Initial species pattern affects invasion resistance in experimental grassland plots

Kathryn A. Yurkonis, Brian J. Wilsey & Kirk A. Moloney

Keywords: Andropogon gerardii; Conspecific aggregation; Monarda fistulosa; Ratibida pinnata; Schizachyrium scoparium; Spatial pattern; Tallgrass prairie

Abstract

Question: Does the spatial patterning of plant species affect plant community dynamics in ways that are independent of effects attributable to species richness or abundances? Does the initial species pattern affect subsequent diversity and invasion in a perennial grassland system?

Location: Field experiment, Iowa State University Horticultural Research Station, Ames, Iowa, USA.

Methods: Experimental plots (4 m²) were planted with seedlings of four grassland species arranged into increasingly larger groups (patches) of conspecific individuals while controlling plot-scale richness and evenness. Available light (photosynthetically active radiation; PAR) at the soil surface was measured each month for three growing seasons after planting. Species’ relative abundances were quantified via point-intercept sampling within each plot at the end of each growing season.

Results: In the three growing seasons after planting, planted species richness and evenness (plot scale) did not vary among plots planted with different species patterns. However, early in the second growing season more light reached the soil surface in plots with initially larger conspecific patches. Invader abundance was also consistently higher in plots planted with initially larger conspecific patches.

Conclusions: Our findings support the hypothesis that invasion resistance increases as communities become more heterogeneous at fine scales and suggest that within-plot heterogeneity should be considered as an additional factor when assessing invasion resistance in perennial plant communities.

Introduction

Communities differ from one another in the number (species richness) and abundances (evenness) of constituent species and both of these attributes affect aspects of diversity maintenance and local invasion (reviewed by Hooper et al. 2005). Communities may also differ in the ways in which conspecific and heterospecific individuals are arranged with respect to one another (Thorhallsdottir 1990; Herben et al. 1993; Purves & Law 2002). Such species patterning may be driven by exogenous (i.e. resource heterogeneity) or endogenous (i.e. localized dispersal and competition) factors (Bolker & Pacala 1997). When species pattern varies among communities established in an otherwise consistent resource environment, this pattern may independently affect diversity maintenance and invasibility (Tilman & Kareiva 1997; Murrell et al. 2001; De Boeck et al. 2006). Although empirical studies have shown that varying endogenous species patterns affects the outcome of competitive interactions among neighbouring individuals in annual systems (Norris et al. 2001; Stoll & Prati 2001; Monzeglio & Stoll 2005) and coral assemblages (Idjadi & Karlson 2007; Hart & Marshall 2009), the effects of altering the spatial pattern of resident species have not been empirically tested in species-rich perennial grasslands, where many studies of the controls affecting diversity maintenance and invasibility have occurred.

Varying fine-scale (within-plot) species patterns while maintaining the same coarser-scale (plot) species richness and evenness may affect plot-scale responses via two pathways. First, varying initial species patterns may affect
subsequent plot-scale species composition and diversity by altering intraspecific interactions among establishing seedlings. Establishing seedlings typically interact with one another over small distances (often at centimetre scales) and are, thus, most strongly influenced by seedlings in their immediate vicinity (Murrell & Law 2003; Vogt et al. 2010). Altering species patterns by increasing the size of patches of conspecific seedlings while maintaining species abundances at the plot scale will increase the frequency of intraspecific interactions among neighbours. If the establishing species differ in their inter- and intraspecific competitive abilities (in magnitude or distance over which interactions occur), then increasing the frequency at which individuals experience intraspecific interactions could affect the plot-scale performance of a focal species (Murrell & Law 2003). At least initially, large conspecific patches may prevent, or at least delay, competitive exclusion of species more strongly affected by interspecific competition than intraspecific competition (weak competitors), and result in reduced abundances of species more strongly affected by intraspecific competition than interspecific competition (strong competitors) (Stoll & Prati 2001; Idjadi & Karlson 2007; Hart & Marshall 2009). However, it is important to note that initial interactions among seedlings are later affected as mature plants disperse locally, interact at different distances (neighbourhood size) (Bolker & Pacala 1999; Law & Dieckmann 2000; Bolker et al. 2003; Racz & Karsai 2006; Murrell 2010), and interact with the exogenous environment. Consequently, it is unclear if effects of species patterning during seedling establishment would persist as communities became more established.

The effects of initial species pattern on subsequent species composition have been empirically tested in a few cases. Stoll & Prati (2001) manipulated the spatial patterning of annual species and found that arranging species into large conspecific patches facilitates persistence of weaker competitors. These findings were further supported by studies of the effects of species patterning in tomato and barnyard grass (Norris et al. 2001), and most recently for corals (Idjadi & Karlson 2007; Hart & Marshall 2009). Hart & Marshall (2009) manipulated the patterns of four coral species and found that some species came to occupy more area when conspecific individuals were grouped into four large patches than when they were randomly arranged. While conducted over short time periods, these experimental results generally support the hypothesis that when species differ in their relative intra- and interspecific competitive abilities, altering fine-scale species patterning while maintaining coarser-scale richness and evenness may affect diversity in the long term. Despite a long-standing interest in how pattern influences process in perennial systems, this hypothesis has not been tested in species-rich, perennial plant communities (Bolker & Pacala 1999; Bolker et al. 2003).

Varying fine-scale species patterns may also affect invasion at the plot scale (Bergelson 1990b; Olsen et al. 2005; De Boeck et al. 2006). Establishment in an open site is generally determined by the density and identity of neighbours around the site (Fowler 1988; Bergelson et al. 1993; Milbau et al. 2007) and is typically higher in sites surrounded by individuals of a few species than in sites surrounded by individuals of several different species because resources in low-richness sites are not as completely consumed (Grubb 1977; Naem et al. 2000; Kennedy et al. 2002). Altering species patterns within a plot may affect the availability of such low-richness sites for invasion. Plots with species arranged into large conspecific patches contain more low-richness sites and, therefore, may be less resistant to invasion than similar plots containing smaller conspecific patches.

In grasslands, light availability often affects invasion success, and establishment is more likely to be successful in locations where more light reaches the soil surface (Milbau et al. 2005; Losure et al. 2007). Thus, light availability at the soil surface may be used as a proxy for understanding potential establishment sites for invaders. Because light use should be lower in low-richness than high-richness sites (Spehn et al. 2000; De Boeck et al. 2006), mean light use at the plot scale should be lower in plots with fewer, larger conspecific patches than in plots with more, smaller conspecific patches. If invaders are responding to the light environment, lower mean light use should be correlated with higher subsequent invader abundance.

In addition to affecting the resource environment for invasion, species patterns may also affect how an invader spreads through an area once established (Bergelson et al. 1993; With 2002). If similar unoccupied sites are located near the establishment site, as would occur when species occur in large conspecific patches, an invader may more quickly colonize those sites than if similar unoccupied sites were further away, as would occur when species occur in small, conspecific patches. Thus, invaders may be more abundant when species occur in large conspecific patches than if the resident species occurred in smaller conspecific patches because plant arrangement facilitates dispersal of established invaders.

Only a few studies have considered effects of species patterns on invasion. Bergelson (1990a) manipulated arrangements of Poa annua and found invasion by two annual weeds was higher when seeds were planted in large conspecific patches than when seeds were randomly arranged. This effect was due to inhibition of invader establishment by litter. Olsen et al. (2005) found that crop planting pattern affected weed recruitment, such that weeds were less abundant when wheat was planted in a
uniform pattern versus in rows. However, we are not aware of any studies that have manipulated pattern in more species-rich communities to test this effect on coarser-scale invasion.

In this study we manipulated species patterns while maintaining plot-scale species richness and evenness to test the effects of altering endogenous species patterns on evenness and invasion. We test the hypotheses that: (1) evenness; (2) light use; and (3) invader abundance will vary among plots with conspecific individuals arranged into increasingly fewer and larger patches. Our findings contribute to our understanding of how endogenous species pattern may affect subsequent community dynamics and are applicable in grassland systems where communities are established in consistent resource environments (i.e. experimental studies and grassland restorations).

Methods

In May 2006, we planted 24 plots (2 m × 2 m with 2-m spacing) with seedlings of four native, tallgrass prairie species in a completely randomized design. Species were planted into increasingly larger conspecific patches among plots, but diversity was kept constant at the plot scale by planting seedlings of all four species in equal abundances in each plot. Plots were planted at the Iowa State University Horticulture Research Station (Ames, IA; Mean annual temperature: 8.8 °C; mean annual precipitation: 837 mm). Vegetation and soils were homogenous across the site prior to planting. The site was originally dominated by Bromus inermis Leyss., established on Clarion fine loam soil derived from glacial till. The area was treated with glyphosate herbicide and disked prior to planting to further homogenize the soil environment prior to planting.

Seedlings of two C4 bunch grasses [Andropogon gerardii Vitman and Schizachyrium scoparium (Michx.) Nash] and two forbs [Ratibida pinnata (Vent.) Barnh. and Monarda fistulosa L.] that are common in local remnant grasslands (Martin et al. 2005) were grown in a greenhouse to ca. equal biomass in a 3:1 sterilized soil:sand mix. A. gerardii did not grow as well as the other species and, as a result, seedling biomass differed among species at planting ($F_{1,20} = 4.72, P = 0.0119$). A. gerardii was smaller than M. fistulosa ($0.038 ± 0.0007$ g vs $0.117 ± 0.029$ g, $F_{1,20} = 6.49, P = 0.0192$) and S. scoparium ($0.151 ± 0.030$ g, $F_{1,20} = 13.09, P = 0.0017$). Seedlings were planted into bare soil in a grid (8 × 8 plants m⁻²) with equal spacing among seedlings (12.5 cm). The seedling density (64 plants m⁻²) mimicked typical plant densities in local remnant prairies (Losure et al. 2007).

Seedlings were planted following a species array generated for each plot with the program QRULE (Gardner & Urban 2007). QRULE is a map-generating program that creates a grid of items based on the desired grid size, the desired proportion of each item in the grid and the input $H$-value, a parameter that affects the likelihood that adjoining grid locations are assigned to the same item. $H$ varies from 0 to 1 (Gardner 1999) and arrays created with a lower $H$-value are less likely to have adjoining grid locations assigned to the same item than those created with a higher $H$-value. Due to the way in which arrays are generated, species arrays created with the same $H$-value vary from one another. Species arrays were produced by asking $n$ to create a $16 × 16$ array of four species in equal proportions and with an $H$-value of 0.0 ($n = 8$), 0.5 ($n = 8$) or 1.0 ($n = 8$). This approach generated a series of arrays where conspecific individuals were arranged into increasingly larger groups (patches) (Fig. 1). For our purposes, a patch was defined as a group of individuals of the same species occupying neighbouring locations in the planting grid, where neighbouring individuals could be directly adjacent to or on a diagonal to one another (Turner et al. 2001) (Fig. 1). Due to the way in which species were assigned to locations in the arrays, A. gerardii individuals were more likely to be surrounded by M. fistulosa individuals than S. scoparium individuals (Type of neighbour, $F_{2,63} = 8.00, P < 0.01$). This difference was more pronounced in arrays with larger conspecific patches ($H = 1.0$) than in arrays with smaller conspecific patches ($H = 0.0$) (Type of neighbour × $H$-value, $F_{6,63} = 81.72, P < 0.01$), as individuals in large conspecific patch arrays were most likely to be surrounded by conspecific neighbours.

Seedlings were watered upon planting and seedlings that died were replanted in early Jun 2006. During the first growing season, plots were weeded to ensure seedling establishment. In subsequent years, all volunteers were allowed to persist to test hypotheses about invasion resistance.

In late summer 2007, 2008 and 2009, species abundances were quantified with point-intercept sampling.

![Fig. 1. Representative planting arrays for plots planted with four common grassland species (each shaded differently) arranged into increasingly larger patches across all species. Each pixel represents one individual (256 plot-1) and a patch consists of a group of similarly shaded adjoining pixels. Planting arrays were created with one of three $H$-values in the program QRULE. (a) $H = 0.0$; area-weighted mean patch size = 0.16 m², (b) $H = 0.50$; area-weighted mean patch size = 0.40 m², and (c) $H = 1.00$; area-weighted mean patch size = 0.68 m².](image-url)
(Jonasson 1988) over the entire plot. In 2007 and 2008, a 1-m² sample frame (1.5-m tall) containing a mobile crossbar with holes drilled at 10-cm intervals was placed over each quadrant of the plot. The frame edges were marked at 10-cm intervals so that the crossbar could be positioned to create a grid of 81 (9 × 9) potential sample points spaced 10-cm apart. Metal pins were dropped vertically through the vegetation at every other point in this grid (40 pins m⁻²). The number of times each species i was touched by a pin was recorded. Relative abundance of species i was calculated by dividing the total touches for species i in a plot (summed across all quadrants) by the total touches in the plot for each sample year. These data were used to calculate evenness \([\frac{1}{S} \sum \frac{p_i}{D_i}\] of the planted species at the plot scale, where \(D = \sum p_i^2\), \(p_i = \) relative abundance of species \(i\), and \(S = \) species richness (Wilsey et al. 2005). At the end of the 2008 growing season, above-ground biomass and litter were removed from each plot in a separate study to assess the utility of using point-intercept sampling to measure biomass-based diversity in these plots. Because it was impossible to recreate the pattern of ramets pre-harvest, harvested biomass was not returned to the plots. In 2009, the same sampling method was used, but the number of sample points was reduced to 20 random locations in each quadrant to accelerate sampling. An analysis of the 2008 data indicated that reducing the number of sample points to 20 would not affect estimates of plot-scale diversity and invasion. The difference between evenness and invader abundance calculated from a sub-sample of the points in 2008 (20 randomly selected from each quadrant) and the full sample sampling effort was not significantly different from zero (Evenness: \(t = 0.4045\), \(P > 0.05\); Invader abundance: \(t = 0.2341\), \(P > 0.05\)).

To test for effects of species pattern on the light environment, we calculated the proportion of available photosynthetically active radiation (PAR) at the soil surface within each plot. In 2007 and 2008, above- and below-canopy (soil surface) PAR was measured each month (May to Aug) at midday (10:00–14:00 CST). Above- and below-canopy PAR was measured in four locations in each plot at each sample date. For each measurement, a Decagon AccuPAR LP-80 Ceptometer (Pullman, WA, USA) was inserted along a diagonal line oriented toward the centre of each quadrant of a plot and a Li-Cor external point sensor (Lincoln, NA, USA) was held above the vegetation. The Ceptometer simultaneously recorded PAR at the external point sensor and at each of 80 sensors arranged along a 90-cm probe. The proportion of available PAR at the soil surface was calculated by dividing the mean soil surface PAR for each quadrant by the associated above-canopy PAR. The proportion of PAR at the soil surface for a plot was the mean of the quadrant values.

### Data analysis

Species patterning was quantified by calculating the area-weighted mean patch size \((\sum S_k^2 / \sum S_k\); hereafter patch size) across all of the patches in the species array for each plot, where \(S_k\) is the size of the kth patch in m². This metric describes the mean area occupied by a group of conspecific individuals when plots were planted. Computing mean patch size in this way reduces the effects of small patch sizes (e.g. containing one or two individuals) on the overall mean (Turner et al. 2001). Large values indicate that conspecific individuals were arranged in fewer groups covering a larger area at planting than in plots with small values.

Figure 2 shows the distribution of the patch size variable for arrays created with each H-value and across all arrays before and after transformation to improve normality. Note that the transformed patch size variable differed among the array categories \((F_{2,21} = 22.8, P < 0.001\), and arrays created with different H-values could have similar mean patch sizes. Plot evenness and invader abundance were consistently similar among array categories (results not shown), indicating that the conditions for generating the patch size gradient did not affect these responses per se.

---

![Fig. 2. Box and whisker plots of the untransformed and natural log-transformed area-weighted mean patch size variable used as a measure of initial species patterning. Means are indicated by a dashed line and outliers are indicated with circles. Separate plots are shown for arrays created with each H-value in QRULE. Percentiles (5th and 95th) could not be calculated for each array category because of the small sample size \((n = 8)\) for each. The distribution of the transformed variable is not significantly different from normal.](image-url)
To test for effects of species patterning on evenness and invader abundance in 2007, 2008 and 2009, we used a repeated-measures ANOVA, with patch size at planting as a continuous effect (proc glim, SAS 9.2, SAS Institute). For these and subsequent analyses, patch size was natural log-transformed and invader abundances arcsine square-root transformed to improve normality.

Finally, monthly mean (natural log-transformed) light (soil surface PAR) was analysed in separate repeated measures ANOVA (SAS 9.2) for 2007 and 2008, with patch size as a continuous effect. Correlation between monthly soil surface PAR and subsequent invader abundance was tested with Pearson correlation with a Bonferroni adjustment for multiple comparisons.

Results

All four planted species persisted in all of the plots over the course of the study. Plot-scale evenness at planting (based on the number of individuals of each species) was similar among plots in the three H-value categories ($F_{2,21} = 0.25, P > 0.05$; mean $= 0.995 \pm 0.0009$) and did not vary with initial patch size ($R^2 = 0.04, F_{1,22} = 0.89, P > 0.05$). At the neighbourhood scale (based on the eight neighbours surrounding ten randomly sampled individuals from each plot), evenness was not correlated with initial patch size ($r = 0.15, P > 0.05$), but species richness was negatively correlated ($r = -0.83, P < 0.001$) and the probability of having conspecific neighbours was positively correlated ($r = 0.80, P < 0.001$) with initial patch size.

Plot-scale evenness at planting was not maintained after the initial planting (Table 1), and plot-scale evenness differed among subsequent sample years ($F_{2,44} = 4.42, P < 0.05$). The effect of initial patch size on evenness also varied among years (Year $\times$ Size: $F_{2,44} = 3.25, P < 0.05$). Plot-scale evenness was marginally lower in plots planted with larger initial patches in 2007 ($R^2 = 0.13; F_{1,22} = 3.34, P = 0.08$), but not in 2008 ($R^2 = 0.01; F_{1,22} = 0.29, P > 0.05$) or 2009 ($R^2 = 0.19; F_{1,22} = 1.80, P > 0.05$).

Invader abundance differed among years ($F_{2,44} = 69.15, P < 0.001$), increasing over time (Table 1). By 2009, invaders dominated the space in the plots, occupying ca. half (52 ± 19%) of the locations originally occupied with a native individual. Invader abundance was positively related to initial patch size in all years, but the slope of the relationship was greater in 2009 than in 2007 and 2008 ($F_{2,44} = 5.01, P < 0.05$; Fig. 3). The most abundant invaders included Bromus inermis, Securigera varia (L.) Lassen and Conyza canadensis (L.) Cronquist, all of which were present at the site prior to this study.

Light environment

Soil surface PAR was similar among months in 2007 ($F_{1,66} = 0.39, P > 0.05$), ranging from 3% of PAR in Jun to 8% of PAR in Jul 2007 (Table 1). The relationship between soil surface PAR and initial patch size differed among months (Month $\times$ Size $F_{3,66} = 2.21, P = 0.13$). Soil surface PAR was positively (marginally) related to initial patch size in May, positively related to initial patch size in Jun, negatively (marginally) related to initial patch size in Jul...

Table 1 Mean plot-scale responses ±1 SE across all plots in an experiment assessing effects of altering species patterning on plot-scale responses. Light is given as proportion of photosynthetically active radiation at the soil surface.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>2007</th>
<th>2008</th>
<th>2009</th>
</tr>
</thead>
<tbody>
<tr>
<td>Evenness</td>
<td>0.72 ± 0.025</td>
<td>0.81 ± 0.023</td>
<td>0.70 ± 0.023</td>
</tr>
<tr>
<td>Invader relative</td>
<td>0.02 ± 0.004</td>
<td>0.21 ± 0.030</td>
<td>0.55 ± 0.053</td>
</tr>
<tr>
<td>Abundance Light</td>
<td>0.042 ± 0.0082</td>
<td>0.178 ± 0.0099</td>
<td>–</td>
</tr>
<tr>
<td>May</td>
<td>0.034 ± 0.0041</td>
<td>0.021 ± 0.0028</td>
<td>–</td>
</tr>
<tr>
<td>June</td>
<td>0.081 ± 0.0037</td>
<td>0.038 ± 0.0029</td>
<td>–</td>
</tr>
<tr>
<td>August</td>
<td>0.075 ± 0.0030</td>
<td>0.044 ± 0.0031</td>
<td>–</td>
</tr>
</tbody>
</table>

Fig. 3. Effect of initial patch size on invader relative abundance in 2007 (note different invader abundance scale), 2008, and 2009 from point intercept sampling of the above-ground biomass in each plot. *P < 0.05.
Effects of species pattern on grassland invasion

K.A. Yurkonis et al.

Discussion

We used a plot-based field experiment to test the hypothesis that endogenous species patterning in a grassland system affects planted species interactions and non-planted species invasion. After four growing seasons, at least some individuals of all of the planted species were still present in all of the plots. Planted species evenness was not related to initial species pattern early in the experiment, when non-planted (invader) species abundances were low, or in subsequent growing seasons when invaders were more abundant. In all years, invader abundance was higher in plots that started with larger conspecific patches. At least over the short-term, initial species pattern appears to affect perennial grassland communities under realistic invasion pressure via effects on invasion resistance, as opposed to effects on planted species interactions.

We did not find evidence that species patterning at establishment affects plot-scale evenness in this system. Several factors could have contributed to this outcome. First, this result could arise if planted species were similar in their inter- and intraspecific competitive abilities and the distances over which inter- and intraspecific interactions took place were equivalent (Murrell & Law 2003). At least in some cases, effects of inter- and intraspecific interactions on seedling establishment in grasslands are similar (reviewed in Goldberg & Barton 1992; Milbau et al. 2007; Vogt et al. 2010). It also appears that, for at least some species, inter- and intraspecific interaction distances are equivalent (Vogt et al. 2010). Second, the effects of initially increased interspecific interactions among establishing seedlings may have been offset by changes in the distances over which individuals interacted (neighbourhood size) as they grew. At planting, the effect of a single seedling on others was likely limited to scales on the order of 5–15 cm (Milbau et al. 2005; Vogt et al. 2010). As seedlings grew, their physical extent and, thus, their neighbourhood size and the number of individuals they interacted with increased. Because plots were similar in composition at larger scales, established individuals may have experienced similar levels of intraspecific interactions among the established study plots.

Finally, the degree to which individuals interacted with conspecific neighbours may have also changed as ramets of the established individuals dispersed into new locations. Several theoretical studies have demonstrated that endogenous heterogeneity can facilitate species co-existence when resident species vary in the extent to which they are affected by inter- and intraspecific competition and their abilities to disperse (via ramets or seeds) locally (Bolker & Pacala 1999; Law & Dieckmann 2000; Bolker et al. 2003; Racz & Karsai 2006; Murrell 2010). In our study, ramets of the planted individuals established in the spaces among the planting locations, altering the neighbourhood composition surrounding the planted individuals. This effect was most striking for *M. fistulosa*, a highly clonal forb. Such local dispersal altered the initial species patterns and likely changed the proportion of intraspecific interactions that resident individuals experienced.

It is unclear if, and to what extent, similarities in inter- and intraspecific competition and changes in the scale and types of interaction affected species composition in these communities. We do not have data concerning inter- and intraspecific competition coefficients and interaction distances for the species in this study, nor do we know how these interactions changed as the planted seedlings established and dispersed through the study plots. Future studies need to investigate if local dispersal and changes in the scale of species interactions over time alter inter- and intraspecific interactions established with the initial species patterns.

Although there was no evenness response, invasion was consistently related to species patterning at establishment.

Fig. 4. Relationship between initial patch size and the proportion of PAR (photosynthetically active radiation) reaching the soil surface in Jun 2007. *P < 0.05, **P < 0.10.

and unrelated to patch size in Aug (Fig. 4). In 2008, soil surface PAR differed among months ($F_{1,22} = 16.29$, $P < 0.001$), ranging from 17% of PAR in May to 2% of PAR in Jun (Table 1), and was not related to initial patch size ($F_{1,22} = 0.16$, $P > 0.05$; Month x Size $F_{3,66} = 1.48$, $P > 0.05$). Finally, yearly invader abundances were not correlated ($P > 0.0025$ for all correlations) with soil surface PAR in the same (2007, 2008) or previous growing seasons (2008, 2009).
Non-planted species were consistently more abundant in plots with initially large species patches than in plots with initially small patches. Our results support the hypothesis that resistance to invasion increases as communities become more heterogeneous at fine scales (Davies et al. 2005; Melbourne et al. 2007). However, it is unclear what mechanisms contributed to this response. Invasion was not related to variation in light environment established with the treatments. It is possible that the scale for measuring light was inappropriate, but this is not likely as previous studies found relationships between light and invasion using the same sampling methodology as in this system (Losure et al. 2007). Invasion may have been related to the ease with which invaders dispersed through a plot once established (Bergelson et al. 1993; With 2002). Bergelson et al. (1993) assessed effects of gap size and distribution on invasion and found that a grassland invader spread more readily when available gaps for establishment were larger and closer together. In our study, locations bordered by the same planted species (spaced 12.5-cm apart) were more closely positioned in plots with larger initial patch sizes than in plots with smaller patch sizes (Fig. 1). Thus, invasion may have increased with initial patch size, as invaders could more readily disperse into similar sites once established. To determine the mechanisms behind the effects of species pattern on invasion, future studies need to investigate how species patterns affect available resources for invaders and consider how initial species pattern affects where invaders establish and disperse once established.

In studying effects of species pattern on plot-scale responses, we must consider what aspects of the species pattern affect the responses of interest. Our study controlled two (richness and evenness) of the five major independent components of spatial pattern in landscape maps identified in Rüitters et al. (1995). We quantified effects of species pattern by assessing plot-scale responses to initial area-weighted mean patch size, which describes a third independent component of spatial pattern (perimeter-area measures) identified in Rüitters et al. (1995) and Gardner & Urban (2007). This area-based metric was used to understand the effects of arranging plants into large, conspecific patches, as often occurs in grassland restorations (Yurkonis et al. 2010). In the arrays (16 × 16 cells) used in this study, the patch size variable was correlated with additional measures that are considered independent in larger arrays in Rüitters et al. (1995) (average patch compaction) and Gardner & Urban (2007) (number of patches). Initial patch size was correlated with the average number of species surrounding any given individual, the proportion of conspecific individuals surrounding any given individual, and with metrics that describe the shape of patches of conspecific individuals (Yurkonis unpubl. data). Although these metrics (i.e. neighbourhood richness, proportion of conspecific individuals and patch shape) may describe ecologically meaningful interactions (Chesson & Neuhauser 2002), we were unable to directly test for their effects with the methods used to generate species arrays in this study. Studies that specifically manipulate such aspects of spatial pattern while holding others constant (i.e. altering patch shape while maintaining size) could provide a more mechanistic understanding of the effects of species pattern on plot-scale responses.

Our findings also have implications for how we view the effects of species patterning in managed and experimental communities established in consistent resource environments. If species are arranged in different ways as a community establishes (e.g. De Luis et al. 2008), then this pattern may affect future invasion, but not planted species interactions, in realistic communities with relatively homogeneous resources. In this sense, arranging species in restored communities into fewer, larger patches (Dickson & Busby 2009) may hinder restoration success because such arrangement may facilitate establishment of undesired species.

Conclusions

Connecting pattern and process in plant communities is challenging because in species-rich communities we cannot easily discern the degree to which individuals are affected by their neighbours. As a few other studies have done (Stoll & Prati 2001; Idjadi & Karlson 2007; Hart & Marshall 2009), we approach the relationship between pattern and process in communities by testing for the overall consequences of altering endogenous species pattern within a grassland community. In a perennial grassland system, it appears that initial species pattern may affect invasion resistance, but not planted species evenness or richness. Future studies need to separate effects of endogenous species pattern on planted species interactions from the effects on invasion resistance to assess if these findings are consistent in communities with less invasion pressure.

Acknowledgements

Many thanks to the Iowa State University Horticulture Station staff who helped to prepare and manage the site. A. Asche, A. Blong, A. Conner, T. Dickson, T. Moeller, J. Reynolds, J. Richter, C. Swenson, K. Wahl and S. Yurkonis assisted in planting and sampling the plots. F. I. Isbell provided valuable feedback throughout the project. Amy Symstad and two anonymous reviewers provided helpful comments on earlier drafts. This project was partially funded by the Iowa Department of Transportation Living Roadway Trust Fund and Prairie Biotic Research Inc.
References


