

Quantifying the influence of environmental texture on the rate of species turnover: evidence from two habitats

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Abstract The environmental texture hypothesis (ETH) proposes that the spatial geometry or texture of the environment influences the rate at which species are accumulated in space or time. Specifically, the ETH suggests that regions, and spatial scales, that exhibit a larger rate of environmental distance decay (DD) should exhibit more rapid rates of species turnover. The ETH should apply over any range of scales where the environment is driving species distributions. To examine the relevance of the ETH at local spatial scales, we tested for a positive relationship between the rate of change in soil chemical properties and vascular plant species composition in grassland and woodland habitats. We recorded presence–absence data along a 1.883 km transect in each habitat and estimated the rate of turnover and environmental DD for spatial lags of 1–41 m. We found that the soil environment explained spatial patterns of species composition more accurately in the grassland habitat compared to the woodland habitat. Consequently the rate of change in soil properties as a function of spatial distance was significantly positively correlated with

the rate of species turnover in the grassland but not the woodland. Our study suggests that one of the central premises of the ETH is relevant for local patterns of species turnover if the environment appears to influence species composition.

Keywords Crosstimbers · Distance decay · Euclidean variogram · Spatial dependence · Spatial autocorrelation · Tallgrass prairie

Introduction

Species composition varies spatially and reflects the combined influences of ecological and evolutionary processes (e.g., Nekola and White 1999; Buckley and Jetz 2008). Historically ecologists related variation in species composition (i.e., patterns of species turnover) almost entirely to the degree of environmental change between samples (e.g., Whittaker 1960). However, it was later recognized that spatial or temporal distance between samples, irrespective of environmental change, was positively correlated with the degree of species turnover (Nekola and White 1999). Legendre (1993) refers to these endogenously driven patterns of species turnover as false gradients of species composition. From a modeling standpoint, the importance of false gradients shifted the focus away from the environment and toward biological processes such as dispersal limitation and patterns of speciation (e.g., Hubbell 2001). The desire to develop

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unified theories of diversity based on relatively few underlying assumptions further directed efforts away from environmental filtering and toward understanding the drivers of inherent spatial autocorrelation in communities (see McGill 2010, for a review).

The environmental texture hypothesis (ETH) is one recent attempt to shift the debate back toward the relevance of environmental heterogeneity on patterns of species turnover (Palmer 2007). Specifically, the ETH suggests that the rate of species accumulation in a spatially explicit sampling scheme is positively influenced by the rate new environments are sampled (i.e., the texture or geometry of the environment influences the rate of species accumulation). The texture of the environment specifically refers to the spatial arrangement of continuous variation in the environment. This hypothesis was proposed as an explanation for the triphasic pattern of the species–area relationship (SAR). At its core the ETH is based upon an assumption that species have different environmental optima that determine where they occur on the landscape (e.g., Gauch and Whittaker 1972). A result of this assumption is that new species are expected to accumulate as new environmental conditions are sampled. Although many studies have recognized that the number of habitats sampled can be an important predictor of species richness (e.g., Rosenzweig 1995; Storch et al. 2003; Triantis et al. 2003), the ETH explicitly predicts a positive relationship between the rate of species accumulation and the rate new environmental conditions are sampled. In other words, if one wishes to understand how rapidly species turnover in space (not simply the magnitude of turnover) it is important to consider the spatial arrangement of the environment (not simply the amount of variability in the environment). In addition, the ETH makes predictions about how the spatial structure of environmental heterogeneity should change as a function of spatial scale. Specifically, the ETH predicts that at local and global scales the environment varies smoothly (i.e., low fractal dimension), which causes rapid accumulation of new species. At intermediate scales the environment is expected to be rougher (i.e., high fractal dimension) in which case new species accumulate more slowly (because many of the species in the region are encountered in the first few samples).

Although the ETH makes several specific predictions related to the triphasic SAR, testing these

predictions is difficult due to a lack of nested richness data which span from regional to global scales. However, testing whether the rate of species accumulation is determined by the rate of change in the environment is logistically feasible because this prediction should apply at any range of scales over which the environment influences species composition. Therefore, the purpose of our study was to test the ETH by examining whether there is a positive correspondence between the rates of environmental and compositional distance decay (DD).

A test of our hypothesis relies on the assumption that the environmental variables we include in the calculation of environmental DD are relevant predictors of species composition. Therefore, the objectives of our study were to: (1) identify relevant environmental variables explaining the spatial structure of species composition, (2) quantify the spatial texture of the environment and species composition, and (3) test for a positive correlation between the rate of environmental and community DD. We accomplished these objectives with data from a grassland and woodland habitat along two 1,883 m transects.

Methods

Study site

We conducted our study on The Nature Conservancy's Tallgrass Prairie Preserve between 36.73° and 36.90°N latitude, and 96.32° and 96.49°W longitude, in Osage County, Oklahoma (Allen et al. 2009). The vegetation of the preserve is composed of approximately 90% grasslands and 10% forests or woodlands. The grasslands are dominated by tallgrass prairie plant species such as *Andropogon gerardii*, *Sorghastrum nutans*, *Sporobolus compositus*, *Panicum virgatum*, and *Schizachyrium scoparium*. Short-grass prairie habitat occurs to a lesser extent on more xeric sites and is dominated by *Bouteloua* spp. The woodland habitats can be classified primarily as Cross Timbers, and they vary in structure from open and savanna like to rather dense closed canopy forests. The two most common tree species are *Quercus stellata* and *Q. marilandica*. The herbaceous layer of the woodlands commonly consists of *Parietaria pensylvanica*, *Oxalis violacea*, *Solidago ulmifolia*, *Andropogon gerardii*, and *Carex gravida*.

Sampling methods

An investigation of DD requires objectively sampled quadrats, otherwise the rate of turnover in species composition may simply reflect the investigators' sampling biases (Palmer 1993). However, in this study we were interested in examining if our hypothesis was robust to habitat type, and therefore several criteria were developed for a constrained objective placement of quadrats within the grassland and woodland habitats: transects were to be oriented in a cardinal direction, not run parallel to roads within a distance of 500 m (crossing was considered acceptable), not intersect any large bodies of water, be located in the bison management unit, and be located almost entirely within their respective habitats (grassland or woodland) according to aerial photography. With these criteria in mind two sets of UTM coordinates for the origin of each transect were selected from a USGS topographic map. Once the initial coordinates for each transect were set all other points were determined by the sampling grid. The grassland transect was oriented north–south, the woodland transect was oriented east–west, and the transects were separated by approximately 9 km. The grassland transect was oriented along a broad but gentle slope which terminated on a large plateau. In contrast, the woodland transect had more topographic heterogeneity as it crossed several dry creeks and rocky hillsides. The transects were sampled in different months due to differences in flowering phenology between the two habitats. The grassland transect was sampled over a 10-day period in early July 2006. The woodland transect was sampled over a 16-day period from May to early June of 2007. We do not expect the differences in the direction of orientation and sampling year will bias our results; however, the differences in topographic complexity may be relevant.

The two transects (grassland and woodland) were both composed of 200, 1 m² square quadrats arranged identically in 10 subtransects (Fig. 1). Each subtransect was separated by a distance of 117 m and covered an extent of 83 m. Within each subtransect, four quadrats were arranged continuously into five sections. Each section was separated by 17 m. Within each 1 m² quadrat we recorded the presence of every vascular plant species rooted within the quadrat, and collected three 10 cm soil cores at 0, 0.5, and 1 m

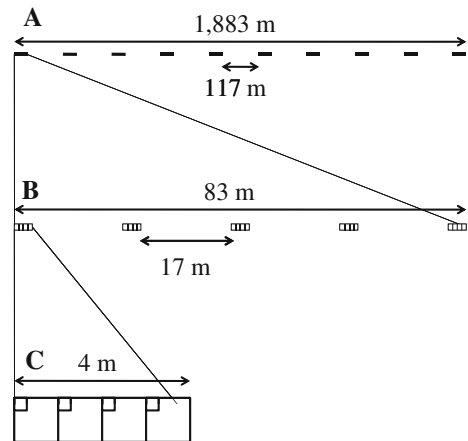


Fig. 1 Diagram of a transect (a), a subtransect (b), and a section (c). Each transect covered a total extent of 1,883 m and was composed of 10 subtransects which each covered an extent of 83 m. The gaps in the transects indicate areas that were not sampled, and the *unfilled squares* indicate where the vegetation and the soil environment was sampled. Each quadrat occupied an area of 1 m², and above-ground biomass was sampled in the 0.01 m² corner subquadrats

perpendicular to the transect. The three cores were aggregated into a single dry sample and sent to Brookside Labs (New Knoxville, OH) to be analyzed for the following soil chemical properties: Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, Al, and P. Samples were sieved to 2 mm prior to analysis, and soil chemical properties were estimated using a Mehlich 3 extractant on a ThermSpec 6500 ICP. We collected all non-woody above-ground biomass below 1.3 m from the corner of each quadrat in an area of 0.01 m² (Fig. 1). The wet and dry mass of the biomass were recorded in the lab. In the woodland, a spherical densiometer (Model A, Forest Densiometers, Bartlesville, OK) was used to estimate the number of grid cells on the densiometer that reflected canopy openings in four cardinal directions. We converted the four readings to percent canopy cover and averaged them. We recorded a single field measurement of slope and aspect using a clinometer and a compass, respectively, for each section at a distance of 10 m from the transect.

Analytical methods

Care must be taken when selecting the choice of metrics for quantifying community DD because different metrics of community (dis)similarity or species turnover carry different interpretations and

sometimes important subtleties (Wilson and Shmida 1984; Vellend 2001; Koleff et al. 2003). Ideally the metric chosen is mathematically intuitive and directly related to the hypothesis under consideration. The semivariance of the Euclidean community variogram (aka, the “variogram of complementarity”) provides one such metric for testing our hypothesis (Wagner 2003, 2004; Bacaro and Ricotta 2007):

$$\begin{aligned}\hat{\gamma}(h) &= \frac{1}{2n_h} \sum_{a,b|h_{ab} \approx h} \|\mathbf{X}_a - \mathbf{X}_b\|^2 \\ &= \sum_i^S \frac{1}{2n_h} \sum_{a,b|h_{ab} \approx h} (x_{ia} - x_{ib})^2,\end{aligned}\quad (1)$$

where $\hat{\gamma}(h)$ is the estimated semivariance at a spatial lag of h , n_h is the number of pairs of samples separated by a distance of h , and \mathbf{X}_a and \mathbf{X}_b are vectors of species abundance or presence/absence in samples a and b , respectively, which are separated by distance h . Note that decomposing Eq. 1 into its species specific components illustrates that the Euclidean community variogram does not consider pairwise covariances between species (i.e., interspecific associations) but simply the sum of the squared differences in the presence of species i in samples a and b across all S species. It is also worth noting that this metric is equivalent to Cody’s (1975) metric of β -diversity (β_c in Koleff et al. 2003).

Equation 1 provides both an intuitive metric of species turnover and a clear link to environmental models of species composition which are necessary for addressing the ETH. When based upon presence–absence data, the semivariance [$\hat{\gamma}(h)$] of the Euclidean community variogram is the expected number of unique species that will be encountered at a given distance from the focal quadrat (Wagner 2003, 2004). This aspect of the Euclidean community variogram makes it a good metric of turnover for our study because our hypothesis is tied to the relationship between the rate of encountering new environments and the rate of encountering new species as a function of distance. In addition, the semivariance can be thought of as a scale-dependent decomposition of the variance–covariance matrix associated with the “linear” ordination techniques: principal components analysis (PCA) and redundancy analysis (RDA). This is beneficial because it provides a direct link between the variance explained by a non-spatial model of the

species–environment relationship and the patterns of semivariance in the environment and species composition (Noy-Meir and Anderson 1971; Wagner 2004).

We used RDA to test whether variance in species composition was related to the environment (ter Braak and Šmilauer 2002; Palmer et al. 2008b). RDA was the natural choice of explanatory model in our study because the total variance of this analysis can be decomposed by the Euclidean variogram into its variance profile (Wagner 2004). The only environmental variables in our analysis were log transformed and then standardized soil chemical properties (ppm). This decision was made in part because other studies have demonstrated that soil chemical properties were strongly correlated with vascular plant composition at our study site (Palmer et al. 2003; Brokaw 2004). In addition, soil chemical properties provide a relatively precise measurement of spatial environmental heterogeneity. We standardized the soil properties by transforming them into z scores because two of the soil variables in the grassland displayed a few strong outliers, and standardization was able to decrease the influence of these variables on the PCA. As many of the soil variables are highly correlated with one another, we summarized the variance in the soil properties with the first four axes of a PCA on the soil variables from each habitat. Four axes were necessary to capture at least 80% of the variance in the soil variables within both habitats. The four orthogonal PCA axes for each habitat type were then used as explanatory variables in the RDA analyses. In addition, we performed a backward stepwise selection of soil properties that minimized the AIC value of the RDA analysis (not shown). These two methods resulted in the same qualitative results and therefore only the environment defined by the PCA axes will be discussed further. The amount of variance explained by the PCA soil axes was quantified as the ratio of the sum of constrained variance over the total variance (R_{RDA}^2). The unbiased or adjusted version of this statistic (R_{RDAadj}^2) was also calculated using Ezekiel’s formulation (Peres-Neto et al. 2006). It should be noted that because we are not factoring out the purely spatial component of compositional variance these estimates of variance explained are inflated (Legendre et al. 2005).

We tested if the RDAs explained significantly more variance in the species composition than

expected due to chance with constrained permutation tests. The permutation algorithm simultaneously carried out random reflections and rotations of the rows (or sites) of the raw site-by-species matrix (Palmer and van der Maarel 1995; ter Braak and Šmilauer 2002). These permutations were designed to maintain the spatial autocorrelation and interspecific associations between the samples but to nullify their spatial dependence (i.e., relationship between a sample and the environment). The permutation scheme was applied separately at three hierarchical scales that corresponded with three of the levels of our sampling design: quadrats, sections, and subtransects (see Fig. 2, for example, the permutation technique applied to subtransects). To isolate the importance of extent, quadrats were randomized within their particular section, sections were randomized within their particular subtransect, and so on.

The permutation algorithm can be thought of conceptually as first breaking the overall site-by-species matrix along its rows into the subunits of interest (e.g., sections). Next, there was a 50% chance that the order of the rows (sites) in a particular submatrix were reversed (the random reflection). Following White and Gilchrist's (2007) analogy, each submatrix was then rolled into a ring with the last quadrat in the series adjacent to the first quadrat in the series and rotated a random number of positions. The rotations between submatrices were independent of one another during each permutation. Finally, each cylinder was broken and the overall matrix was reconstructed for usage with the observed site-

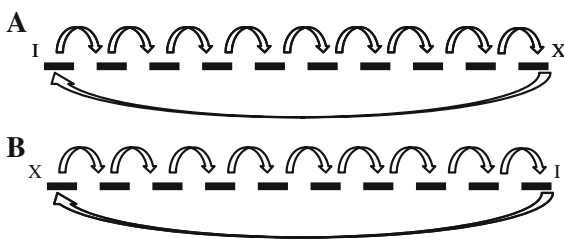


Fig. 2 Diagram of the random rotation and random reflection permutation scheme. A single random shift without a reflection (a) and a single random shift with a reflection (b) applied to the 10 subtransects. The Roman numerals indicate the orientation of the transect. Although the position of each subtransect was shifted, the spatial order of the samples within each subtransect was as observed in the empirical sample with the exception of the subtransect that must be returned to the beginning of the series

by-environment matrix in an RDA. This permutation scheme only preserves a fraction of the original spatial autocorrelation because the cylinder is broken at different positions (White and Gilchrist 2007). The test statistic for this analysis was the F value (Legendre and Legendre 1998, p. 608). When testing a model at the subtransect scale there were only 20 possible spatial orientations (including the empirical ordering), and therefore it was possible to perform a complete permutation test in which every possible permutation was enumerated. In this case, the smallest possible P value was 0.05 ($=1/20$). Complete permutation tests were impractical for all other tests and 999 permutations were conducted instead. To judge significance, we used a Bonferroni corrected α value of $\alpha = 0.05/n$, where n is the number of tests performed on a single data set.

We quantified the rate of change in the environment as a function of spatial lag by first calculating the multivariate Euclidean variograms for the variables of interest. A weighted least squares regression model was used to estimate the slope of the relationship between the log of the semi-variance in the environment on the log of spatial lag. The weights of the model were determined by the number of pair-wise comparisons that were available for a given spatial lag. The number of pair-wise comparisons (for both species composition and the environment) were 15, 15, 40, 20, 22, and 30 at spatial lags of 1, 2.33, 19, 21.4, 35.55, and 41 m, respectively. These spatial lags were chosen such that (1) the number of pair-wise comparisons per each lag were as equitable as possible, and (2) the maximum spatial lag was less than half the length of a transect (88 m), the unit of replication. In general, ordinary least squares regression models agreed closely with the weighted regression model (not shown).

The same general approach was used to calculate the rate of species turnover as a function of spatial lag. We quantified spatial community turnover with Euclidean variograms (Wagner 2003, 2004). As with the environmental variograms, we log transformed the semivariance of species composition and spatial lag before estimating the slope of the relationship with a weighted linear regression model.

We chose to examine the variograms in log–log space because if patterns of DD are relatively linear in log–log space then it suggests that they may be scale invariant which would aid in our ability to

predict patterns outside the domain of our sampling scales (Bell et al. 1993). In addition, we expected that much of the change in composition and the environment may take place rapidly at relatively small scales given the small grain of our sampling unit (1 m²) and in order to better qualitatively and quantitatively characterize this pattern, a log transformation of spatial lag was beneficial.

We tested if a positive relationship between the rate of change in the environment and the rate of change in species turnover existed between the subtransects with constrained but spatially random permutation tests. The spatial positions of each subtransect were randomly swapped, but the order of quadrats within each subtransect were kept fixed in the observed spatial arrangement. The test statistic for this randomization test was the *t* value for the slope of the OLS regression model of the rates of species turnover on the rates of environmental DD. Only data on 9 of the 10 subtransects were included in the test of the ETH for each habitat due either to compromised soil samples or to exposed bedrock which prevented soil coring. This missing environmental data precluded the calculation of spatial lags at intermediate scales for the subtransects in which they occurred and therefore these specific subtransects were not used to estimate the rates of DD. The vegetation information from these subtransects (which was complete) was still used in the randomization procedures.

Results

In the grassland average species richness was 18.02 with a range of 7–33 and in the woodland it was

13.62 with a range of 0–29. The woodland habitat had higher gamma diversity with 40 more species than the grassland habitat (211 species in the woodland compared to 171 in the grassland). Total compositional variance was similar in the two habitats (Table 1). Total variance in the standardized, log-transformed soil properties was also similar in the two habitats: 9.31 and 9.01 in the woodland and grassland, respectively. Average aboveground dry biomass in the grassland was 25.88 g compared to 5.86 g in the woodland. Average canopy cover in the woodland was 60%, but ranged from 0 to 90%.

Environmental control of species composition

The species composition in the grassland responded more strongly to variance in soil properties (Table 1). Specifically, the RDA explained 12% of the variance in grassland species composition and was either significant or marginally significant at each of the three scales of randomization. In contrast, the RDA in the woodland explained 5% of the variance in species composition and was only significant or marginally significant at the section and subtransect scales, respectively.

Geometry of the environment and species turnover

The log–log variograms for both the environment and species composition were generally well described by linear models in log–log space (Figs. 3, 4). The estimated semi-variance for both the environment and species composition did not consistently deviate from the regression line in either the positive or negative direction for a certain spatial lag which would be

Table 1 The results of the RDA and permutation tests on the sum of all canonical eigenvalues for the two habitat types

Habitat	Total variance	R^2_{RDA}	R^2_{RDAdj}	<i>F</i>	<i>P</i> values		
					Quadrat	Section	Subtransect*
Grassland	11.08	0.14	0.12	7.59	0.001	0.001	0.050
Woodland	10.25	0.07	0.05	3.65	0.794	0.005	0.050

The first four axes of a PCA on the soil chemical properties from a particular habitat were used as explanatory variables in each model, respectively. The permutations were spatially constrained at three scales: quadrats, sections, and subtransects (see “Analytical methods” section for more details). All tests were conducted with 999 permutations except for those at the subtransect scale in which a complete permutation test on all 20 possible constrained orderings of the data was considered. The Bonferroni corrected α value for each habitat is 0.017 (=0.05/3)

* The smallest possible *P* value is 0.05 (=1/20)

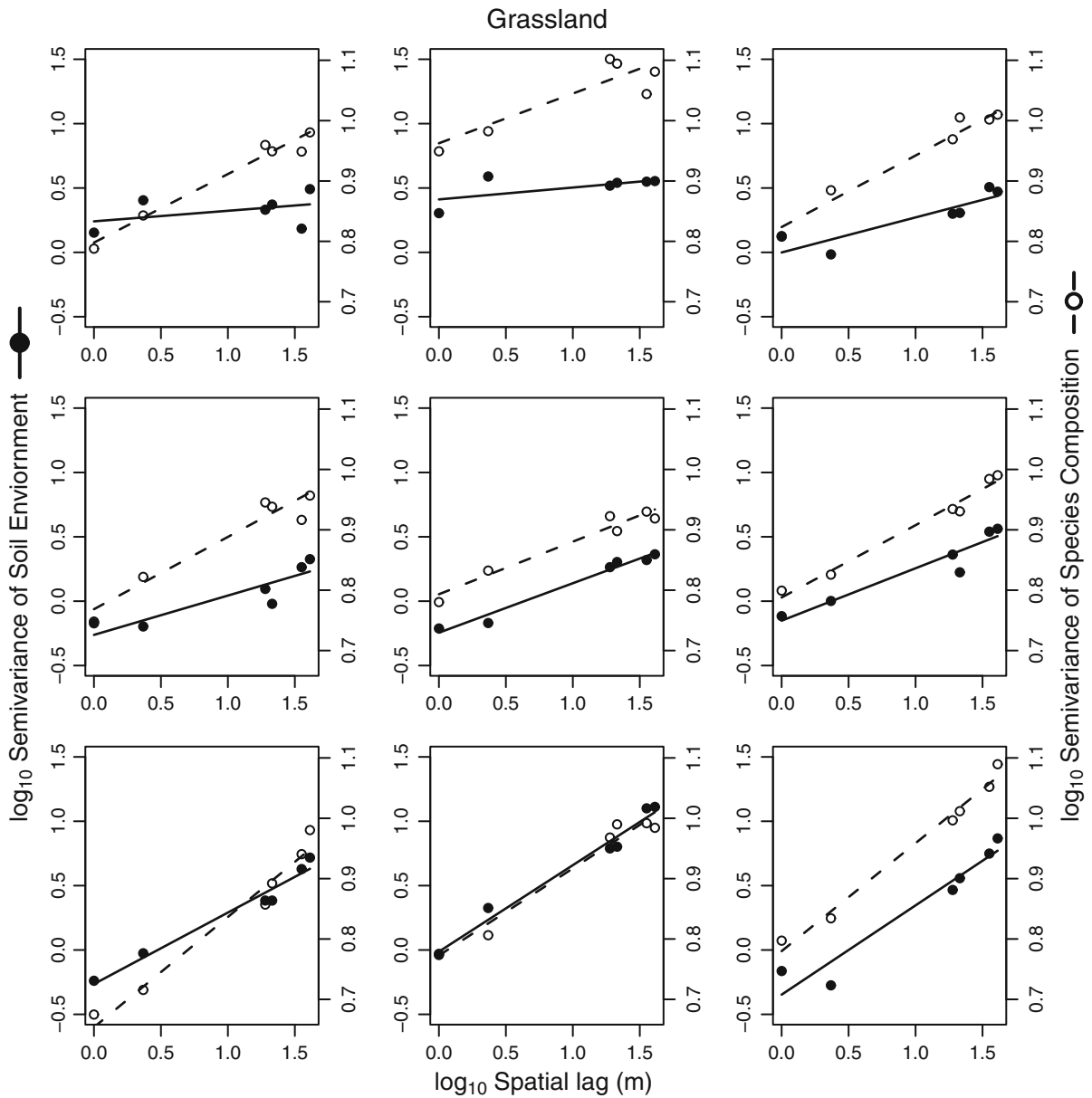


Fig. 3 The environmental and community Euclidean variograms for the nine subtransects in the grassland habitat. The figures are ordered left to right and top to bottom in increasing rate of environmental distance decay. The axis on the left applies to the degree of difference in the selected

environmental variables and the axis on the right applies to the degree of species turnover in species composition. All axes are log10 transformed and the fitted lines are weighted linear regression models

indicative of spatial dependence. However, we refrain from describing them as self-similar or scale free because considerable variation exists around some of the regression lines (given that this is a log–log scale). The average rate of DD (i.e., the weighted OLS regression slope of the log–log variogram) for the

grassland was 0.38, which was higher than the average rate of environmental decay observed in the woodland (0.30); however, in both habitats the subtransects displayed a range of environmental decay rates (Figs. 3, 4, 5). The rate of community turnover was positively correlated with the rate of environmental

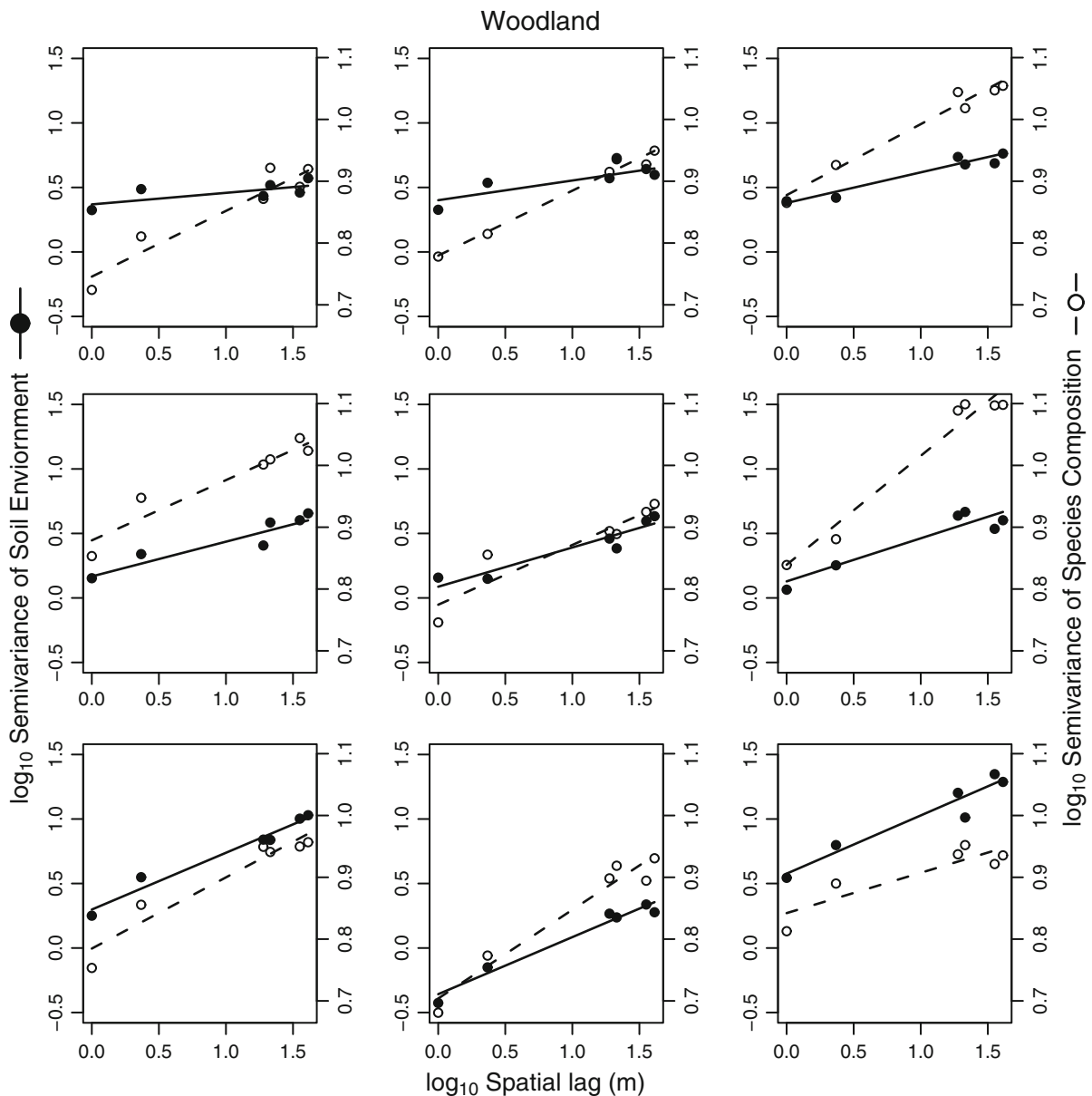


Fig. 4 The environmental and community Euclidean variograms for the nine subtransects in the woodland habitat. The figures are ordered left to right and top to bottom in increasing

rate of environmental distance decay. See Fig. 3 for additional explanation of the graph

DD in only the grassland habitat, and there was no relationship in the woodland (Fig. 5). In both habitats the relationship was rather noisy.

Discussion

We hypothesized that if the environment structures community composition, then the rate of DD in the

environment should be positively correlated with the rate of DD in species composition. Our results suggest that in both habitats the rate of community DD increased with the rate of environmental DD, however, we observed a significant positive correlation only in the grassland habitat. The lack of significant correlation in the woodlands did not strongly support or strongly contradict our hypothesis.

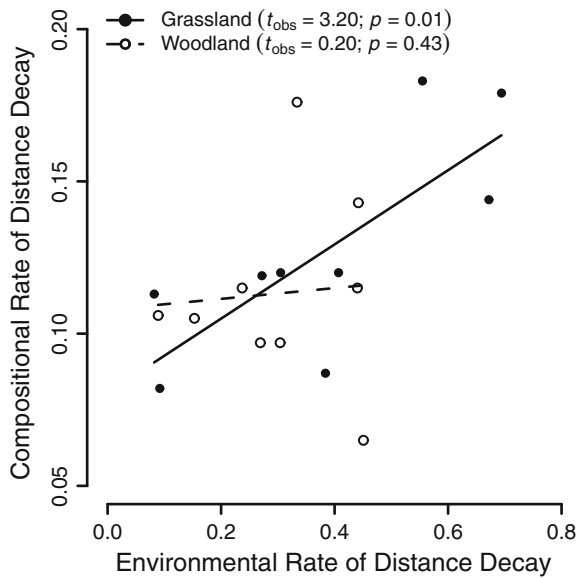


Fig. 5 Relationship between the rates of compositional and environmental distance decay. The solid regression line is for the grassland subtransects (*solid circles*), and the dotted regression line is for the woodland subtransects (*open circles*). The P values are based on 999 constrained permutations (see “Analytical methods” section for more details)

Our results suggest that one of the central premises of the ETH may be relevant at local spatial scales.

Implications for the ETH and future tests

Our study was stimulated in large part by the ETH, which hypothesizes that the triphasic pattern of the SAR is due to changes in the geometry of the environment as a function of spatial grain (Palmer 2007; Qian et al. 2007). An underlying premise of the ETH is that the rate at which unique species are accumulated (z of the SAR) is determined by the rate at which new environments are sampled. Many conceptual models and empirical studies include a metric of environmental or habitat diversity when attempting to predict species richness (e.g., Storch et al. 2003; Triantis et al. 2003); however, the hypothesis we addressed suggests that it is not simply the total variability in the environment (i.e., the number of habitats sampled) but the spatial (or temporal) structure of that variability which is relevant to understanding the rate of species accumulation or turnover. If the environmental variability is strongly spatially structured it will have a steep

Euclidean log–log variogram, which is characteristic of an environmental gradient (Palmer 1988), and new species should accumulate rapidly.

Although the ETH was first suggested as an explanation of the triphasic SAR that is only observed across many orders of magnitude in area, our study suggests that the underlying assumption that the geometry of the environment influences the rate of species turnover may be also relevant for vascular plants at local scales (1–50 m²). However, it should be noted that our study’s relatively small sample size of 20 transects distributed over two habitat types limits the regional generality of our results. If our sampling design captured a larger range of spatial scales, the ETH would predict that the log–log variograms for both the environment and species composition would display a scale-dependent deceleration in the relative rate of accumulation of new species and new environments as a function of spatial scale. A potential future test of the ETH is to examine if this is indeed the case and if the scale at which the environment changes geometry corresponds with a change in the rate of species turnover. However, a strong obstacle in performing such a test would be that the same environmental variable that is relevant at local scales is not necessarily the most important at regional scales.

Variograms and different metrics of species turnover

We used Euclidean variograms to estimate the rate of compositional turnover and environmental change between two sampling units. We chose this metric because when based upon presence/absence data the semivariance is the expected number of unique species between two sampling units. Euclidean variograms also provide a spatial decomposition of the variance explained by RDA. In addition, the mathematical properties of variograms are generally well understood due to their rich history in the field of geostatistics, unlike newer methods of studying species turnover such as dissimograms and correlograms (Journel and Huijbregts 1978; Wagner 2003). Over the scales we examined both the environmental and compositional variograms generally appeared linear in log–log space. This justifies in part our usage of linear regression to estimate the slopes of these relationships, but we hesitate to refer to them as self-

similar. Palmer (1988) demonstrated that considering variation in the slope of the log–log variogram (via fractograms) can yield additional insight into the geometry of species composition even when the relationship appears approximately linear.

Wagner (2004) noted that although the Euclidean community variogram has many useful properties (some of which we have mentioned here), it may be best suited for describing species turnover over relatively short environmental gradients in which species are expected to display linear responses to the environment. If species display unimodal responses to an environmental gradient, then it is typically argued that weighted averaging ordination techniques such as correspondence analysis (CA) or canonical correspondence analysis (CCA) offer a superior representation of community variation (Gauch 1982; ter Braak 1986; ter Braak and Prentice 2004). Therefore, Wagner (2004) developed the chi-square community variogram which is a spatial decomposition of the chi-squared variance covariance matrix utilized by CA and CCA. We refrained from the interpretation of the chi-squared variogram in our study because the semivariance of this method does not have an intuitive link to the expected number of unique species between two samples. In a study of several different data sets, Schlup and Wagner (2008) found that the Euclidean and chi-squared variograms generally agreed with one another. However, in their study increasing quadrat grain consistently increased the semivariance of the Euclidean variogram but not the chi-squared variogram. In addition to the chi-squared variogram, it may prove insightful to examine other transformations of the community data matrix (e.g., Hellinger transformation) prior to computing the community variogram (Legendre and Gallagher 2001). More case studies and theoretical developments are required to better understand the differences and appropriateness of various types of community variograms.

Habitat differences

The spatial geometry of the soil environment appeared to exert a stronger influence on the rate of species turnover in the grassland than in the woodland. This was expected, in part, because the RDAs indicated that in the woodland species composition was less related to the soil environment than in the

grassland. Given how little of the total variation the woodland RDA explained (5%), it seems likely that other environmental variables or biological mechanisms may be shaping community spatial patterns that were not included in the analysis. In the woodland, heterogeneity in degree of light limitation may have influenced understory plant composition given the range of overstory canopy cover we observed in our study (0–94%, standard deviation ca. 25%). However, additional RDA analyses (not shown) indicated that average canopy cover explained only a small additional portion of the total variability (<0.1%). The woodlands were also more topographically complex than the grasslands and crossed several small gullies or arroyos, which may have decreased the relative importance of measures of the soil environment. However, here again additional analyses utilizing slope and aspect (not shown) indicated that these variables also only contributed a small fraction of explained variance. Moisture and nutrient availability are also known to shape herbaceous understory community composition (Ludwig et al. 2004; Galhidy et al. 2006; Graves et al. 2006), but we did not collect information on either of these variables. There are many other potential biological drivers of community structure in our study system which include, but are not limited to, Janzen-Connell effects, herbivory, competitive exclusion, dispersal limitation, variation in growth forms, extent of rooting zone, and patterns of vegetative reproduction.

An alternative explanation for the weaker environmental signature in the woodland is that historical drivers are playing a stronger role in this habitat. Both habitats were in the bison management unit but they differed in frequency of prescribed burning. The woodland sites were located in a management unit that experienced a more frequent burning regime (seven spring burns in the past 7 years) than the management unit in which grassland site was located (two burns in the past 7 years). Because of the greater opportunity for fire exclusion in the forest (due to rockiness and bare patches without fuel) it is unknown if the actual frequency of fire at the woodland sites was lower than what was reported by The Nature Conservancy. It seems reasonable that a high fire frequency in the woodlands may have contributed to decreased response in the understory vegetation to the soil environment. However, a study conducted on the understory of a mixed-oak forest

found that frequency of fire explained relatively little total variation in species composition (Hutchinson et al. 2005). Reilly et al. (2006) found that a single wildfire increased (not decreased) the correlation between species composition and the environment. However, this finding was primarily due to a strong gradient in elevation which influenced the severity of the fire. In addition, differences in fire frequency likely resulted in differing spatial patterns of bison grazing both within and between the two habitat types due to the positive fire–grazing interaction (Fuhlendorf and Engle 2004). Like fire, grazing has the potential to increase or decrease the heterogeneity of community structure and potentially influence the community–soil relationship (Adler et al. 2001).

A third possible explanation is that because the vegetation was sparser in the woodlands, the rarefaction or sampling effect may be exerting a stronger influence in this habitat. The rarefaction effect is due to the necessary link between the number of individuals sampled and the number of species observed (Palmer et al. 2008a; McGlenn and Palmer 2009, 2010). The rarefaction effect will exert the strongest influence on the probability of observing a particular species at fine grains (e.g., 1 m² quadrats). Even if species are responding strongly to the environment our ability to detect this will be inhibited if the density of individuals is relatively low. If the number of individuals of each species is recorded in each sample then the expectation of species turnover due only to rarefaction effects can be developed. A simple randomization approach would be to place all individuals into a pool of potential colonists and randomly select the observed number of individuals without replacement for each quadrat. However, this may not be an option for many vegetation studies (including the present study) because many plants exhibit clonal growth which makes estimating the number of unique individuals (or genets) logistically unfeasible. An alternative solution is to sample at multiple grains such that the ecological pattern may be observed at presumably different levels of the rarefaction effect.

Conclusions

Not only does species composition vary spatially across landscapes, but so does the rate of species

turnover. If species composition is related to measured environmental variables (as in the grassland habitat), then the rate of change in the environment will be positively correlated with the rate of species turnover. Therefore, the texture of the environment can help to explain variation in the rate of species turnover across spatial scales in objectively placed samples. Future work on linking the environment to patterns of turnover should consider the strengths of the Euclidean variogram, which is appropriate for non-contiguous samples, provides an intuitive definition of turnover, and is linked to environmental models of species composition. The chi-squared variogram may be a useful metric of turnover as well, but more work is necessary to understand its properties. At local scales, the rarefaction effect may decrease the ability to detect environmental signatures and should be considered as a potential confounding factor in comparative studies.

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