



Landscape composition and configuration have scale-dependent effects on agricultural pest suppression

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ABSTRACT

Increasing landscape heterogeneity (composition and configuration) can enhance natural enemy populations and support pest suppression in agricultural landscapes. Using a network-based data mining approach, we examined independent gradients of landscape composition and configuration at six spatial scales that were associated with pest suppression services measured at 32 sites in Michigan and Wisconsin, USA. We compared the relative effects of landscape composition and configuration across scales with those of local crop type (corn or grassland). We found that multiple gradients of configurational heterogeneity were independent of composition and strongly associated with pest suppression, with different configuration metrics being predictive of pest suppression depending on the spatial scales and regions considered. Landscapes that were more configurationally heterogeneous at smaller spatial scales consistently supported higher pest suppression. In Michigan, pest suppression increased in landscapes with high edge contrast between annual crops and surrounding habitats and high edge density of grassland within 250–500 m radii. In Wisconsin, pest suppression increased with large core area of grassland and high field density within a 250 m radius. The main compositional effect we found was a positive relationship between grassland cover and pest suppression occurring at larger spatial scales (1000–1500 m) and occurring in Wisconsin but not in Michigan. Our findings demonstrate that effects of landscape composition and configuration on pest suppression differ across spatial scales and vary regionally. The network-based data mining techniques used here could be useful for disentangling intercorrelated landscape metrics in a variety of other contexts in landscape ecology.

1. Introduction

Agricultural intensification has transformed Earth's landscapes, with around 40 % of terrestrial surfaces already converted from unmanaged systems to cropping or grazing (FAO, 2019). While humans rely on agricultural landscapes to provide food and other ecosystem services, as landscapes become increasingly simplified, their ability to provide these services can be compromised (Dainese et al., 2019; Rusch et al., 2016; Tschamntke et al., 2005). In particular, grassland and other semi-natural habitats often support essential ecosystem services in agricultural landscapes (Bengtsson et al., 2019). For example, they provide habitat for predatory and parasitic arthropods that suppress crop pests (Grab et al., 2018), reducing the demand for insecticides (Meehan et al., 2012) and in some cases increasing yields (Gagic et al., 2019). As a result, understanding how landscape structure influences the provision of pest suppression services in intensified agricultural landscapes is increasingly important.

The potential for pest suppression in a given field varies partly as a function of the surrounding landscape. Landscape structure is comprised of two components: composition, which describes the amounts and diversity of different land cover types, and configuration, which refers explicitly to their spatial arrangement in the landscape (Fahrig et al., 2011). Until recently, most research on landscape-scale predictors of pest suppression focused on the effects of landscape composition. In some cases, pest suppression potential in a focal field improves with increasing amounts of semi-natural habitats (Meehan et al., 2012), decreasing amounts of cultivated land (Rusch et al., 2016), and increasing crop diversity (Redlich et al., 2018) in the surrounding landscape. However, in some circumstances, natural habitats surrounding crop fields fail to enhance pest suppression (Tschamntke et al., 2016), and a recent prominent review indicates that crop pests and predator abundance respond inconsistently to landscape composition (Karp et al., 2018).

Landscape configuration can also influence pest suppression and

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could do so by multiple mechanisms (Haan et al., 2019). Since natural enemies can spillover across boundaries between managed and unmanaged systems (Rand et al., 2006; Tscharntke et al., 2012), the edge density or spatial arrangement of habitats in the landscape may influence pest suppression independently of the amount of habitat present. Similarly, organisms that use resources from multiple cover types at different life stages or times of year may benefit from ‘landscape complementation’ (Dunning et al., 1992): the degree of intermixing among cover types in the landscape will influence the spatial arrangement and accessibility of resources and therefore could also influence pest and natural enemy populations.

Recent research illustrates some of the ways landscape configuration can influence pest suppression. In South Korean landscapes where composition and configuration were uncorrelated, several natural enemy taxa were positively influenced by increasing configurational complexity, quantified as edge density (Martin et al., 2016), and the effects of configuration were larger than those of composition. Other examples include rice agroecosystems, where the connectivity of bunds (grassy embankments) influenced parasitoid abundance (Dominik et al., 2018), and wheat fields, where field size influenced the abundance of different functional groups of spiders and carabids (Gallé et al., 2018). In some cases, proximity to semi-natural habitats can inhibit pest suppression, especially if predators are adapted to open field conditions (e.g., Berger et al., 2018; Aristizábal and Metzger, 2019).

There are several challenges associated with understanding the effects of landscape configuration on pest suppression. First, landscape configuration is constrained by and often highly correlated with composition, so these two types of metrics are easily confounded in landscape-scale studies where experimental manipulation is impractical (Fahrig et al., 2011). Second, configuration can be described using dozens of different and often highly inter-correlated metrics and can, therefore, be challenging to describe in practical terms. Ecologists are often caught between choosing one or two configuration metrics they think could be biologically meaningful (and risk missing important patterns) or testing a wide range of predictors whose various meanings and correlation structures can obscure their ecological relevance (Li and Wu, 2004; Kupfer, 2012). Finally, identifying the spatial scales at which configuration (or composition, or both combined) affects pest suppression most strongly is difficult, since different taxa respond to different spatial scales according to their dispersal abilities and habitat use preference (With and Crist, 1995).

The purpose of this study was to investigate the effects of landscape configuration on the provision of natural pest suppression services in the Midwest United States and to evaluate the importance of considering multiple spatial scales. We used data from a previous study (Meehan et al., 2012), which focused specifically on the effects of landscape composition on pest suppression in bioenergy production landscapes and found positive effects of increasing grassland cover. Using high-resolution imagery, we re-analyzed these data with the goal of evaluating the relative contribution of landscape configuration and tested the sensitivity of pest suppression services to these variables at multiple spatial scales (Chiavacci et al., 2018). Effects of landscape configuration on pest suppression in this region are mostly unexplored, so rather than choosing a small number of landscape metrics *a priori*, we began with a large number and used data mining techniques to distill out a smaller number of uncorrelated metrics to use as predictors. Specifically, we asked three questions: (1) What are the independent aspects of local and landscape complexity that are associated with pest suppression? (2) What are the effects of spatial scale on the relative importance of landscape composition and configuration? (3) How do individual configuration metrics predicting pest suppression vary by region and spatial scale?

2. Materials and methods

The experiment generating the pest suppression data analyzed here

was conducted during the summer of 2010 at 32 study sites, covering a compositional gradient from annual- to perennial-dominated landscapes in the Midwest U.S. (Meehan et al., 2012). Of those, 16 sites were located in southern Wisconsin, 16 in southern Michigan, and in each state 8 sites were located in corn fields and 8 in grasslands. The purpose of the original study was to assess how changes in landscape composition stemming from the adoption of bioenergy cropping systems will affect pest suppression; data collection occurred in corn and grassland because they represent typical annual and perennial bioenergy crops, respectively. Within each site, predation rates on three sentinel pest species were measured using platforms that held pests in the canopy (for eggs of corn earworm, *Helioverpa zea*, and for larvae of fall armyworm, *Spodoptera frugiperda*) or on the ground (for larvae of wax moth, *Galleria mellonella*). Natural pest suppression was measured as a single index based on averaged predation rates across taxa since removal rates of different sentinel prey were positively correlated with one another. Characteristics of field sites and experimental design are described in detail by Werling et al (2011) and Meehan et al. (2012). The original study related pest suppression to landscape composition (the percentages of land cover types) at different spatial scales around fields, based on USDA Cropland Data Layer (CDL 2009, 56 m). However, the initial analysis indicated those levels of spatial resolutions (30–56 m) were too coarse to characterize small, fragmented patches (e.g., grasslands) and consequently produced less accurate configurational measures (Fahrig et al., 2015). Therefore, in the present study, we used the same pest suppression data but recharacterized landscape structure using high-resolution land cover data (1 m × 1 m) to investigate the relative effects of landscape composition and configuration across multiple spatial scales. The overall workflow used in this study is shown in Fig. 1 and detailed below.

2.1. Building land cover maps

We mapped the land cover types within a 1500 m radius around each site using heads-up digitizing in ArcGIS 10.2.2 (ESRI) based on high-resolution aerial imagery from National Agriculture Imagery Program (NAIP 2010, 1 m, available at NRCS, <https://nrcs.app.box.com/v/naip/folder/19554895429>). We then cross-referenced with historical Google Earth imagery and verified with local experts to finalize the land cover data. The maximum radius was chosen based on relevant landscape scales in previous studies (Thies et al., 2003; Gardiner et al., 2009). Land cover features were classified into four categories: annual crops, forest, grassland, and others. In the study region, annual crops, principally corn, soybeans, and wheat, dominate the landscapes (mean ± SE; MI: 34.36 ± 28.59 %; WI: 41.30 ± 19.37 %), closely followed by various types of forest (MI: 34.09 ± 22.12 %; WI: 13.90 ± 15.38 %), including evergreen and mixed forest, forested hedgerows, riparian forest, isolated trees, and forested wetlands. The grassland category consisted of herbaceous-dominated cover types, including agricultural grasslands (e.g., hayfields, pasture), sparse and weedy scrub, shrublands, herbaceous wetland, and open woodland (MI: 10.01 ± 22.06 %; WI: 32.18 ± 15.42 %). Other land covers, including developed areas, water, paved road, mowed grass, orchard, and bare, were not used in the analysis.

2.2. Quantifying landscape heterogeneity (composition and configuration)

In addition to composition metrics, we developed a list of configuration metrics describing patch size and density, edge characteristics, patch shape, connectivity, contagion/interspersion, and core area, based on our understanding of how they may influence natural enemies and therefore pest suppression (Table 1). All metrics were calculated at the class level (annual crops, grassland, and forest) across six spatial scales (250, 500, 750, 1000, 1250, and 1500 m radii) in FRAGSTATS 4.2 (McGarigal et al., 2012) based on raster-format land cover data of 1-m resolution, except mean field size and field density which were

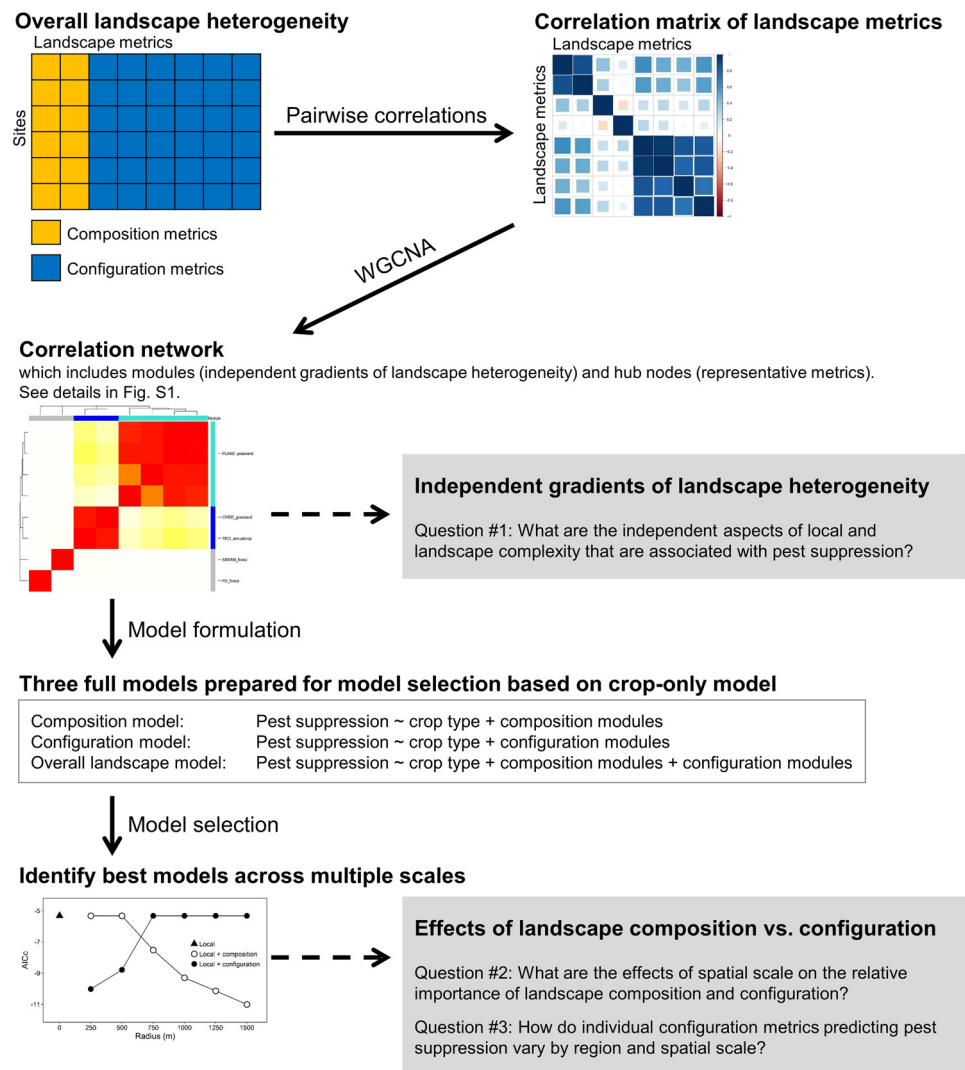


Fig. 1. Overview of multiscale modeling process combined with weighted gene correlation network analysis (WGCNA) used to address our research questions (gray boxes). Detailed interpretation of correlation networks, modules, and module representatives is presented in Fig. S1.

Table 1

The list and description of variables expected to impact pest suppression within corn fields and grasslands, including the local crop type, one landscape composition metric, and 14 configuration metrics. All landscape metrics were calculated for three land cover types (annual crops, grassland, forest) located within six spatial scales (250, 500, 750, 1000, 1250, and 1500 m) around each site, using digitized 1-m resolution land cover data and FRAGSTATS 4.2, except mean field size and field density which were only calculated for annual crops, using digitized field boundaries and ArcGIS 10.2.2. Some metrics were summarized based on the mean (MN) and area-weighted mean (AM) of patch distribution of specific cover type in the landscape.

Category	Variable	Abbr.	Unit (range)
Local	Focal habitat type	crop	corn = 0, grassland = 1
Composition	Percentage of landscape	PLAND	% (0, 100)
Size & density	Mean patch size	AREA (_MN, _AM)	ha (> 0)
Size & density	Mean field size (annual crops only)	MeanFieldSize	ha (> 0)
Size & density	Patch density	PD	number per 100 ha (> 0)
Size & density	Field density (annual crops only)	FieldDensity	number per 100 ha (> 0)
Edge	Contrast-weighted edge density	CWED	m per ha (≥ 0)
Edge	Total edge contrast index	TECI	percent (0, 100)
Shape	Perimeter-area fractal dimension	PAFRAC	NA (1, 2)
Shape	Related circumscribing circle	CIRCLE (_MN, _AM)	NA (0, 1)
Connectivity	Connectance index	CONNECT	percent (0, 100)
Connectivity	Similarity index	SIMI (_MN, _AM)	NA (≥ 0)
Contagion/interspersion	Clumpiness index	CLUMPY	NA (-1, 1)
Contagion/interspersion	Interspersion & juxtaposition index	IJI	% (0, 100)
Core area	Core area index distribution	CAI (_MN, _AM)	% (0, 100)
Core area	Core area percentage of landscape	CPLAND	% (0, 100)

calculated for annual crops only in ArcGIS based on digitized field boundaries. Metrics that required user-defined parameters were defined as follows: Calculations for core area were based on a 20-m edge depth according to prior studies in this system which showed edge effects for predators and parasitoids decline after 15–20 m into crop fields (Dyer and Landis, 1997; Woltz et al., 2012). Metrics based on the distribution of suitable habitat pixels within a specified distance of a focal point and an eight-neighbor rule used a 100 m search radius. Finally, edge contrast weights between grassland and forest, annual crops and forest, annual crops and grassland were assigned values of 0.5, 0.7, and 1, respectively, based on their expected benefits to natural enemies and on evidence that grasslands are particularly important suppliers of natural enemies (Meehan et al., 2012). Detailed descriptions of all metrics can be found in McGarigal et al. (2012).

2.3. Identifying independent gradients of landscape heterogeneity

At each spatial scale, we began with an initial set of up to 53 metrics characterizing composition and configuration of annual crops, grassland, and forest in the landscapes, which were possibly inter-correlated. To identify a subset of independent metrics at each scale, we employed a widely used data mining method, weighted correlation network analysis, also known as weighted gene co-expression network analysis (WGCNA; Langfelder and Horvath, 2008). WGCNA can be used for finding modules (clusters; coded by different color names) of highly correlated nodes (variables) by constructing a network based on pairwise correlations and summarizing such clusters using intramodular hub nodes. In this study, we constructed a WGCNA network at each scale, separately, to identify independent landscape gradients based on clusters of highly correlated metrics and to determine the representative metrics (see details in Supplementary material). According to Tissier et al. (2018), WGCNA performance depends on parameter settings for network construction and works better for predictors, which are highly associated with the response variable. Therefore, metrics not correlated with pest suppression (Pearson's $r < 0.4$) were removed before network construction, as well as metrics highly correlated with local variables (local habitat type and/or focal field size; Pearson's $r > 0.7$). Three types of metric modules were defined for each network: (1) composition modules, that primarily characterized composition-related heterogeneity and included composition metrics and if present, a few configuration metrics highly correlated with composition; (2) configuration modules, characterizing gradients of configurational heterogeneity that were independent of composition and composed of configuration metrics only; and (3) one grey module, which did not represent a real module as it included metrics that were uncorrelated but cannot be clustered into other modules. In our case, grey modules of all WGCNA networks were made up entirely of configuration metrics. Thus, each metric in the grey module represents an individual gradient of configurational heterogeneity with itself as the representative metric. For composition and configuration modules, composition and configuration metrics with the highest intra-modular connectivity (k_{Within}) were selected, respectively, as the representative metrics. WGCNA analysis was repeated for each spatial scale using R package WGCNA (Langfelder and Horvath, 2008).

2.4. Model selection

The responses of pest suppression (i.e., average pest removal rate) to local crop type and compositional and configurational landscape heterogeneity measured at different spatial scales were analyzed using linear models (function *lm* in R package *stats*). The predictors were crop type and a list of metrics representing independent compositional and configurational gradients of landscape heterogeneity across scales. All metrics were centered and scaled using means and standard deviations before analysis. Data from the two regions (Michigan and Wisconsin) were analyzed separately. For each region, we used the crop-only model

as a null model because this local effect has already been shown to substantially influence pest suppression (Meehan et al., 2012).

At each scale, three full models were developed based on the crop-only model by adding representative metrics of composition only, configuration only, and both components of landscape heterogeneity. For each full model, models with all combinations of predictors were compared via AICc using the function *dredge* in R package *MuMIn* (Barton, 2018) and only models within $\Delta AICc < 2$ of the top model were selected as the final models (Table S1). The analysis was repeated independently for each full model at each scale. As local crop type has no spatial scale and landscape metrics correlated with local variables were removed, the explanatory power of landscape heterogeneity can be directly compared (1) within scales to identify the relative effects of landscape composition and configuration, and (2) across scales to detect the scale-dependent pattern and the most relevant spatial scale for pest suppression.

3. Results

3.1. Independent gradients of landscape heterogeneity related to pest suppression

The WGCNA analysis identified a preliminary list of independent gradients of compositional and configurational landscape heterogeneity within each of the six spatial scales (see representative metrics in Table 2), which enabled us to compare the relative effects of landscape composition and configuration on pest suppression. First, there was a strong compositional gradient ranging from low to high proportion of grassland (PLAND2) within scales of 750–1500 m in both regions (Pearson's r between PLAND2 and pest suppression, Michigan: 0.41–0.57, Wisconsin: 0.75–0.80; Table 2). This was expected as the sites were originally selected to capture this gradient (Meehan et al., 2012). In addition, we found multiple configurational gradients, independent of composition, across all scales except 1250–1500 m in Michigan and 1500 m in Wisconsin. In Michigan, pest suppression was positively correlated with decreasing mean field size and core area of annual crop patches (CAI_AM1) within scales of 250–500 m, and also positively correlated with increasing edge contrast between annual crops and surrounding habitats (TECI1) and increasing edge density of grassland-related boundaries (CWED2) within scales of 250–750 m. In Wisconsin, pest suppression decreased when grassland patches were narrower and more elongated (CIRCLE_MN2 approached 1) at 250 m and increased with increasing core area of grassland patches (CAI_MN2) at 250–500 m. Similarly, pest suppression was positively correlated with increasing edge contrast between annual crops and adjacent habitats (TECI1) at scales of 250–1000 m. However, edge contrast of annual crops was positively correlated with the core area of grassland patches (CAI_AM2; Pearson's $r = 0.54$) at 500 m and negatively correlated with the core area of annual crop patches (CAI_MN1; Pearson's $r = -0.55$) at 1000 m.

Though not included in the model selection, many configuration metrics at larger scales (750–1500 m) were clustered into the composition module and were strongly and positively correlated with grassland composition (PLAND2) in both regions. Examples included core area (CPLAND2, CAI_MN2), mean patch size (AREA_MN2), edge density (CWED2), and shape complexity (CIRCLE_MN2, PAFRAC2) of grassland, and edge contrast of annual crop patches (TECI1).

3.2. Effects of landscape composition vs. configuration

The relative effects of landscape composition and configuration on pest suppression were region-specific and scale-dependent (Fig. 2, Table S1). In Michigan, final composition models – either crop-only (at scales of 250–1500 m) or in combination with the proportion of grassland (PLAND2; at scales of 1000–1500 m) – performed similarly to the crop-only model ($\Delta AICc < 2$; Table S1); this held true across all

Table 2

The list of representative metrics of compositional and configurational landscape heterogeneity for model selection. Modules were coded with different color names across states (MI = Michigan, WI = Wisconsin) and scales (250, 500, 750, 1000, 1250, and 1500 m radii). The number after metric abbreviations in column 'Metric' relates to the land cover type: 1 = annual cropland, 2 = grassland, 3 = forest. See Table 1 for metric abbreviations. Other abbreviations: kWithin – intramodular connectivity, GS – gene significance measure defined as the correlation between one metric and pest suppression, p.GS – *p* values of GS, moduleCorR – module significance defined as the correlation between the module eigengene and pest suppression, p.moduleCorR – *p* values of moduleCorR.

State	Radius (m)	Module	Module type	Metric	kWithin	GS	p.GS	moduleCorR	p.moduleCorR
MI	250	turquoise	Configuration	CAIAM1	0	−0.52	0.037	−0.53	0.035
MI	250	turquoise	Configuration	MeanFieldSize1	0	−0.45	0.077	−0.53	0.035
MI	250	brown	Configuration	TECI1	0	0.45	0.078	0.51	0.042
MI	250	brown	Configuration	CWED2	0	0.44	0.085	0.51	0.042
MI	250	blue	Configuration	CIRCLEMN2	0	−0.64	0.008	0.63	0.009
MI	250	blue	Configuration	CLUMPY2	0	0.51	0.044	0.63	0.009
MI	500	turquoise	Configuration	CAIAM1	1.03	−0.61	0.012	−0.63	0.009
MI	500	blue	Configuration	TECI1	0.41	0.73	0.001	0.71	0.002
MI	500	grey	Configuration	IJI1	0.01	0.49	0.053	0.62	0.011
MI	500	grey	Configuration	CIRCLEMN3	0.00	−0.46	0.076	0.62	0.011
MI	500	grey	Configuration	PD3	0.01	0.45	0.080	0.62	0.011
MI	750	turquoise	Composition	PLAND2	1.20	0.57	0.021	0.55	0.028
MI	750	blue	Configuration	TECI1	0.44	0.72	0.002	0.73	0.001
MI	750	grey	Configuration	CAIMN3	0	−0.44	0.089	0.50	0.050
MI	750	grey	Configuration	PD3	0	0.44	0.091	0.50	0.050
MI	1000	turquoise	Composition	PLAND2	1.51	0.56	0.024	0.58	0.018
MI	1000	grey	Configuration	SIMIAM3	0	0.62	0.011	0.66	0.006
MI	1000	grey	Configuration	IJI3	0	−0.47	0.067	0.66	0.006
MI	1250	turquoise	Composition	PLAND2	1.05	0.50	0.049	0.51	0.041
MI	1500	turquoise	Composition	PLAND2	0.92	0.41	0.115	0.50	0.048
WI	250	turquoise	Configuration	CAIMN2	0	0.72	0.002	−0.70	0.002
WI	250	turquoise	Configuration	CIRCLEMN2	0	−0.64	0.008	−0.70	0.002
WI	250	grey	Configuration	FieldDensity1	0.06	0.55	0.027	0.62	0.011
WI	250	grey	Configuration	MeanFieldSize1	0.25	−0.49	0.052	0.62	0.011
WI	250	grey	Configuration	CONNECT1	0.01	−0.48	0.060	0.62	0.011
WI	250	grey	Configuration	TECI1	0.23	0.41	0.116	0.62	0.011
WI	500	turquoise	Configuration	CAIMN2	0.39	0.68	0.003	0.72	0.002
WI	500	grey	Configuration	CONNECT3	0	0.40	0.121	0.40	0.121
WI	750	blue	Composition	PLAND2	1.38	0.75	0.001	0.70	0.002
WI	750	grey	Configuration	TECI3	0	−0.53	0.036	−0.67	0.005
WI	750	grey	Configuration	TECI1	0	0.48	0.060	−0.67	0.005
WI	1000	turquoise	Composition	PLAND2	2.34	0.77	0.000	0.79	0.000
WI	1000	blue	Configuration	CAIMN1	0.20	−0.52	0.037	0.58	0.019
WI	1250	turquoise	Composition	PLAND2	2.08	0.80	0.000	0.79	0.000
WI	1250	grey	Configuration	CAIMN1	0	−0.43	0.095	−0.43	0.095
WI	1500	turquoise	Composition	PLAND2	2.07	0.80	0.000	0.74	0.001

spatial scales (compare the triangle dot and solid line with open circles in Fig. 2a). In contrast, final configuration models (the solid line with closed circles in Fig. 2a) at scales of 250–1000 m ($\Delta AICc > 2$; Table S1) but not 1250–1500 m had more explanatory power than the crop-only model. Thus, configuration models within scales of 250–500 m were most predictive for pest suppression in Michigan ($\Delta AICc < 2$ of all models across scales), explaining 43–49 % more variation than the crop-only model. In Wisconsin, final composition models performed better than the crop-only model at scales of 750–1500 m ($\Delta AICc > 2$; Fig. 2b, Table S1). In contrast, final configuration models were more predictive at scales of 250–500 m. Thus, the configuration model at 250 m and composition models at scales of 1000–1500 m were most predictive for pest suppression in Wisconsin ($\Delta AICc < 2$ of all models across scales), where 32–38 % more variation was explained than the crop-only model. In both regions, however, no improvements were found when representative metrics of both compositional and configurational heterogeneity were included in the model selection, compared to the final composition or configuration models at the respective scale ($\Delta AICc < 2$).

3.3. Significant landscape metrics

Model selection allowed us to narrow the preliminary list of landscape metrics that had initially been identified using WGCNA. Based on the most predictive models (Tables 3–4), significant landscape metrics, and spatial scales at which they were relevant varied between the two regions. In Michigan, pest suppression rates were higher in grasslands

($R^2_{adj} = 0.57, p < 0.05$) and significantly increased with decreasing core area of annual crop patches (CAIAM1; $R^2_{adj} = 0.22, p < 0.05$; Fig. 3a) and increasing grassland-edge density (CWED2; $R^2_{adj} = 0.14, p < 0.05$; Fig. 3b), especially grassland-annual crop boundaries, at the scale of 250 m. Pest suppression also increased when grassland patches in the landscape occurred as simple, non-elongated shapes (CIRCLE_MN2 approached 0; $R^2_{adj} = 0.36, p < 0.05$; Fig. 3c). In addition, pest suppression in Michigan increased with decreasing core area of annual crop patches (CAIAM1; $R^2_{adj} = 0.33, p < 0.05$; Fig. 3d) and increasing edge contrast between annual crops and surrounding habitats (TECI1; $R^2_{adj} = 0.50, p < 0.05$; Fig. 3e) at 500 m radius. In contrast, pest suppression rates in Wisconsin significantly increased with increasing core area of grassland patches (CAIMN2; $R^2_{adj} = 0.48, p < 0.05$; Fig. 3f) and increasing field density ($R^2_{adj} = 0.26, p < 0.05$; Fig. 3g) at 250 m radius. However, at larger spatial scales, configuration metrics did not enter the final models. Instead, pest suppression rates significantly increased with the increasing proportion of grassland (PLAND2) at scales of 1000–1500 m (all $R^2_{adj} \geq 0.57, p < 0.05$; Figs. 3h–j) and were higher if the focal field was grassland rather than corn ($R^2_{adj} = 0.51, p < 0.05$).

4. Discussion

Pest suppression is a valuable ecosystem service in agricultural landscapes. This study adds to a growing body of evidence that pest suppression is influenced by landscape configuration in addition to composition and that in some circumstances landscape configuration can be as or more predictive than composition (also see Bailey et al.,

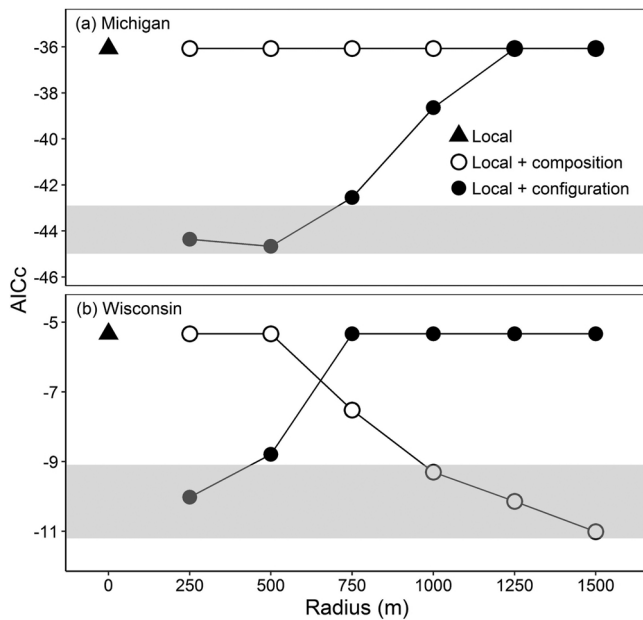


Fig. 2. The lowest AICc values of best models at each spatial scale are shown for different model types: local crop-only (filled black triangle), landscape composition (filled white circle) and configuration (filled black circle) models in (a) Michigan and (b) Wisconsin. The models with $\Delta AICc < 2$ of all models were highlighted with shaded area.

2010; Martin et al., 2016; Schüepp et al., 2014). By applying weighted correlation network analysis (WGCNA), we found that multiple aspects of configurational heterogeneity were strongly associated with pest suppression, independent of landscape composition. Overall, pest suppression was consistently higher in landscapes that were more configurationally heterogeneous at smaller spatial scales. The expected positive composition effects driven by a higher proportion of grasslands in the surrounding landscapes were found to be region-specific and occurred only at larger spatial scales when present.

4.1. Independent gradients of landscape heterogeneity related to pest suppression

We used WGCNA to identify a set of compositional and configurational landscape gradients that were independent of one another and

then fed the representative metrics into the model selection procedure to identify the models that best explained pest suppression in each region and at each spatial scale. While we mostly interpret relationships between pest suppression and the metrics based on the final landscape models (see 4.3 below), some broader insights can also be gained from examining the broader suite of variables selected through WGCNA analysis. For example, for all metrics that were relatively important for pest suppression (Pearson's $r \geq 0.40$), their directions remained stable across scales and regions, except for one case (the elongation metric of forest, CIRCLE_MN3, which was negative in Michigan and positive in Wisconsin). This supports the prior observations that analysis at one scale can often suffice to determine the direction of landscape effects (Martin and Fahrig, 2012; Martin et al., 2016).

4.2. Effects of landscape composition vs. configuration

In this study, the relative importance of landscape composition and configuration for pest suppression was scale-dependent (Jackson and Fahrig, 2014). When present, effects of composition occurred at larger spatial scales (WI: 750–1500 m), while configuration effects in both regions were more relevant at smaller spatial scales (MI: 250–1000 m; WI: 250–500 m). This is in line with the hypothesis that scales of effect for habitat configuration or fragmentation should be smaller than those for habitat amount (prediction 10; Miquet et al., 2016). It is also important to note that the most predictive scales differed when composition or configuration was considered in isolation. For example, in Wisconsin, the best scales identified based on final composition and configuration models were 1000–1500 m and 250 m, respectively. This result affirms the need to account for both composition and configuration simultaneously when determining the scales where they exert the most significant influence on ecological processes (Martin et al., 2019). Moreover, both composition and configuration effects on pest suppression may interact with species' traits such as dispersal ability and habitat use, and that the strength and direction of landscape effects could differ among functional groups (Martin et al., 2019; Perović et al., 2017).

4.3. Significant configuration metrics

Several configuration metrics were correlated with pest suppression in Michigan. In general, they point to the importance of local grasslands and larger pest suppression capacity in configurationally complex landscapes at smaller spatial scales. First, at scales of 250–500 m, pest suppression was enhanced when surrounding landscapes contained

Table 3

The coefficient estimates, 95 % CI, p values of predictors, the variation explained (R^2 / R^2_{adj}), and AICc values of the final models ($\Delta AICc < 2$ of all models across the scales) in southern Michigan. The number after metric abbreviations related to the land cover types: 1 = annual cropland, 2 = grassland, 3 = forest. Metric abbreviations: CAIAM – area-weighted mean core area index, CIRCLEMN – mean related circumscribing circle index, CWED – contrast-weighted edge density, TECI – total edge contrast index. The p values were bold when respective predictors were significant at $p < 0.05$.

Model ID	1			2			3			4		
Model type	Configuration			Configuration			Configuration			Configuration		
Radius (m)	250			250			500			500		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	0.62	0.52 – 0.72	< 0.001	0.80	0.71 – 0.88	< 0.001	0.59	0.48 – 0.69	< 0.001	0.64	0.53 – 0.74	< 0.001
crop	0.08	0.02 – 0.14	0.026				0.10	0.05 – 0.14	0.002	0.08	0.04 – 0.13	0.004
CWED2	0.21	0.11 – 0.30	0.001	0.23	0.14 – 0.32	< 0.001						
CIRCLEMN2	–0.19	–0.31 – –0.07	0.010	–0.27	–0.36 – –0.18	< 0.001						
CAIAM1				–0.13	–0.22 – –0.03	0.024	–0.14	–0.25 – –0.04	0.019	–0.13	–0.23 – –0.04	0.018
TECI1							0.14	0.05 – 0.23	0.013	0.15	0.06 – 0.23	0.007
CIRCLEMN3										–0.07	–0.15 – 0	0.092
Observations	16			16			16			16		
R^2 / R^2_{adj}	0.854 / 0.817			0.856 / 0.820			0.859 / 0.824			0.892 / 0.853		
AIC	–44.131			–44.363			–44.671			–43.661		

Table 4

The coefficient estimates, 95 % CI, *p* values of predictors, the variation explained (R^2 / R^2_{adj}), and AICc values of the final models ($\Delta AICc < 2$ of all models across the scales) in southern Wisconsin. The number after metric abbreviations related to the land cover types: 1 = annual cropland, 2 = grassland, 3 = forest. Metric abbreviations: CAIMN – mean core area index, FieldDensity – annual crop field density, PLAND – percentage of land cover types. The *p* values were bold when respective predictors were significant at $p < 0.05$.

Model ID	1			2			3			4		
Model type	Configuration			Composition			Composition			Composition		
Radius (m)	250			1000			1250			1500		
Predictors	Estimates	CI	<i>p</i>	Estimates	CI	<i>p</i>	Estimates	CI	<i>p</i>	Estimates	CI	<i>p</i>
(Intercept)	0.21	0.10 – 0.32	0.003	0.18	0.06 – 0.31	0.013	0.20	0.08 – 0.31	0.006	0.21	0.11 – 0.32	0.002
crop				0.20	0.03 – 0.37	0.038	0.19	0.02 – 0.36	0.049	0.19	0.04 – 0.35	0.033
PLAND2				0.47	0.14 – 0.80	0.015	0.46	0.16 – 0.75	0.010	0.45	0.18 – 0.73	0.007
CAIMN2	0.54	0.31 – 0.78	0.001									
FieldDensity1	0.47	0.18 – 0.76	0.007									
Observations	16			16			16			16		
R^2 / R^2_{adj}	0.728 / 0.686			0.716 / 0.672			0.730 / 0.689			0.744 / 0.705		
AIC	–10.024			–9.300			–10.142			–11.011		

crop fields with a smaller core area (edge was defined as a 20-m buffer from the patch boundary; Figs. 3a, d). Core area shrinks as patch size decreases and/or as patch shape complexity increases; either of these will result in a landscape with more field edge habitats relative to field interiors. Since natural enemies find overwintering structures, alternative prey, nectar resources, and shelter in other habitats near crop fields (Landis et al. 2000, Herse et al., 2018), landscapes with more edge habitats could provide more spillover of natural enemies into crops. These landscapes could also be more hospitable to natural enemies due to complementation effects (Dunning et al., 1992; Reiss et al., 2009). We also note that in our study, the relationship between pest suppression and core area of crop fields was shaped in part by data from a single site (Fig. 3a), but without this point, the direction of the effect would be unchanged.

Pest suppression in Michigan also increased with total edge contrast between annual crops and other cover types at 500 m (Fig. 3e), particularly when annual crop patches in the landscape shared more edges with adjacent grasslands. This is consistent with previous findings of the importance of grassland habitats (e.g., Werling et al., 2014) and suggests their usefulness as reservoirs of natural enemies may be highest when they are directly adjacent to annual crops. Along the same lines, pest suppression rates in Michigan were also higher in landscapes with a higher grassland-edge density at 250 m (Fig. 3b). Finally, pest suppression rates were lower in landscapes with grassland patches made up of complex shapes (i.e., higher when grassland shapes were more compact at 250 m; Fig. 3c), suggesting that grasslands with simpler shapes may be more effective reservoirs of natural enemies.

Pest suppression in Wisconsin responded to surrounding landscapes differently from that in Michigan. First, it was higher when landscapes contained higher field density at 250 m (Figs. 3f–g). A higher field density indicates smaller field sizes, which is in line with recent evidence that decreasing crop field sizes can benefit within-field biodiversity and the provision of ecosystem services such as pest suppression (Fahrig et al., 2015; Sirami et al., 2019). Second, pest suppression was higher when landscapes contained grassland patches with a larger core area, also at a scale of 250 m. Large grassland patches may provide better habitat for taxa that favor core habitat and then spill over into other habitat patches. Overall, the important configuration metrics and respective models that predict pest suppression were diverse and varied between the two states. We suspect that these differences are due to the two states having rather distinct physical geographies, farming practices, and landscape structures. For example, the landscapes we investigated differed strongly between the two states in terms of amount of grassland (MI: 10.01 ± 22.06 %; WI: 32.18 ± 15.42 %) and forest (MI: 34.09 ± 22.12 %; WI: 13.90 ± 15.38 %).

This illustrates the importance of region-specific landscape contexts

in predicting how landscape heterogeneity affects natural enemy communities and the provision of pest suppression services.

4.4. Conclusions and management implications

Our results add to a body of knowledge that could inform the design of agricultural landscapes to maximize biodiversity and ecosystem services (Geertsema et al., 2016; Landis, 2016). The adoption of bioenergy cropping systems in many regions, including the Midwest U.S., is expected to drive large-scale changes in landscape composition and configuration (Wright and Wimberly, 2013). Previous work in this system has indicated that the addition of perennial polycultures of biomass crops onto marginal lands has the highest potential to increase multiple ecosystem services (Robertson et al., 2017; Landis et al., 2018), while increasing the cover of annual bioenergy crops would likely have the opposite effect (Werling et al., 2014). In this study, we found evidence for the benefits of increased configurational heterogeneity; thus, the adoption of bioenergy cropping systems is an opportunity to reconfigure landscapes more favorably. Recent advances in yield mapping in combination with remotely-sensed data allow farmers to identify portions of crop fields that consistently underperform in terms of yield and account for the greatest amount of nitrogen loss from Midwestern cropping systems (Basso et al., 2019). Implementing precision conservation practices on consistently low yielding portions of annual crop fields has the potential to increase both profitability and environmental outcomes (Capmourteres et al., 2018). Where low-yielding zones occur inside annual crop fields, conversion of these areas to perennial crops would enhance configurational complexity in agricultural landscapes, and benefit pest suppression services.

Despite our increasing knowledge of the effects of landscape configuration on pest suppression and other ecosystem services such as pollination (Isaacs and Kirk, 2010; Ekroos et al., 2016), we still know little about the mechanisms that drive these patterns. Additional research that focuses on manipulative experiments to test mechanistic hypotheses is needed to establish these relationships. In addition, landscape structure is likely to affect several ecosystem services simultaneously. Future studies could test how suites of ecosystem services – including pest suppression, pollination, denitrification, and others – are affected by changes in landscape configuration (Haberman and Bennett, 2019).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to

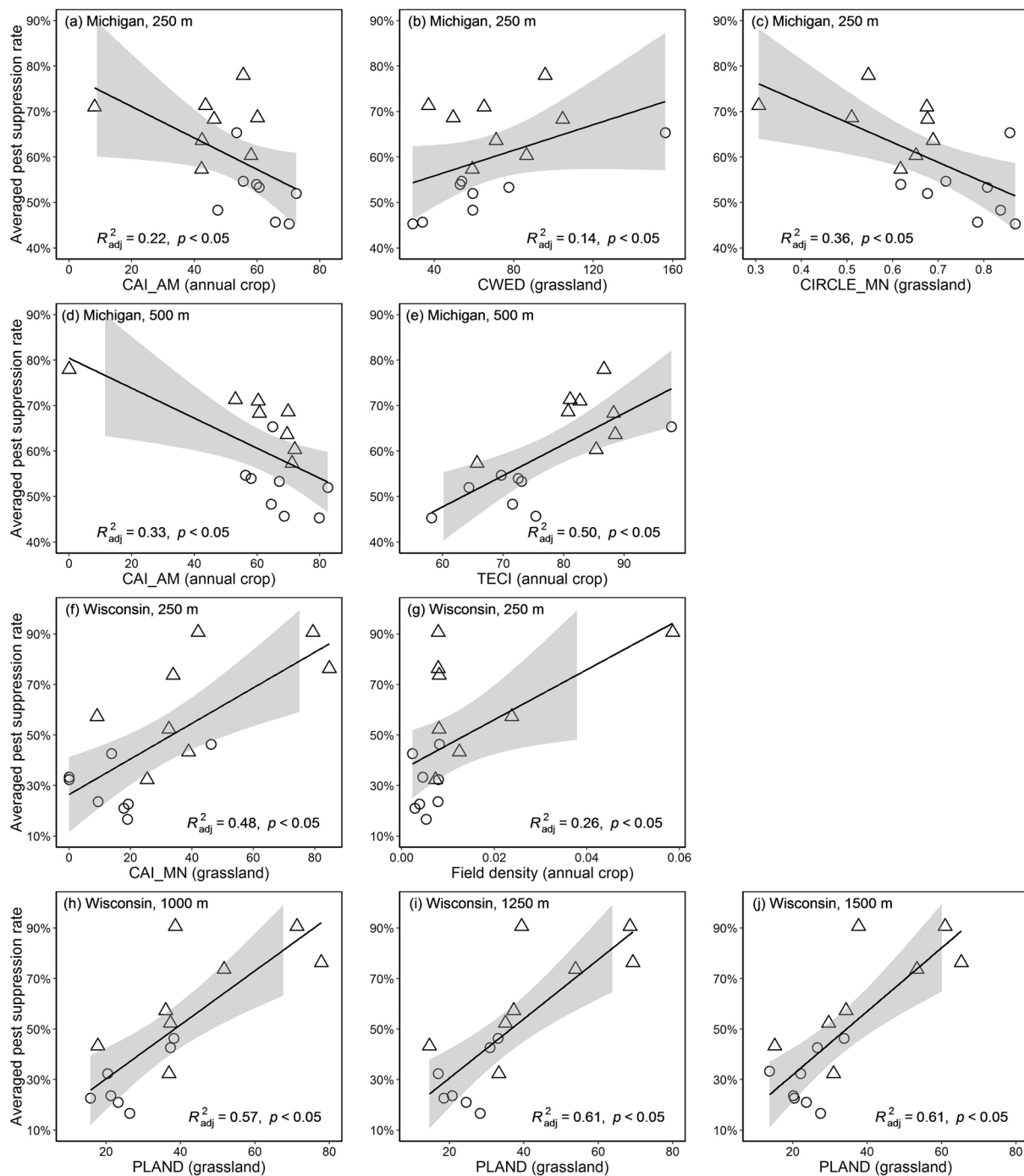


Fig. 3. The Linear regressions of pest suppression and important landscape metrics in the final models (Tables 3–4). The solid line represents the regression line, the shaded area denotes 95 % confidence interval, dots in circle represent corn fields and triangle for grassland. The land cover types were added in parentheses after metric abbreviations. Metric abbreviations: CAIAM – area-weighted mean core area index, CAIMN – mean core area index, CIRCLEMN – mean related circumscribing circle index, CWED – contrast-weighted edge density, PLAND – percentage of land cover types, TECI – total edge contrast index.

influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.107085>.

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