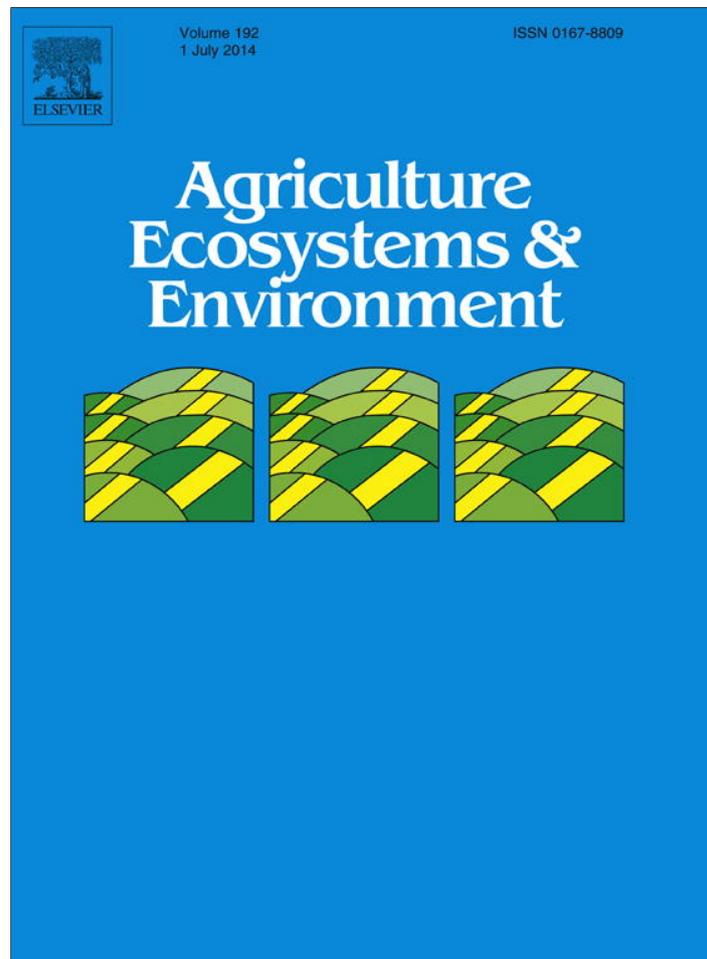


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Using hedgerows as model linkages to examine non-native plant patterns



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ABSTRACT

Non-native plant distribution and community composition, along with an array of environmental factors, were examined in 31 hedgerows, an archetypal class of conservation linkage, in the northern part of California's Central Valley. Row crop, orchard, and vineyard agriculture dominate this area, and hedgerows have been popular for well over a decade. Seven groups of explanatory data (environmental, historical, landscape, management, spatial, structural, and biological) were used to determine the strongest correlates of spatially-explicit patterns of non-native plants within and immediately surrounding hedgerows. In 15 hedgerows, a field experiment tested the effect of degree of shading on non-native plant diversity and cover.

The results of this project showed that: (1) Hedgerows harbored a flora of non-native plants richer than the surrounding matrix and that invasion was spatially structured. (2) Edges were more invaded than interiors in terms of both non-native richness and percent cover. (3) Differences between edges and interiors were likely due to shade. (4) Community-level patterns were most strongly correlated with the environmental, historical, structural and/or landscape explanatory variables. (5) Matrix types affected the non-native plant community in different ways, and the direction of those relationships was influenced by plant dispersal mode.

This research revealed that hedgerows can function as barriers to plant invasion if managed appropriately. Results supported the idea that these features may function as invasion conduits but perhaps not as major sources for invasion into agricultural fields. Specific recommendations are made regarding key factors (management, site, and species characteristics) influencing invasion, with particular emphasis on the role of shade, matrix characteristics, and plant dispersal mode.

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1. Introduction

Conservation linkages, also known as habitat or wildlife corridors, are connective lands designed to allow native species (plants and animals) to move, thus negating some of the negative effects of pervasive habitat fragmentation and climate change (e.g., Hilty et al., 2006; Schippers et al., 2009; Beier, 2012). Agricultural hedgerows were chosen as the model linkages for this study because they embody basic structural characteristics of conservation linkages of particular interest (high perimeter: area ratio). Hedgerows are linear plantings or remnants of shrub or low tree species which run along edges of agricultural fields. They can provide or support ecosystem services (e.g., pollinator services) and native species habitat (Marshall and Moonen, 2002; Donald and

Evans, 2006; Roy and de Blois, 2008) and may also enhance landscape connectivity for native species (Sitzia, 2007; Schippers et al., 2009; Van Geert et al., 2010).

Conversely, because they are typically embedded in working landscapes, hedgerows can be a source of concern for many agriculturalists because of their potential to harbor economically harmful non-native plant species (Sosnoskie et al., 2007; De Cauwer et al., 2008; Brodt et al., 2009). Several studies have examined spatial and compositional distribution of non-native plants in field margins, hedgerows, and windbreaks and have found that these linear features can function as refugia for non-native plant species (Sosnoskie et al., 2007; Boutin et al., 2008; Liira et al., 2008; Petit et al., 2013). Deckers et al. (2008) detailed the potential conduit function of hedgerows by showing that an invasive tree species' movement through a hedgerow system is mediated through the perching behavior of its main dispersal agents, birds.

This research used a blend of observation and experimentation to examine potential major influences on non-native plant communities within the context of model landscape linkages, a novel

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approach. Data collection and analysis focused on key aspects of the matrix, linkage, and species ecology, essential elements for an evaluation of invasive plant patterns in linkages (Wilkerson, 2013). The specific research questions were:

1. Are there differences in non-native plant distribution patterns between the different spatial axes of the hedgerow (edge vs. interior and ends vs. middles)?
2. If such differences exist, are they attributable to differences in light availability?
3. How do differing matrix types and other site variables relate to non-native plant richness and abundance patterns within the hedgerow and the immediately adjacent matrix?
4. Do non-native plant patterns in hedgerows differ depending on dispersal mode?

2. Methods

California's Central Valley, a large, mostly flat valley that dominates the interior of the state, is a mosaic of agricultural fields and rangeland interspersed with restored or remnant natural habitat. Non-native plants are pervasive throughout the landscape, and hedgerows are well distributed throughout the northern part of the Valley. Private landowners, NGOs, and government agencies have actively encouraged agriculturalists to maintain or restore hedgerows with native woody and herbaceous species (Earnshaw, 2004; Brodt et al., 2009; Long and Anderson, 2010).

Thirty-one hedgerows were chosen for the descriptive study. Of those, 15 were used in the experimental shade study. Hedgerows were selected based on similarity of management methods and planted native species and also based on a diversity of ages, from just-planted to 15 years old. All fell within three contiguous counties (Yolo, Solano, and Colusa) that have similar topography and land use/land cover types, and most non-native plants were annual grasses or forbs. The entire agro-ecological study area was 1400 km². The selected hedgerows ran along active field and/or orchard edges and had a farm road on one side. They ranged between 2–7 m in width and 120–800 m in length. All the study hedgerows ended sharply in either agricultural fields, or more often, dirt roads.

Selected hedgerows had generally the same planted shrub and tree species, most commonly *Sambucus nigra*, *Heteromeles arbutifolia*, *Cercis occidentalis*, *Baccharis pilularis*, *Ceanothus* spp., and *Quercus lobata* and occasionally native grasses *Stipa pulchra*, *Elymus glaucus*, *Elymus triticoides*, and *Muhlenbergia rigens*. Site preparation and management of the hedgerows were largely similar, including tilling, pre-planting herbicide, weed removal, seasonal watering via drip lines, and continued weed management.

2.1. Data collection

In the height of the spring flowering season (mid April–early June) of 2009 and 2010, observational data was collected from 31 hedgerow sites. The sampling design differentiated between middle vs. ends and interior vs. edges (Appendix 1A). “Edge” was defined as the outer 1 m of a hedgerow and “interior” the center line of the planting, at least 2 m from either edge. There were no “interior” quadrats in narrow (<3 m wide) hedgerows. Hedgerows “ends” were clearly demarcated by the cessation of hedgerow plantings. Five sampling sites were delineated along evenly spaced portions of each hedgerow. At each sampling site, a 10 m-long transect and a 1 m² quadrat imbedded within the transect were surveyed, and the frequency and aerial percent cover, respectively, of all native and non-native plant species was recorded. Fifteen transects and quadrats were surveyed for each of the 15 wider

hedgerows, and five transects and quadrats for each of the 16 narrower ones. All focal species were non-native to California and usually to North America and are referred to only as non-native because not all have been classified as invasive by local evaluation sources (e.g., Cal-IPC, 2006).

Data was also collected at three matrix sampling sites: the two ends and the midpoint of the hedgerow (Appendix 1A). All species' frequencies were recorded along transects perpendicular to the hedgerow up to 27 m into the matrix (e.g., if the hedgerow ran N-S, matrix transects ran E-W). At each of the two end collection areas, additional transects were run to capture that edge type (e.g., if the hedgerow ran N-S, these transects would also run N-S.) For baseline data, six hedgerows were located that had been planted the winter prior to data collection (referred to as 0-year-old hedgerows). Presence–absence data was collected in the same way as described below (5 sampling sites with 10 m transects).

Explanatory data were grouped into seven categories (Table 1) and were chosen based on the research questions above and their usefulness for land managers, as well as on similar multivariate plant community analyses (e.g., Deckers et al., 2004; Hyvönen et al., 2005; Bassa et al., 2011). Historical and management data were collected via surveys sent to each grower about the hedgerow(s) on their property. Soil environmental data came from SoilWeb, an online tool using U.S. Department of Agriculture and National Council for the Soil Studies soil survey data (<http://casoilresource.lawr.ucdavis.edu/soilweb/>). Landscape, structural, and biological variables were collected with vegetation data. Definitions for all matrix land-use types are included in Appendix 1B. To account for spatial autocorrelation, spatial variables were derived from a cubic trend surface regression equation based on *x* and *y* coordinates: $z = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$ (Borcard et al., 1992).

Each non-native plant species was placed into one or more dispersal mode categories (cf. Cal-IPC, 2006; DiTomaso and Healy, 2007; Hintze et al., 2013). Because many species had more than one major mode of dispersal, wind vs. animal/bird vs. water vs. gravity-dispersed species could not be compared in one analysis.

2.2. Experimental set-up

To complement the observational study and delve more into the mechanics of this spatial phenomenon, a shading study was designed to test the direct effects of shade on non-native plant diversity and cover. Three mesh weights of shade cloth made of black knitted polypropylene were chosen to create different light levels that resembled levels found within existing hedgerows. Light level data was measured using a PAR (photosynthetically active radiation) ceptometer which measures the portion of the light spectrum that plants use for photosynthesis. All light measurements under the shade cloths and within hedgerows were made between hours of 13:00 and 15:00 within a three-week period in early winter. Light levels beneath the 90% cloth (meant to block 90% of sunlight) were closest to the mean light level found in the interiors of mature hedgerows (40 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The 60% (285 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and 30% (660 $\mu\text{mol m}^{-2} \text{s}^{-1}$) cloths spanned the range of light levels found along the edges of mature and within the interior of younger (narrow) hedgerows. Based on the results from preliminary analysis, it was hypothesized that the 90% and 60% shade cloths would decrease the diversity and cover of non-native plants whereas 30% shade would actually increase those metrics through a facilitative effect (e.g., Baumeister and Callaway, 2006; Semchenko et al., 2012).

In November 2011, after the first heavy rain of the 2011–2012 “rain year”, shade cloth-covered sample plots were erected in 15 hedgerows where observational data had previously been

Table 1
All explanatory variables used in CCA and pCCA for observational non-native plant patterns within hedgerows. All variables are grouped into seven explanatory groups. Each variable was either coded as a dummy variable (0/1) if categorical or as a continuous variable.

Explanatory variable group	Variables	Abbreviation	Type of variable	Description
Environmental	Alfisol	Alf	0/1	Soil type
	Vertisol	Vert	0/1	
	Mollisol	Moll	0/1	
	Entisol	Ent	0/1	
	Inceptisol	Incept	0/1	
	Elevation	Elev	continuous	Elevation of site (m)
History	Age	Age	continuous	Years since planting
	Crop-history	Crophist	0/1	Land use history of hedgerow site
	Unused-history	Unuhist	0/1	
	Edge-history	Edgehist	0/1	
	Tilling prep	Tillprep	0/1	Types of pre-planting site preparation
	Herbicide prep	Herbprep	0/1	
Other prep	Othprep	0/1		
Management	2 years or less water	2yrwater	0/1	Watering regime
	More 2 years of water	more2wat	0/1	
	2–3 years maintenance	3yrmaint	0/1	Weed maintenance
	Continual maintenance	contmaint	0/1	
	Herbicide use	herbicide	0/1	
Structure	Length	length	continuous	Length of hedgerow (m)
	E-W	EW	0/1	Orientation of hedgerow
	N-S	NS	0/1	
	Other	Othorient	0/1	
	Narrow	Narrow	0/1	Width class of hedgerow
	Wide	Wide	0/1	
Landscape	Grassland	Grass	0/1	Matrix type
	Ditch	Ditch	0/1	
	Edge	Edge	0/1	
	Row crop	Rowcrop	0/1	
	Orchard	Orch	0/1	
	Vineyard	Vine	0/1	Paved road directly adjacent to hedgerow
	Slough	Slough	0/1	
	Paved road	Pavedrd	0/1	
	No. hedges 50 m	Hedge50m	continuous	
No. hedges 100 m	Hedge100m	continuous	Other hedges in proximity	
No. hedges 200 m	Hedge200m	continuous		
Biological	Bush	Natbush	continuous	Percent cover within sampling unit
	Tree	Nattree	continuous	
	Native grass	Natgrass	continuous	
	Native forb	Natforb	continuous	
Spatial	9 in total, not all listed		continuous	Variables from trend surface regression equation

collected. The hedgerows were selected to span an even spread of age. In each hedgerow, six 1.5 m × 1.5 m shade cloths frames were installed, two replicates of each shade level, set 0.5 m above the ground via wooden stakes. Each experimental plot was situated in gaps of at least 2 m width between planted bushes. To allow for a full germinating and growing season, shade experiments were maintained until May 2012. Data were then collected on species-specific aerial percent cover under the central 1 m² of the cloth. Six 1 m² cover quadrats in unshaded blocks within the hedgerow were used as controls.

2.3. Statistical analysis

To determine how the spatial axes of the hedgerow impacted non-native species pattern, linear mixed model were used with the spatial axes as a fixed effect nested within hedgerow name (i.e. location), a random factor. Non-native species data was grouped into grasses, forbs, and then all species combined. For the shade experiment, the non-native abundance and cover data also was analyzed using a linear mixed model with hedgerow age, position (middle vs. end), and shade cloth level as fixed effects nested within hedgerow identity, a random effect. For the non-native plant data collected in the matrices, non-parametric analyses were used to

evaluate relationships between non-native richness and cover and the explanatory variables, and distance from hedgerow was added as an explanatory variable. All analyses were conducted using JMP 9.0.0 (2012).

To quantitatively determine the roles of matrix and other explanatory groups in determining non-native species patterns, iterations of indirect and direct gradient ordination analyses were conducted (Leps and Smilauer, 2003). All multivariate ordination analyses used the statistical package CANOCO for Windows 4.5 (ter Braak and Smilauer, 2002). Species in only one hedgerow (>5% of sites) were excluded from all data analysis due to the sensitivity of canonical analysis to rare species (ter Braak and Smilauer, 2002; Leps and Smilauer, 2003), and remaining rarer species were down-weighted. Preliminary analyses, using Detrended Correspondence Analysis (DCA) for both presence–absence and cover (log-transformed), produced gradients of more than 4 SD for Axis 1, indicating the appropriateness of a unimodal model (Canonical Correspondence Analysis, CCA) (ter Braak and Smilauer, 2002).

The first ordination analysis stage consisted of an overall CCA on species composition, presence–absence and cover separately, with data constrained by all explanatory variables with spatial axis variables as covariables. Due to high multi-collinearity between variables, several variables were excluded from further analysis

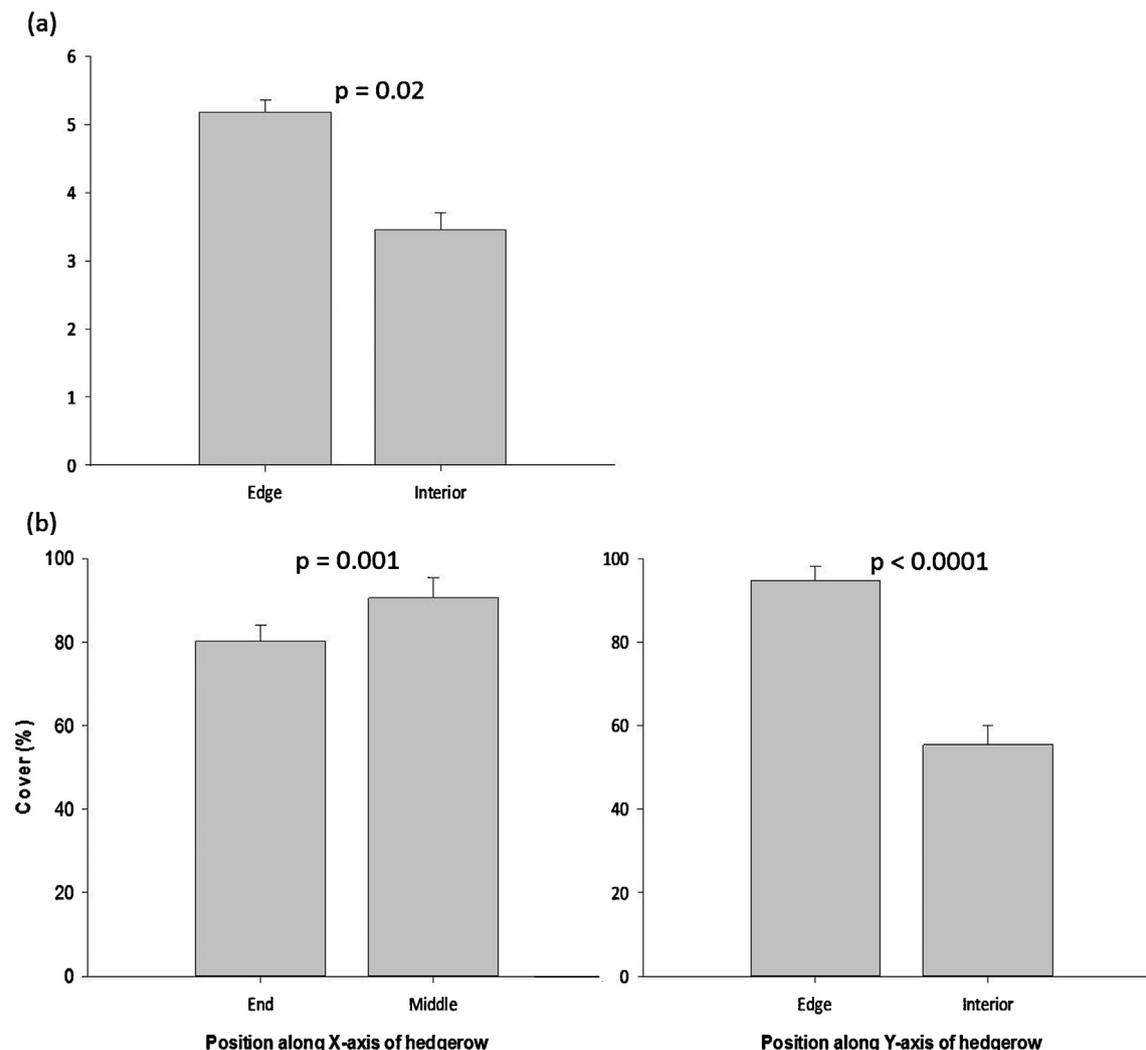


Fig. 1. Spatially-explicit differences between non-native plant (a) richness and (b) cover along the X- and Y-axes of the hedgerows. Error bars are standard error (SE).

based on their Variance Inflation Factors (ter Braak and Smilauer, 2002). With the reduced set of explanatory variables, the stepwise forward selection option was selected. Only variables with a p -value of 0.01 or less were retained as significant (Okland and Eilertsen, 1994). The significance of Axis 1 and each explanatory variable was tested with a Monte-Carlo permutation test (199 unrestricted permutations) (ter Braak and Smilauer, 2002).

To quantify the effect of each group of significant explanatory variables on non-native species, the second stage in the ordination analysis consisted of a variance partitioning approach using partial CCA (pCCA) (Borcard et al., 1992; Okland and Eilertsen, 1994; Cushman and Wallin, 2002). For variance partitioning, the overall analysis was conducted in two steps: (1) CCAs of species composition data constrained by each group of explanatory variables and (2) pCCAs of the species data constrained by each group but using the other explanatory groups as covariables.

In the last stage of the ordination analysis, results from the pCCA analyses were used to identify the specific ways in which individual variables related to non-native plants. Individual explanatory variables were related to overall non-native richness and cover using non-parametric statistics in JMP 9.0.0 (Spearman rank correlation for continuous variables, Chi-square for categorical and Wilcoxon/Mann-Whitney for binary). All significant variables identified in the pCCA analysis within the environmental, historical, structural, and landscape explanatory groups were included.

Edge and interior were included as covariables as they were the most consistently significant spatial axis effect found in the spatial component analysis.

For a comparative study, native plant species richness and cover patterns were also analyzed in relation to the explanatory variables. There were too few non-planted native species to run a full ordination analysis as detailed above. However, non-parametric tests were run for individual relationships between native plant richness and cover and the variables within the key explanatory groups identified by the non-native species pCCA. Only overall patterns herbaceous non-planted native species (14 species in total) were analyzed.

To determine how dispersal mode interacts with the observed non-native plant patterns, non-parametric statistical tests described above were re-run using only the landscape variables (i.e. matrix types and presence of nearby hedgerows). This time, non-native species data was grouped into four dispersal groups: wind, water, animal/bird, and gravity. Only richness data was analyzed.

3. Results

One hundred and six herbaceous species were counted across the 31 hedgerows, 63% of which were categorized as non-natives – 19 grasses and 48 forbs (see Appendix 2A). Only 16 of those

non-native species present had a 25% or more occurrence probability in any given hedgerow (see Appendix 2B). On average, 82% of the species richness and 86% of the cover in the herbaceous community consisted of non-native species. Most non-natives were closely associated with California's agricultural systems and are species that are highly disturbance-tolerant and adapted to open habitats.

In the 0-year-old hedgerows (baseline data), there were a total of 26 non-native species across six sampled sites. Of those 26 species, all but one belonged to the 16 most commonly occurring species in the older hedgerows (see Appendix 2C). However, two of the sites were both organic (no pesticides) and not actively managed (along fallow grasslands). When those two sites were excluded, there were only 18 non-native species in the 0-year-old hedgerows, and these species did not include several of the most prevalent invasive grasses and forbs found in the older hedgerows.

3.1. Differences between hedgerow spatial components

Edges had 24.5% mean higher non-native richness and 40.8% higher cover than interiors ($df = 1$, $F = 1.92$, $p = 0.02$ and $df = 1$, $F = 5.45$, $p < 0.0001$, respectively) (Fig. 1) and middles had 14.7% greater non-native plant cover than ends ($df = 1$, $F = 2.01$, $p = 0.001$) (Fig. 1). Sampling sizes were unequal within the spatial axes but even when sampling size was corrected, the patterns described above were still statistically significant. Both of the spatially explicit patterns for cover were driven by grasses and not by forbs. There were no significant differences in overall species richness between hedgerow ends and middles ($df = 1$, $F = 1.10$, $p = 0.33$).

3.2. Direct effects of manipulated shade

The highest level of experimental shading reduced non-native species diversity and abundance by 72–74% ($F = 30.98$, $p < 0.0001$ and $F = 87.91$, $p < 0.0001$) (Fig. 2). The effect of the intermediate level of shading was either between the highest and lowest/control (Fig. 2a) or was not significantly different from the lowest shading level or the control sites (Fig. 2b). Thatch (dead plant material) and bare ground were 61–77% higher under the highest (90%) shading ($F = 37.64$, $p < 0.001$ and $F = 41.17$, $p < 0.0001$).

3.3. Patterns and key explanatory variables for cover in matrix

Far fewer non-native species were found in the matrix than in the hedgerows. Only 16 non-native species were found in the matrix habitats, 11 of which were among the most commonly found species in the hedgerows (see Appendix 2D).

Examining non-native patterns in the matrix confirmed that non-native plant cover dropped sharply as distance away from the hedgerow into the adjacent matrix habitat increased ($\chi^2 = 80.15$, $p < 0.0001$). While the cover declined continually up to 30 m away from the hedgerow, there was a noticeable decrease between 5 and 10 m away (mean non-native cover declining from 41% to 35%) and a sharper drop between 10 and 15 m (from 35% to 27%). Orientation was important for non-native cover ($\chi^2 = 19.10$, $p = 0.0003$), particularly for grasses. Matrix habitats along the north sides of hedgerows had greater non-native cover than did matrix habitats along other sides. Matrix type was also an important correlating factor ($\chi^2 = 240.17$, $p < 0.0001$). The strongest difference in total non-native cover was between grassland, vineyard, edge and ditch habitats (greater cover) vs. slough and row crop habitats (lower cover). For matrix type definitions, see Appendix 1B.

3.4. Key explanatory variables for cover, richness and diversity

For the presence–absence CCA (from transect data), 27 statistically-significant variables were kept in the final analysis

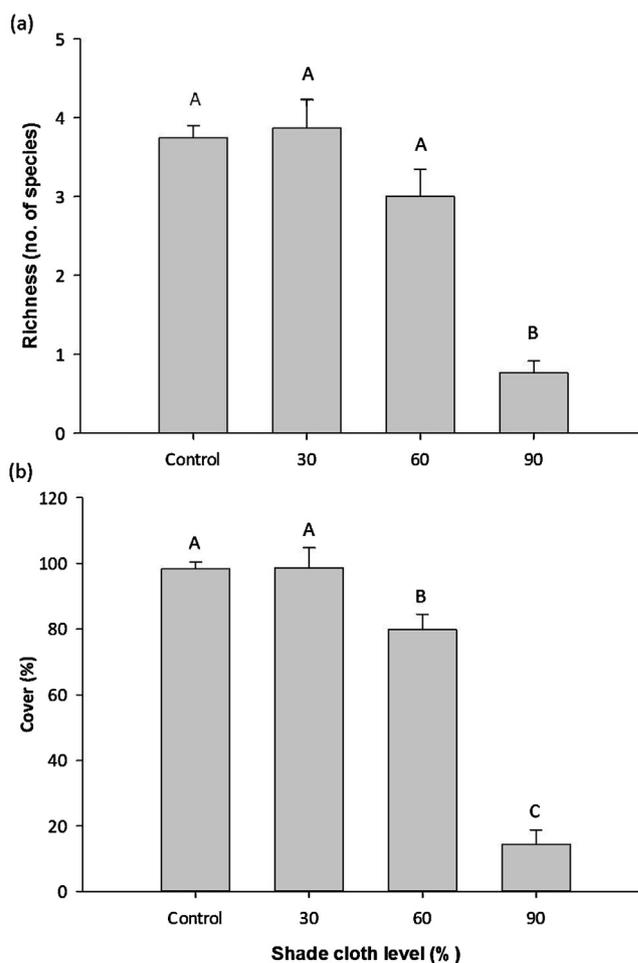


Fig. 2. Effect of shade cloth on non-native (a) richness and (b) cover. Letters represent significantly different Tukey groups ($p < 0.05$). Error bars are standard error (SE).

with at least one variable in each of the seven explanatory groups (see Appendix 3A). All of the remaining variables were statistically significant ($p = 0.01$ or less) as were all of the axes (Monte-Carlo permutation test). The CCA captured 35.5% of the datasets' variation (see Appendix 3A). Axis 1 explained 5.8% of variation in species composition and 16.1% of species–environment relations. The addition of Axis 2 explained nearly twice as much variation.

When analyzing species cover patterns, 34 statistically-significant explanatory variables were kept in the CCA capturing 33.3% of the dataset's variation (see Appendix 3B). Twenty-eight variables were statistically significant ($p = 0.01$ or less) as were all of the axes. Axis 1 explained 5.9% of species variation and 17.7% of species–environmental variation; Axis 2 added a similar amount of variation explanation.

Despite that idiosyncrasy, the pCCA's revealed several strong patterns in richness and cover data. For richness, the environmental, structural and landscape variable groups explained the largest portions of the data variation (5.8–6.5% each, see Appendix 3C). For cover, environmental and landscape groups also explained large portions but the historical variables were more descriptive than structural data (4.9–13.8% each, see Appendix 3D).

For the environmental explanatory group, there was a significant positive relationship with alfisol and vertisol soil types, and overall cover whereas both richness and cover were negatively correlated with entisol and inceptisol soil types (Table 2). Width and orientation were both significantly correlated with richness, although length was not, despite its significance in the CCA and

Table 2

Relationship of all individual explanatory variables with total herbaceous, grass, and forb non-native species richness and cover. Only the four explanatory groups that explained the most species variation in pCCA analyses for richness and cover, separately, were examined.

Explanatory group	Variable	Relationship with total herbaceous non-native species richness	Non-native total species cover	Non-native grass richness	Non-native grass cover	Non-native forb richness	Non-native forb cover
Environmental	Alfisol	ns	Z = -2.76**	Z = 0.01**	Z = -4.79**	ns	ns
	Vertisol	ns	Z = 3.56**	Z = -2.40*	Z = 2.26*	ns	Z = 2.13*
	Entisol	Z = -2.86**	Z = -2.25*	ns	ns	Z = -3.94***	Z = -3.07**
	Inceptisol	Z = -2.74**	Z = -4.28*	Z = -3.12**	Z = -3.09**	ns	Z = -5.75***
Historical	Age		$\rho = -0.16^*$		ns		$\rho = -0.16^*$
	Tilling prep		Z = -3.19**		ns		Z = -4.99***
	Other prep		Z = 3.12**		Z = 4.35***		
Structural	Orientation	$\chi^2 = 26.86^{***}$		$\chi^2 = 26.72^{***}$		$\chi^2 = 29.03^{***}$	
	Width	Z = 4.98***		ns		Z = 6.71***	
Landscape	Grassland	Z = 3.10**	ns	Z = 4.62***	Z = 2.02*	ns	ns
	Edge	ns	ns	ns	ns	Z = 3.27**	ns
	Row crop	ns	ns	Z = -2.25*	Z = -3.10*	Z = 2.07*	ns
	Orchard	Z = -2.10*	ns	ns	ns	Z = -3.00**	ns
	Vineyard	ns	Z = -2.17*	ns	ns	ns	Z = -3.22**
	Slough	Z = 2.16*	Z = 2.00*	ns	Z = 1.91*	Z = 3.54**	Z = 2.94**
	Paved road	ns	Z = -1.91*	ns	ns	ns	ns
	No. hedges w/i 50 m	ns	$\rho = -0.10^*$	ns	ns	ns	ns
	No. hedges w/i 200 m	ns	ns	ns	ns	$\rho = 0.13^*$	ns

ns, not significant.

Z-values are from Wilcoxon/Mann–Whitney tests, χ^2 values are from Kruskal–Wallis Chi-squared tests, and ρ values are from Spearman rank correlations.

* $p \leq 0.05$.

** $p \leq 0.01$.

*** $p < 0.001$.

pCCA. Narrower hedgerows had higher non-native richness than wider ones whereas hedgerows with an N-S orientation had highest richness (Table 2). Age was negatively correlated with non-native cover (Table 2). Of the three preparation types, only herbicide preparation was not significantly correlated with cover (Table 2). Both tilling preparation and other common preparations were correlated with greater non-native cover.

The relationships between cover patterns and landscape variables differed slightly from those between richness and landscape variables (Fig. 3 and Table 2). For richness, hedgerows adjacent to grasslands and sloughs had more non-natives and that pattern was driven by grasses and then forbs, respectively. When adjacent to orchards, hedgerows had lower non-native richness, due to forbs. In hedgerows adjacent to row crops, grass richness increased whereas forb richness decreased resulting in a non-significant pattern for non-natives overall. For cover, hedgerows adjacent to sloughs were again significantly correlated with an increase in total non-native cover, driven by forbs. Vineyards were associated with lower total non-native cover, driven by forb patterns. Paved roads were actually negatively correlated with non-native cover, an unexpected finding. For cover, the presence of more hedgerows within a 50 m radius was correlated with a decrease in non-native cover.

The response type and directions listed above for the individual ANOVAs were not different between the two spatial axes (i.e. between edge vs. interior or end vs. middle). However, for richness, several of the focal variables were more often significantly associated with edges than interiors. For cover, edges and ends often drove the significant associations with focal variables.

3.5. Effect of key explanatory variables on native plant richness and cover

For native richness, only the relationships with variables within the environmental, structural and landscape explanatory groups

were analyzed as those were the key ones identified in the non-native richness pCCA. There were fewer significant relationships between native species and explanatory variables (for full details, see Appendix 4). Many of the significant relationships were in the same direction as they were with the non-native plants, and there were a few relationships that were significant for native plants that had been non-significant for non-natives. The one instance that patterns were opposite was that native cover was positively correlated with the presence of paved roads ($Z = 4.10, p < 0.0001$) whereas non-native cover decreased when adjacent to paved roads.

3.6. Dispersal mode effects

The type and direction of the patterns between different dispersal groups along the spatial axes was the same or non-significant. Wind-dispersed species richness was positively associated with hedgerows that had a grassland matrix ($Z = 2.91, p = 0.004$; Fig. 4a). Bird/animal-dispersed species were positively associated with grassland matrices but negatively associated with orchard matrices ($Z = 4.05, p < 0.0001$ and $Z = -1.96, p = 0.05$, respectively; Fig. 4b). Water-dispersed species were positively associated with the presence of sloughs ($Z = 2.38, p = 0.02$; Fig. 4c). A greater number of hedgerows within 50 m was positively associated with water-dispersed species richness ($\rho = 0.12, p = 0.03$) whereas gravity-dispersed species were negatively associated with more hedgerows at that radius ($\rho = -0.14, p = 0.01$). At greater distances (hedges within 100 m), only water-dispersed species were related, positively, to greater numbers of nearby hedgerows ($\rho = 0.14, p = 0.01$).

4. Discussion

As hypothesized, non-native plant diversity and abundance dropped sharply in hedgerow interiors despite hedgerows'

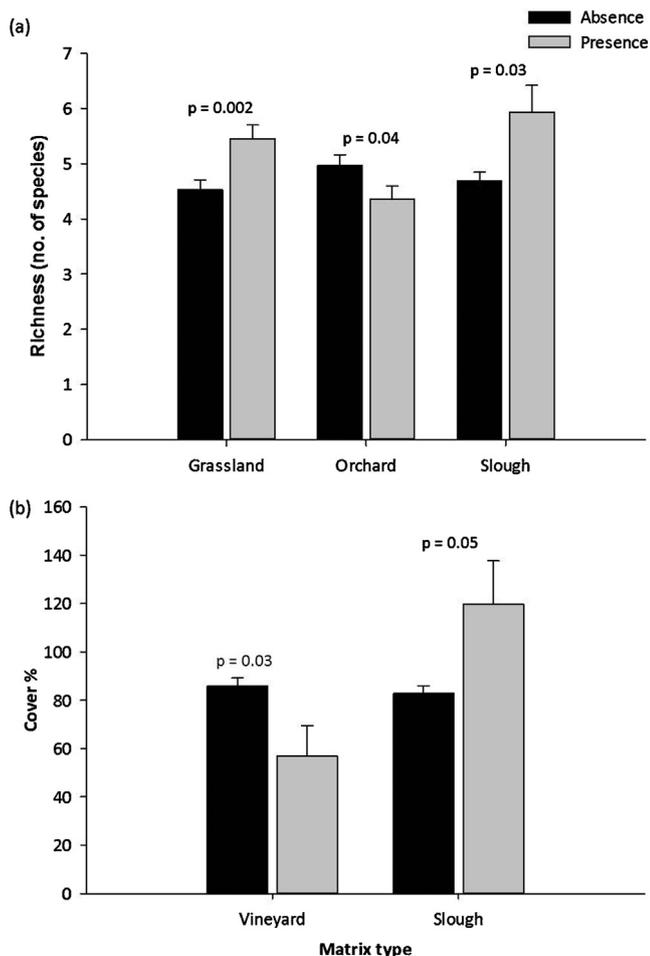


Fig. 3. Relation between matrix types and total non-native plant (a) richness and (b) cover. Only matrix types that had statistically significant relationship to non-natives are shown. Error bars are standard error (SE).

narrowness. The lower non-native abundance at the ends of hedgerows seems counter-intuitive because hedgerow ends inherently had more edge and often more vehicular traffic than the middles. While it was hypothesized that the full sun exposure common at hedgerow ends might explain the lower abundance of non-natives, the shade experiment did not show any facilitative effect of low-level shade.

This study indicates that hedgerows could function as barriers to plant invasion if their structure throughout the length and width resembled that of a hedgerow interior. Deep shade (90% level) had a strong negative impact on non-native richness and abundance which helps explain why these narrow features had strong edge and interior differences. The differences between edge and interior, despite the fact that their narrowness (at most 7 m across) might have suggested that they would be “all edge,” actually indicate that hedgerows could be designed or managed to function as complete barriers to plant invasion, disrupting non-native plant connectivity in the broader landscape. Greater inclusion of fast-growing, dense native shrub species or double rows of shrub plantings could achieve that ideal barrier function.

While this study was not designed to assess movement of non-native plants, certain results indicate that hedgerows have the potential to act as conduits for invasion. In this focal area, hedgerows oriented along the north–south axis had greater non-native diversity than ones running along the east–west axis.

This was supported by the observation that non-native richness in the matrix was higher in crops, orchards, or grasslands that ran along east and north sides of hedgerows. These patterns may have been due to prevalent wind directions in this area; hedgerows might be acting as “drift-fence” corridors (Fried et al., 2005; Wilkerson, 2013). Proximity to other hedgerows should be another consideration for hedgerow design, especially when designing for connectivity conservation. Connectivity between various landscape elements (e.g., hedgerows or matrix types) can influence non-native plant diversity (Petit et al., 2013). There were strong correlations between higher water-dispersed species richness and greater numbers of nearby hedgerows. Non-native plants with that dispersal syndrome may be more easily transported in denser clusters of hedgerows, an important connectivity consideration.

With respect to the concern that agriculturalists have regarding weed ingress into their crops, hedgerows did not seem to function as major sources of plant invasion into the matrix. Species richness declined abruptly when moving away from a hedgerow into the agricultural matrix. De Cauwer et al. (2008) similarly found that the risk of “contaminating” the field crop with weeds from a planted herbaceous field margin was limited to a distance of just a few meters away from sown grass strips into the crop. This finding is supported by other studies on weed ingress (Blumenthal and Jordan, 2001; Cordeau et al., 2011). Actively managing field margins by planting hedgerows or sowing wildflowers or native grasses may strongly decrease non-native seed exchange between margins and matrix (Petit et al., 2013). Concerns over non-natives in hedgerows may thus focus more on their effect on conservation goals rather than agricultural ones.

Other studies that examined plant species composition in hedgerows found that increased land-use intensity in the agricultural matrix can skew vegetation composition toward invasive, annual species (Schmitz et al., 2007; Bassa et al., 2011). However, this study found that non-native plant richness and/or cover actually decreased when adjacent to some heavily-used matrix types, namely orchards, row crops, and vineyards. The matrices associated with greater invasion overall (grasslands and sloughs) had low structural profiles and may have been less heavily managed than vineyards and orchards. Grasslands and sloughs also likely provided greater habitat for birds and animals (i.e. more dispersers) than other matrix types. Indeed, wind- and bird/animal-dispersed species were positively associated with grassland matrices.

The other explanatory variables explored in this study will also help better design, site, plant, and manage hedgerows to minimize invasion. Managers and owners should consider soil properties when choosing hedgerow sites as this study indicated that certain soil types might facilitate or adversely affect non-native plant communities. Key historical variables involved prepping methods, and the results indicated that the very methods meant to diminish plant invasion, namely tilling and disking or surface scraping (“other” preparation) were associated with higher levels of non-natives. These common weed management methods can actually facilitate plant invasion by uncovering dormant seed banks or creating easily invaded habitats (Recasens et al., 2005; Sosnoskie et al., 2007). However, volunteer native and non-native species were affected in similar ways by the explanatory variables examined in this research.

Considerable deliberate thought has gone into the subject of minimizing invasion in hedgerows and other field edge native plantings, especially in this study’s region (Earnshaw, 2004; Long and Anderson, 2010), yet land managers and agriculturalists can take into greater consideration specific hedgerow, matrix, and non-native species characteristics to minimize both the incursion and proliferation of non-native plants.

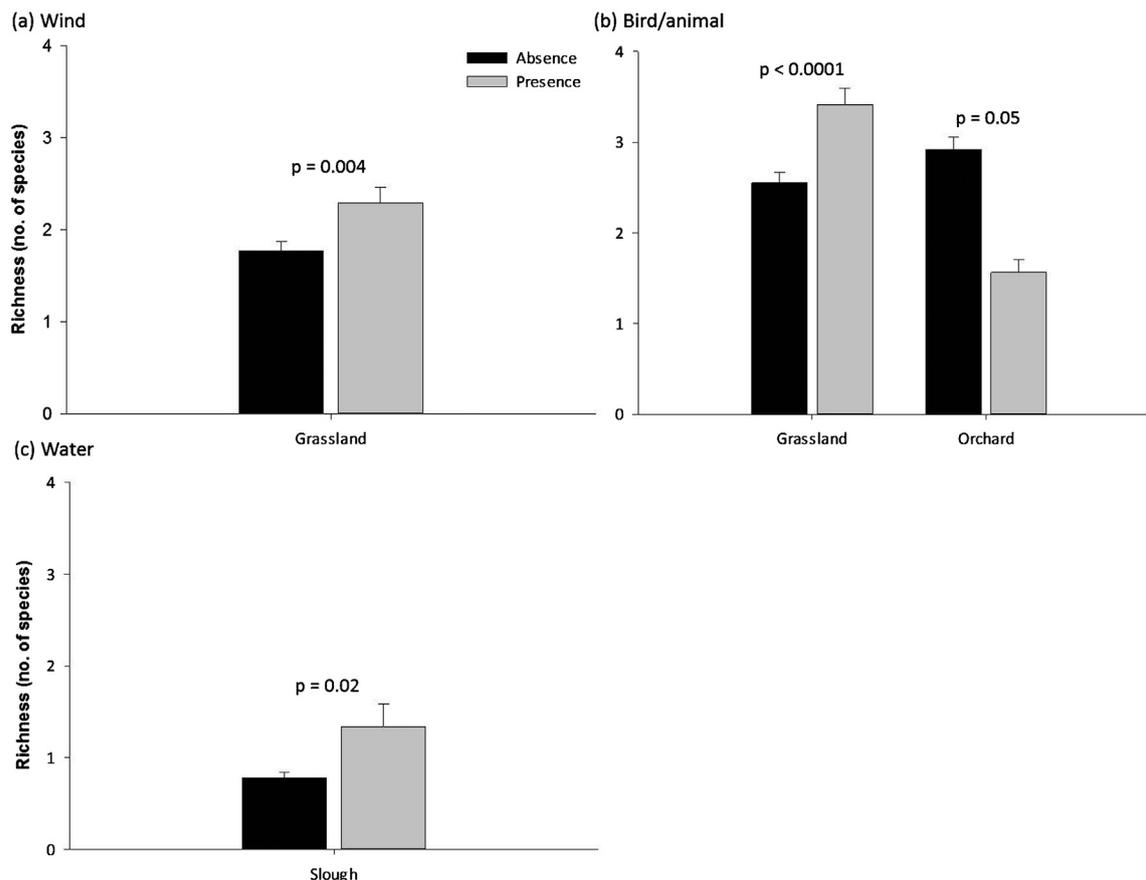


Fig. 4. Relation between matrix types and differently-dispersed non-native plant groups: (a) wind-dispersed, (b) bird/animal-dispersed, and (c) water-dispersed. Only matrix types that had a statistically significant relationship with dispersal groups are shown. Error bars are standard error (SE).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2014.03.044>.

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