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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

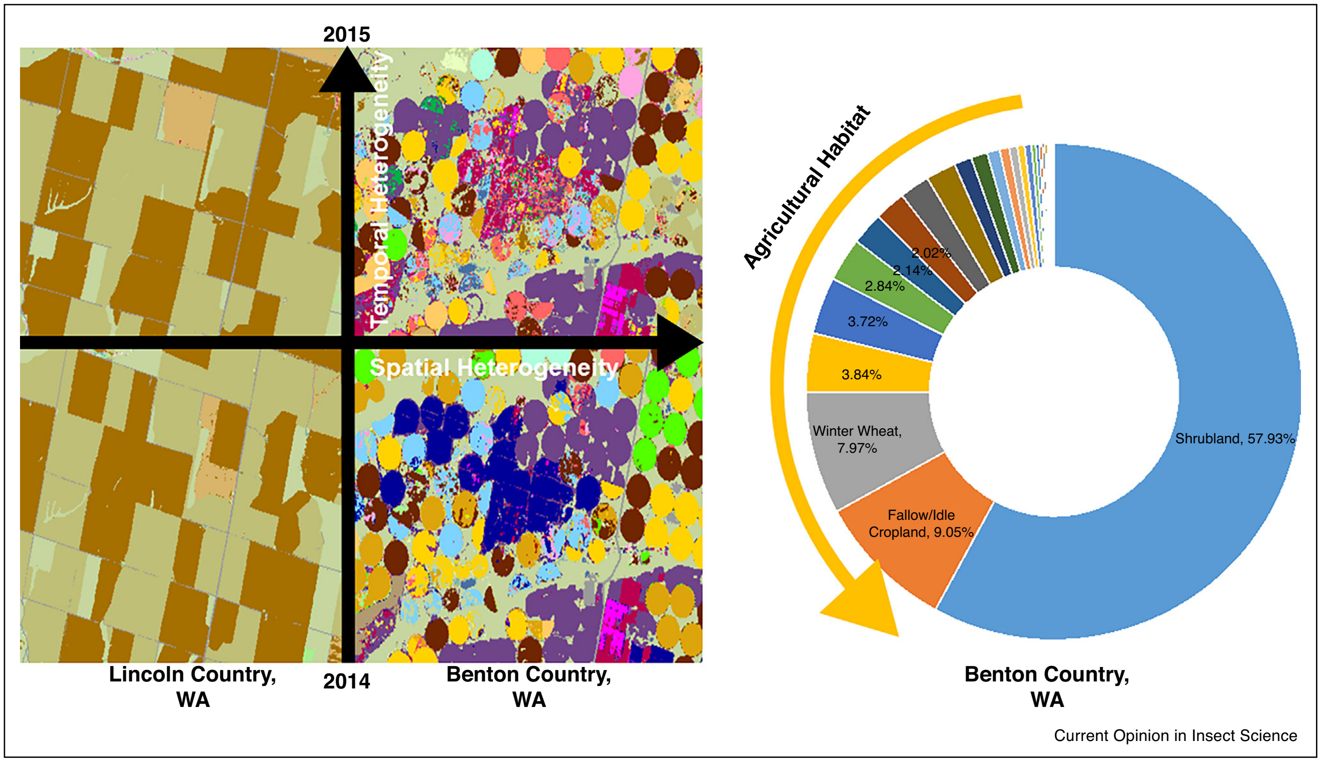
Biological control relies on diverse communities of natural enemies that disperse into crop fields to control pests [1,2••]. As such, the composition of landscapes surrounding crop fields can strongly impact biological control [1]. More complex landscapes, where crop fields are surrounded by a high proportion 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•]. Conversely, simplified landscapes often have reduced biological control [2••]. 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••] (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••,14•], 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••,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 interesting 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

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