat types; the two panels on the right illustrate complex landscapes with multiple habitat types. Moving from the bottom two panels to the top two panels represents temporal change that might be expected in a landscape over two seasons, as farmers rotate crops or modify the landscape in other ways. The pie chart shows the percentage of the total landscape covered by each habitat type in the complex landscape. This shows the diversity of habitat types that fall under the 'agricultural' umbrella.

processes interact with local management practices to influence biological control. We also describe how studies that incorporate temporal complexity provide greater insight into the timing of natural enemy movement into crop fields and resulting biological control. Modern decision support tools can incorporate variation in spatial and temporal conditions that affect biological control across landscapes, while providing recommendations for growers. We conclude by suggesting future directions for researchers interested in promoting biocontrol at the landscape level.

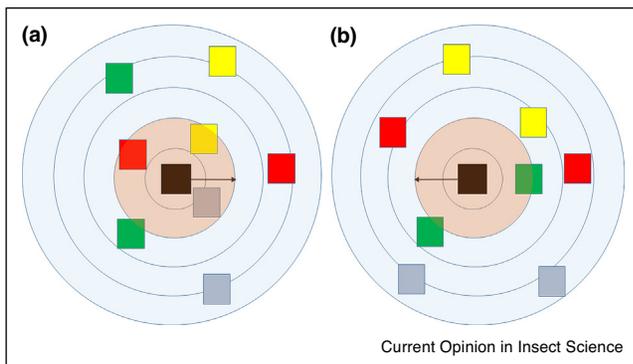
### Landscape heterogeneity

The most common method to classify landscape complexity is a binary system where all habitat patches are classified as either 'semi-natural/natural' or 'agricultural/developed' [21]. Such systems are commonly referred to as the habitat-matrix paradigm [22,23]. Once all habitat patches are classified, landscape complexity is calculated as the proportion of semi-natural/natural habitat (Figure 1). While there is no definitive standard for what defines a 'simple' landscape, a common approach is

to define landscapes with less than 20% non-crop habitat as 'simple' and those with greater than 20% non-crop habitat as 'complex' [21].

Binary classification schemes are prevalent in part because of statistical issues associated with more complex characterizations of landscapes. For example, classifying landscape diversity based on the richness (*i.e.*, number of unique habitat types) or evenness (*i.e.*, relative abundance of different habitat types) can be confounded by the scale of measurement (Figure 2), because the likelihood of detecting rare habitat types increases at greater scales (Figure 2). Similarly, landscapes with greater habitat richness typically have lower habitat evenness because they include more rare habitat types; thus, determining which landscape is more 'diverse' becomes problematic. Moreover, if all habitats in a landscape are evaluated for their effects on natural enemies and biological control, the associated statistical models will often be overly complicated and lack power, making it difficult to determine the key factors that truly drive biological control [23]. A constant challenge for researchers is therefore to develop

Figure 2



Graphical depiction of the effects of the scale of measurement on measures of landscape complexity. Shown are two landscapes, (a) and (b), around two sampled fields (black squares). The colored squares represent different habitat types in the landscape. Landscape (a) has high diversity, with four unique habitat types in the landscape, at any spatial scale of measurement (shown with the different rings). In contrast, the diversity of landscape (b) depends on the scale of measurement. At the smallest scale landscape (b) has only one unique habitat, and the number of unique habitats increases with the scale of measurement.

models that are simple and interpretable but which also provide high explanatory power.

Another major drawback of such schemes is that they treat all agriculture and all natural habitat uniformly, thereby obscuring the contribution of particular habitat types on natural enemies and biological control [14,24–26]. It is clear, for example, that not all ‘non-crop’ habitat equally promotes natural enemy spillover into crop fields. For example, Inclán *et al.* [14] found strong evidence that tachinid parasitoids moved readily into apple orchards from forest habitat, regardless of overall landscape composition. However, while tachinids also dispersed from grasslands into apples, this only occurred in landscapes dominated by apples. These results suggest that forests consistently served as a source of tachinids into apple orchards, but the effectiveness of grasslands as a source of parasitoids depended on landscape composition [14]. To address this disparity, some authors have argued that landscape complexity should be based on the ‘functional diversity’ of habitats [23]. For example, rather than identifying crop and non-crop habitats researchers might classify habitats as ‘suitable’ or ‘unsuitable’ for natural enemy survival and reproduction. Functional habitat diversity might in turn be a more useful method for dealing with inherent variability across systems related to how natural enemies and pests perceive and respond to landscape features [23].

Classifying landscapes based on the acreage of particular habitat types may also overlook the role of landscape structure in mediating pest and natural enemy

communities. Landscapes are composed of a diverse matrix of habitat types with varying connectivity (Figure 1). A study of insect movement between native vegetation patches, canola, and cereal crop fields found that aphid parasitoids predominantly moved between the native patches and canola, while caterpillar parasitoids moved primarily into canola from cereal fields [27]. Indeed, it has also been shown that the amount of border a crop field shares with semi-natural habitat is positively correlated to overall natural enemy biodiversity [28]. Insects often have limited dispersal, such that habitats directly adjacent to crop fields have a greater impact on insect communities than the complexity of the surrounding landscape [29,30]. For example, in a study of natural enemy communities overwintering in semi-natural habitat, local variables like habitat, soil, and management had a stronger influence on community composition than landscape-level variables [30].

While farmers typically have limited control over their surrounding landscape, growing evidence suggests strong linkages between local management and landscape heterogeneity. Some studies have shown that farmers, particularly in simple landscapes, may be able to promote biological control through on-farm diversification [1]. For example, planting floral strips along field borders tends to produce large effects on boosting natural enemy populations in simple landscapes, but reduced impacts in complex landscapes [31]. Other management practices, such as conservation tillage, have also been shown to promote biological control in simple but not complex landscapes [32]. Local land management practices, such as intensive pesticide use, can also mediate the impacts of landscape complexity on natural enemy communities [16]. More studies are needed, however, to determine if the effects of local management on biological control are consistently stronger in simple compared to complex landscapes.

To improve our understanding of linkages between landscapes and biological control, researchers must continue to move beyond binary landscape classifications. This is particularly important in regions where the diversity of habitats is high, such that binary classifications obscure overall landscape structure. Moreover, it is clear that while farmers might have limited control over the landscape around their fields, they might be able to modify their management practices based on the composition of their landscape to maximize biological control.

### Temporal heterogeneity

Landscapes experience temporal heterogeneity both within and across seasons, such as the gradual development of formerly rural areas or through crop rotations [15]. These changes are important because natural enemy movement into crop fields from surrounding habitat is affected by plant phenology, including the relative suitability of crop and non-crop habitats. For example,

González *et al.* [33<sup>\*</sup>] showed that forests served as a source of natural enemies into soybean fields, but this effect diminished as soybeans senesced. However, quantifying land-use change within seasons is difficult, because most publicly accessible land cover datasets are produced once per year. This is problematic in regions where multiple crops are grown in a year. Moreover, factors such as crop senescence are difficult to ascertain from satellite images. For these reasons, ground-truthing and local knowledge of changing landscape conditions can aid researchers in understanding how temporal change might affect biological control. Researchers in regions with considerable within-season variation should also classify landscapes based on satellite images or aerial photos that are produced more than once per year.

Temporal variation of landscapes can also impact biological control by affecting the timing of natural enemy arrival in fields, and overlap between natural enemies and pests [34<sup>\*\*</sup>]. For example, natural enemies of aphids (coccinellids and carabids) were more abundant and diverse in wheat fields surrounded by complex landscapes, and colonized crops earlier, strengthening biological control [34]. Literature reviews have similarly suggested that natural enemies that arrive earliest into crop fields are the most effective at providing biological control [35]. In contrast, Neuville *et al.* [36<sup>\*</sup>] found that the parasitoid *Diaeretiella rapae* tends not to arrive in fields until its host, the cabbage aphid *Brevicoryne brassicae*, has reached its peak population density, such that the pests are capable of inflicting considerable crop damage by the time the parasitoid arrives. When the authors experimentally manipulated parasitoid arrival to happen simultaneously with the aphid, the highest parasitism success

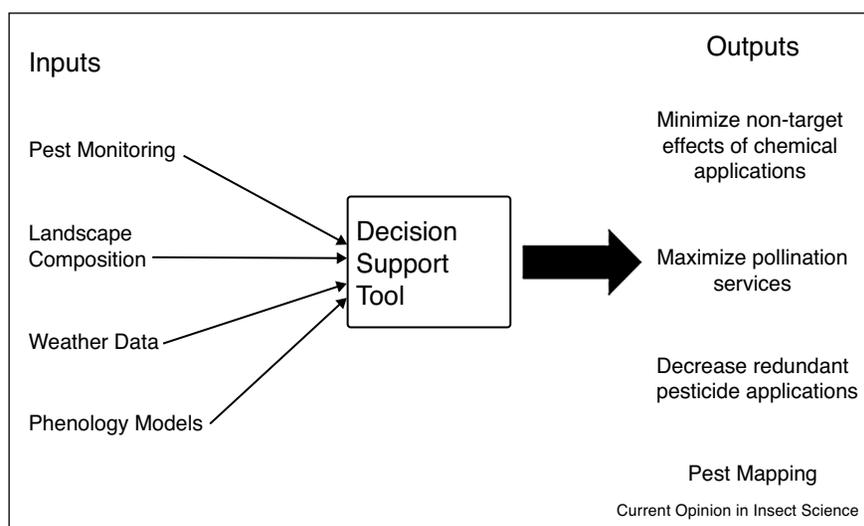
rate and lowest plant damage was observed. However, not all biological control systems follow similar temporal patterns, and such temporal effects are likely to be context-dependent.

To better understand how temporal heterogeneity of landscapes impact biological control, more long-term studies of biological control are needed. For example, while not directly related to landscape complexity, a 10-year study on cereal leaf beetle, *Oulema melanopus*, showed how temporal variability can affect biological control [37]. In warmer springs, the beetle colonizes fields earlier in the year. However, the phenology of the parasitoid, *Tetrastichus julis*, did not change based on warming springs. In warm years, this led to the parasitoid arriving after the pest established, weakening biological control [37]. If natural enemy populations similarly adapt less quickly to changing landscape conditions, such that pests 'escape' control in parts of their range as land-use changes, it could weaken biological control [38]. By structuring more landscape biological control studies to look at long term trends, we can better determine the sensitivity of biological control services to temporal changes across landscapes.

### Decision support systems

While biological control involves the basic ecology of natural enemy and pest populations, it is at its core an applied science. To be effective growers must be aware of biological control and implement farming practices that promote abundant and diverse natural enemy communities across space and time. Moreover, growers must consider how the timing and intensity of their management practices (such as the use of insecticides) can impact

Figure 3



Inputs and outputs associated with decision support systems. These systems integrate data on abiotic and biotic factors to generate recommendations for growers that can be used to guide management practices and maximize the effectiveness of biological control.

biological control both on their farms and across farming landscapes.

Modern decision-support systems are effective tools that address these issues by integrating spatial and temporal landscape complexity into models that provide recommendations for growers (Figure 3). One example is the 'Decision Aid System' (DAS) for tree fruit growers in Washington State [39,40]. The DAS system incorporates real-time weather data and phenology models to predict how populations of pests and natural enemies vary across space and time. Based on these models, the system provides recommendations to best manage pests while maximizing the impacts of natural enemies. For example, growers get recommendations on pesticides that minimize non-target effects based on the time of the season and their location.

Decision support systems are critical tools that may allow farmers to get targeted predictions about pests and natural enemies based on their location in a broader landscape. The ability to deliver such real-time information can help reduce pesticide sprays, increasing the effectiveness of biological control and farmer profitability. As technology develops, decision-support systems will continue to be an effective means of integrating complex spatial and temporal landscape data to improve biological control in many crop systems.

## Conclusion

Increasing complexity of agricultural landscapes is generally beneficial for natural enemies and biological control. However, our understanding of the impacts of landscapes on biological control has been hampered by using simple classification schemes for both spatial and temporal complexity. Advances in remote sensing and fine-scale land cover datasets are making it easier to create detailed pictures of overall landscape composition, and resulting impacts on natural enemy population dynamics, dispersal into crops, and pest control. As landscapes continue to be modified by humans and climate change, decision-support systems are useful tools that can help growers make management decisions that promote biological control while considering spatial and temporal complexity. Future research should continue to assess specific spatial and temporal factors that promote biological control across landscapes. Only with a nuanced understanding of how natural enemies move across landscapes to control pests can we truly understand how to design landscapes and local farming systems to maximize this key ecosystem service.

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