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Research Article

Interactions between past land use, life-history traits and understory spatial heterogeneity

Jennifer M. Fraterrigo[1,2,*], Monica G. Turner[1] and Scott M. Pearson[3]
*[1]Department of Zoology, University of Wisconsin, Madison, WI 53706, USA; [2]Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011-3221, USA; [3]Department of Biology, Mars Hill College, Mars Hill, NC 28754, USA; *Author for correspondense (e-mail: jmfrater@iastate.edu)*

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Abstract

Past land use has contributed to variability in the distribution of herbaceous species by reducing plant abundance and altering species' chances of recolonizing suitable habitat. Land use may also influence plant heterogeneity by changing environmental conditions within stands. We compared the variability of understory herb abundance in southern Appalachian forests with different land-use histories to examine how past land use influenced plant heterogeneity. The cover of eleven focal species or genera was estimated and mineral soil concentrations were determined during 2001 and 2002 in eight stands that were farmed, logged, or had no disturbance history (reference) in western North Carolina. Analysis of the coefficients of variation revealed that the abundance of understory plants was more heterogeneous in disturbed stands compared with reference stands. However, when nutrient availability differences were accounted for by detrending the plant cover data, understory variability within stands declined, and no differences between disturbed and reference stands could be distinguished. This finding suggests that nutrient availability has important effects on plant heterogeneity, which depend on past land use. Species dispersal, seed size, and phenology also explained variability in the spatial heterogeneity of plants, but generally only before soil nutrient differences were statistically controlled. In addition to demonstrating that past land use has long-term effects on plant heterogeneity, these results indicate that soil nutrients may play different roles in determining vegetation patterns in historically altered and unaltered forests.

Introduction

Research on environment–vegetation relationships has identified many abiotic factors that influence plant distributions and abundance. At broad scales, for example, climate, elevation, topography, light, and soil resources have been associated with understory patterns (Struik and Curtis 1962; Beals and Cope 1964; Leach and Givnish 1999), whereas locally, patterns have been linked with fine-scale soil resource gradients, overstory characteristics, and microtopographic features (Bratton 1976; Hicks 1980; Beatty 1984). However, studies seeking to evaluate environment–vegetation relationships

have occasionally yielded more equivocal results, suggesting that other factors can confound these relationships (e.g., Reed et al. 1993; Richard et al. 2000; Frelich et al. 2003). Over the short term, disturbance can produce additional variation in vegetation patterns by increasing opportunities for species recruitment, altering successional states, and altering environmental conditions (Hobbs and Mooney 1985; McIntyre and Lavorel 1994). Although there is the potential for these changes to have long-lasting effects on vegetation patterns, little is known about the persistent effects of disturbance on the spatial organization of plants.

Land use is one form of disturbance that can generate long-lasting changes in the distribution of understory vegetation. By altering the arrangement of suitable habitat, land use has resulted in a complex mosaic of stands that differ in composition, and in many cases, lack or have a reduced abundance of dispersal-limited species (Peterken and Game 1984; Verheyen and Hermy 2001b; Bellemare et al. 2002). Within stands, differences in environmental conditions may further modify vegetation patterns by acting as a secondary filter (Dupré and Ehrlén 2002; Verheyen et al. 2003). Soil resources are likely to be foremost among the factors that affect understory patterns. They play a vital role in plant recruitment and productivity and can be altered by past land use (Honnay et al. 1999; Verheyen and Hermy 2001b). In particular, past land use can change both the average amount of soil nutrients (Compton and Boone 2000; Dupouey et al. 2002) and the spatial patterning of soil nutrients (Robertson et al. 1993). For example, Fraterrigo et al. (2005) showed that previous agricultural and silvicultural activities continue to enhance the within-site and among-site variability of soil carbon, nitrogen, phosphorus, calcium, potassium, and magnesium in southern Appalachian forests for at least 50 years after land abandonment. Within sites, nutrients tend to be more evenly distributed in intensively used areas compared with reference undisturbed stands, whereas among sites, nutrients tend to be more spatially heterogeneous (Fraterrigo et al. 2005). Despite these differences, the role of soil nutrients in altering understory plant distributions in historically modified forests remains poorly understood.

Investigations of how past land use influences understory vegetation patterns may be hampered by spatial processes that affect the distribution plants and soil nutrients. Recent work has demonstrated that heterogeneity in nutrient supply can increase the yield of individual plants and plant populations compared with their growth under homogeneous conditions (Wijesinghe and Hutchings 1999; Day et al. 2003a, b), and scale and spatial dependencies have often been found to obscure the relationship between nutrient and plant distributions (Reed et al. 1993; King et al. 2004; Mancera et al. 2005). Plant life-history characteristics, such as dispersal capacity, clonal spreading, seed size, and phenology, can also affect vegetation patterns by influencing plant recruitment and establishment potential. For example, Miller et al. (2002) found greater spatial dependence among plant species that had limited dispersal capacities or belonged to early temporal guilds. An approach that simultaneously considers the spatial arrangement of plant abundance and soil nutrients may therefore be essential for understanding how past land use influences vegetation patterns through changes in environmental conditions.

Previous studies show that multi-scale analyses of vegetation patterns can help to distinguish the factors that shape plant communities. Analyses of fine-scale patterns can show how plants respond to changes in the local distribution of soil resources that are not evident at broader scales (Bell and Lechowicz 1994; Farley and Fitter 1999). They can also highlight interactions with species life-history traits that influence plant distributions through neighborhood effects (Frelich et al. 1998; Schwarz et al. 2003) or by mediating local plant–environment associations (Greig-Smith 1979). Compared across the landscape, vegetation patterns may also provide insights about how disturbance affects plant communities at broad scales. In the case of former land use, within-stand vegetation patterns may be similar because of nutrient homogeneity, whereas among-stand patterns may be dissimilar, indicating that human practices have changed the conditions underpinning plant distributions.

The objective of this research was to compare the variability of understory plant abundance within and among stands to determine how past land use, through its modification of nutrient distributions, influences vegetation patterns. The study was conducted in a section of the southern Appalachian Mountains that has undergone

extensive transformation during the past century due to the presence of humans. Here, historical land use has initiated scale-dependent changes in soil nutrient heterogeneity, including a decrease in within-stand and an increase in among-stand nutrient variability (Fraterrigo et al. 2005). Thus, we hypothesized that there would be less within-stand variation and more among-stand variation in the abundance of understory plants in historically disturbed stands compared with undisturbed stands. Based on earlier studies, we also anticipated that certain life-history traits would modulate these patterns. In particular, we predicted that species dispersal capacity, propensity for clonal spreading, seed size, and phenology would influence patterns of plant abundance regardless of land-use history due to their influence on plant recruitment and establishment.

Methods

Study area description and data collection

We located eight stands in cove-hardwood forests of the Southern Blue Ridge Physiographic Province within the French Broad River Basin of western North Carolina, USA. Canopy trees in each stand are representative of the mixed mesophytic forest type described by Braun (1950) and include tulip tree (*Liriodendron tulipifera*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), oak (*Quercus* spp.), basswood (*Tilia americana*), hickory (*Carya* spp.), and yellow birch (*Betula alleghaniensis*). While hemlock (*Tsuga canadensis*) and rhododendron (*Rhododendron maximum*) were encountered, we avoided them when establishing study areas because these species acidify the soil and inhibit understory growth. Soils are well to moderately drained, derived predominately from granite, gneiss and mica-schist (Typic Dystrudepts).

The land-use history of this region includes extensive disturbance by agriculture and timber extraction and subsequent natural reforestation beginning in the mid-1900s following widespread land abandonment (Yarnell 1998; Davis 2000). The specific management history of each stand was determined from landowner interviews conducted by Pearson et al. (1998), rigorous examination of historical records, physical evidence (e.g., stand-age distribution, fences, stumps, road beds), and a chronosequence of aerial photographs developed by Wear and Bolstad (1998). For stands described as former farms ($n = 2$), historical practices began in 1850 and consisted of 80–85 years of cropping and grazing on level or moderately steep, cleared lands where stumps were removed and forage grasses were seeded. Previously logged stands ($n = 3$) were clearcut around 1950 (SAMAB 1996; Davis 2000). There is no evidence to suggest that these areas were burned (e.g., no charcoal was recovered). Stands without a history of intensive human disturbance were employed as references ($n = 3$) when they occurred near historically farmed or logged stands.

Within each stand, we located a 20×20-m area that was representative of the stand and differed minimally from other areas in its abiotic and biotic characteristics (i.e., plots had similar light environments and species composition). A cyclic design was used to describe soil and vegetation distributions in each area across different spatial scales. The cyclic sampling design is derived from time series analysis and enables the detection of autocorrelation between samples for a range of distance intervals using a minimum number of sampling points (Clinger and Van Ness 1976). This is possible because distance intervals between samples (i.e., lags) are repeated as multiples of the smallest interval several times throughout the plot. Given that soil cores require a great deal of time and effort to collect and process, we decided on a sampling scheme for soils first, and then applied the same scheme for collecting plant data. We chose a repeating series that samples 3 of every 7 points in the east–west direction, and 4 of every 12 points in the north–south direction, with 4 additional points placed at greater distances within the area sampled (see Fraterrigo et al. 2005 for illustration). The smallest lag between points was 1 m and the largest was 27.6 m. Although this design did not afford a large sample size relative to other ecological studies, it enabled us to thoroughly characterize within-stand soil and plant distributions.

The upper 15 cm of mineral soil was collected from each sampling point ($n = 40$ per stand) during June 2001 with a 5.2-cm diameter cylindrical PVC corer. Laboratory procedures for determining bulk density, pH, loss-on-ignition, total nitrogen, acid-extractable phosphorus, and extractable potassium, calcium and magnesium are

Table 1. Life-history characteristics and groupings by trait of species and genera studied.

Species or genus[a]	Dispersal mechanism[b]	Dispersal capacity	Root morphology[b]	Spread potential	Seed size (mm)*	Seed size group	Flowering phenology[b]	Temporal guild
Arisaema triphyllum	Ingested	Long	Fibrous rhizome	Low	3.5	Large	March–April	Early
Aster divaricatus	Wind	Long	Creeping rhizome	High	3.3	Large	July–Sept.	Late
Astilbe biternata	Adhesive	Long	Fibrous rhizome	Low	2.0	small	May–July	Late
Cimicifuga racemosa	Passive	Short	Fibrous rhizome	Low	1.5	Small	May–July	Late
Disporum lanuginosum	Ants	Short	Elongate rhizome	High	6.0	Large	April–May	Early
Goodyera pubescens	Adhesive	Long	Creeping rhizome	High	0.7	Small	May–July	late
Galearis spectabilis	Passive	Short	Short rhizome	Low	0.5	Small	April–July	Early
Osmorhiza spp.	Adhesive	Long	Fibrous rhizome	Low	1.1	Small	April–May	Early
Polygonatum spp.	Ingested	Long	Elongate rhizome	High	4.0	Large	April–June	Early
Prenanthes altissima	Wind	Long	Fibrous rhizome	Low	6.0	Large	Aug–Oct.	Late
Sanguinaria canadensis	Ants	Short	Thick rhizome	Low	3.0	Large	March–April	Early

[a]Nomenclature follows Gleason and Cronquist (1991).
[b]From Matlack (1994), Radford et al. (1964), and Mabry et al. (2000).
*Determined by averaging the length, width, and depth of an individual seed.

described by Fraterrigo et al. (2005). We estimated the percentage cover of all herbaceous understory species, as well as 11 herbaceous species or genera (Table 1), in the same locations ($n = 40$ per stand) during early June 2002 using 1-m^2 quadrats and a scale that emphasized accuracy for low coverage (Gauch 1982): absent, 0.5, 1, 2, 3, 4, 5, 8, 10, 15, 20, 25–100% by increments of 5%. This scale has been employed by others studying the distribution of herbaceous plants in forest understories (Scheller and Mladenoff 2002). We selected species or genera that were likely to be present in each stand (unpublished data, S. Pearson and M. Turner) so that balanced comparisons could be made among areas that differed in history. The taxa represented a range of life-history attributes and were therefore also suitable for investigating the relative influence of dispersal syndrome, clonality, seed size, phenology on spatial patterning (Table 1). In each quadrat, we also recorded the percentage cover of shrubs 0.5–1 m tall to assess whether shrub distributions could have affected the patterns of understory plant abundance.

We also sampled litter depth and forest canopy closure to determine if these factors varied with past land use. Litter depth was estimated by measuring the depth of undecomposed organic matter at the center of four 5×5-m subplots within each 20×20-m plot. We determined canopy closure by digitizing the amount of open sky visible in hemispheric photographs of the forest canopy. One photograph was taken at each corner of each plot with a fish-eye lens mounted on a 35-mm camera. Photographic negatives were scanned and processed to classify photographs into open sky vs. shaded pixels. The proportion of open-sky pixels in the image was arcsine-transformed to improve normality of the data.

Statistical analyses

We averaged shrub cover, litter depth, and canopy closure for each stand and compared them using analysis of variance (ANOVA), with past land use as a fixed effect. To quantify soil variability, we calculated coefficients of variation (CV) for each soil nutrient and for bulk density for each stand. Within-stand patterns of variability were evaluated by analyzing the CVs in a one-way ANOVA model with past-land use as a fixed effect. To evaluate among-stand patterns of variability, we analyzed CVs with Levene's test for equality of variances (Levene 1960). In this approach, a dispersion variable is derived from the dependent variables by calculating the absolute difference of each response from the mean response for the group (the standard deviation of the values) and an ANOVA is performed on this variable. Levene's test has been shown to be a robust and statistically powerful method for determining whether data meet homogeneity of variance assumptions (Schultz 1985). Recently, it has been used to assess the significance of changes in the variance of ecological systems before and after disturbance (Cottingham et al. 2000). One-way

models with land-use history as the fixed effect were used for all soil variables.

The variability of plant abundance in each stand was initially described with semivariograms to test for spatial autocorrelation (Matheron 1963). Percent cover data for the all herbaceous species were transformed by taking the fourth root of observations to normalize them. Semivariograms were constructed to a maximum distance of 20 m with 10 lags (i.e., bins for distances between sample points), giving an average of 76 pairs of points per lag (min = 23; max = 117). The cyclic sampling design permitted consideration of lag distances greater than one-half the maximum sampling distance (27.6 m), as there were ample pairs at these distances (23–117 pairs). Semivariograms were standardized by dividing the semivariance by the sample variance (Rossi et al. 1992).

We found no evidence of spatial autocorrelation and thus proceeded with a non-spatial analysis of variability using the CV of total herbaceous cover and the summed cover of taxa grouped by dispersal ability, clonal spreading propensity, seed size, and phenology for each stand to assess the influence of these traits on vegetation patterns (Table 1). CV were also calculated for each of the response variables after removing the effect of soil nutrient availability with a local regression model. Local regression ensured a high level of correspondence between dependent and independent variables by weighting the predicted values most heavily by neighboring observations (Cleveland and Devlin 1988; Trexler and Travis 1993).

CV were employed as described above to evaluate within-stand and among-stand variability in plant abundance. A one-way model with land-use history as a fixed effect was used to compare the within-stand variability of total herbaceous cover. A two-way model, with land-use history, trait, and the interaction of these terms as fixed effects, and stand nested in land-use history as a random effect, was used to compare the within-stand variability of taxa grouped by traits. Stand was included as a random variable to account for the fact that more than one trait could occur in a stand. Levene's test was used to evaluate among-stand patterns of variability. One-way models with land-use history as a fixed effect were used for all plant response variables, as Levene's test is currently not available for more complex models.

Of the two farmed plots sampled, only one plot contained a sufficient number of the selected species or genera to permit its inclusion in the analyses. Vegetation patterns in the remaining plots ($N = 7$) were therefore compared on the basis of whether or not they had been subjected to human practices in the past, and not on the basis of their specific land-use history. To ensure that our results were not biased by this approach, we reanalyzed the data without the farmed plot. No appreciable differences in trends were detected when the farmed plot was excluded, so farmed and logged plots were combined in all analyses.

Results

Neither litter depth nor light intensity varied with past land use. Mean litter depth was 6.9 cm (±1.1 SE) in disturbed stands and 4.8 cm (±1.3) in reference stands ($F = 1.61$, $p = 0.26$). Canopy closure was dense in all stands, ranging from 90 to 92% closure ($F = 0.51$, $p = 0.51$). However, shrub cover was significantly higher in reference stands. Mean shrub cover was 12% (±3) in disturbed stands and 23% (±3) in reference stands ($F = 6.32$, $p = 0.05$).

Soil nutrient heterogeneity

Differences in the variability of soil nutrient concentrations with land-use history depended both on the element and spatial scale being considered. Generally, however, we found that within-stand variability in disturbed stands tended to exceed that in reference stands (Table 2). The concentration of soil organic matter (as described by loss-on-ignition) was significantly more variable in disturbed areas than reference areas. Differences in variability for potassium, calcium, and magnesium were marginally significant (Table 2). Given the small sample size, however, statistical tests for these nutrients had limited power ($1-\beta$ ranged from 0.31 to 0.48).

As expected, among-stand nutrient variability was generally greater between disturbed areas than reference areas (Table 2). Differences in dispersion were marginally significant for soil pH, phosphorus, and potassium. Soil nitrogen showed the opposite

Table 2. Average coefficient of variation and dispersion from the mean for mineral soil (0–15 cm depth) nutrient concentrations. Within-stand variability was evaluated using one-way analysis of variance, whereas among-stand variability was assessed with Levene's test (Levene 1960). Land-use history was a fixed effect in all models.

Soil property	Coefficient of variation (%)		Within-stand variability		Dispersion from mean		Among-stand variability	
	Disturbed	Reference	*F*	*p*	Disturbed	Reference	*F*	*p*
Bulk density (g/cm^3)	24	28	0.51	0.51	6.31	1.77	2.73	0.16
pH	7	5	0.13[a]	0.72	2.59	1.02	4.53	0.09
Loss-on-ignition (%)	25	15	30.1	0.003	2.15	1.09	1.03	0.36
Nitrogen (g/kg)	26	21	0.50[a]	0.48	1.17	5.38	11.3	0.02
Phosphorus (mg/kg)	35	24	0.85	0.40	15.7	3.91	3.74	0.11
Potassium (mg/kg)	36	27	5.54	0.06	5.19	2.55	3.25	0.13
Calcium (mg/kg)	50	35	3.67	0.11	7.89	7.20	0.03	0.87
Magnesium (mg/kg)	40	30	3.22	0.13	5.32	4.81	0.03	0.87

[a]Because Levene's test indicated the homogeneity of variance assumption was not met for these variables, we performed a non-parametric Mann–Whitney–Wilcoxon test instead of ANOVA to test for differences in within-stand variability. Accordingly, we report the chi-square test statistic instead of the *F* statistic.

pattern, however, being significantly more variable among reference stands than disturbed stands.

Within-stand plant heterogeneity

We found little indication of spatial dependence in understory plant abundance, especially after the effects of nutrient availability were considered (Figure 1). Thus we proceeded with the non-spatial analysis of plant abundance patterns. This analysis provided strong evidence of an effect of past land use on understory vegetation patterns. The variability of total plant cover within stands was significantly greater in historically disturbed areas ($F = 31.0$, $p = 0.003$). However, when differences in nutrient availability were accounted for by detrending the cover data, this pattern was no longer evident (Figure 2), which suggested that nutrient distributions largely explained differences in within-stand variability between disturbed and reference stands.

Additional support for the importance of nutrient variability was found when within-stand patterns of understory abundance were considered with respect to life-history traits. Nearly all the traits investigated were significantly related to within-stand understory variability prior to detrending the cover data (Figure 2). The abundance of short-distance dispersers was significantly more variable than long-distance dispersers ($F = 10.8$, $p = 0.02$), as was the abundance of small-seeded plants compared with large-seeded plants ($F = 9.28$, $p = 0.03$), and late-blooming plants compared with early-blooming plants ($F = 5.49$, $p = 0.06$). Yet, after the effects of nutrient availability were removed, these traits were no longer explained differences in variability. The low power of these tests due to the small sample size and large error variance ($1\text{-}\beta$ ranged from 0.20 to < 0.10 for past land use and traits) may have constrained our ability to detect differences.

Although past land use had a slight effect when plant abundance was grouped by seed size ($F = 4.19$, $p = 0.09$), generally it did not directly account for differences in the variability of plant abundance in these models. A marginally significant interaction between past land use and seed size ($F = 4.55$, $p = 0.08$) and past land use and phenology ($F = 4.90$, $p = 0.07$) suggested that past land use may have influenced the within-stand variability of small-seeded and early-blooming plants (Figure 2), but limited power made it difficult to assess this relationship statistically.

Among-stand plant heterogeneity

Past land use did not significantly affect the among-stand variability of total herbaceous cover, regardless of whether differences soil nutrient availability were considered. However, the relationship between past land use and among-stand variability in the abundance of species with

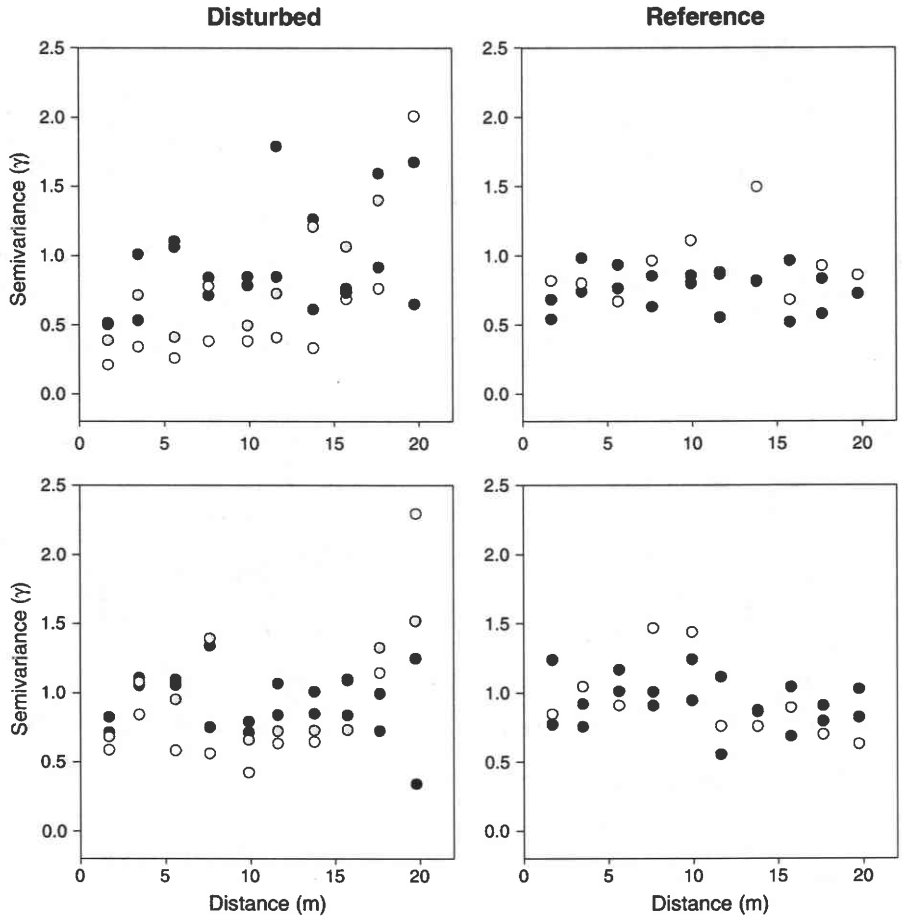

Figure 1. Semivariograms illustrating the random spatial pattern of understory abundance in historically altered and reference cove-hardwood forests in western North Carolina. Individual plots are indicated by different colored dots (N = 4 disturbed plots, N = 3 reference plots). Semivariograms in the two top panels are based on the percent cover of all herbaceous plants. The effect of nutrient availability on cover was removed prior to generating the semivariograms in the two bottom panels.

particular life-history characteristics suggested that nutrient availability did influence some vegetation patterns at the landscape-scale (Figure 3). The abundance of short-distance dispersers was significantly more variable among reference stands than disturbed stands (F = 15.3, p = 0.01). Yet, in the detrended model, past land use had no effect. The abundance of late-blooming species was also significantly more variable in reference than disturbed stands (F = 9.59, p = 0.03), but only prior to detrending. In contrast, past land use influenced the variability of low spreading species after nutrient differences were accounted for (F = 6.24, p = 0.05), such that their abundance was more variable among stands with a disturbance history compared with reference stands (Figure 3). The among-stand variability of the cover of species differing in seed size did not vary with land-use history.

Discussion

This study sought to compare the heterogeneity of understory plant abundance within and among stands that differed in land-use history to determine

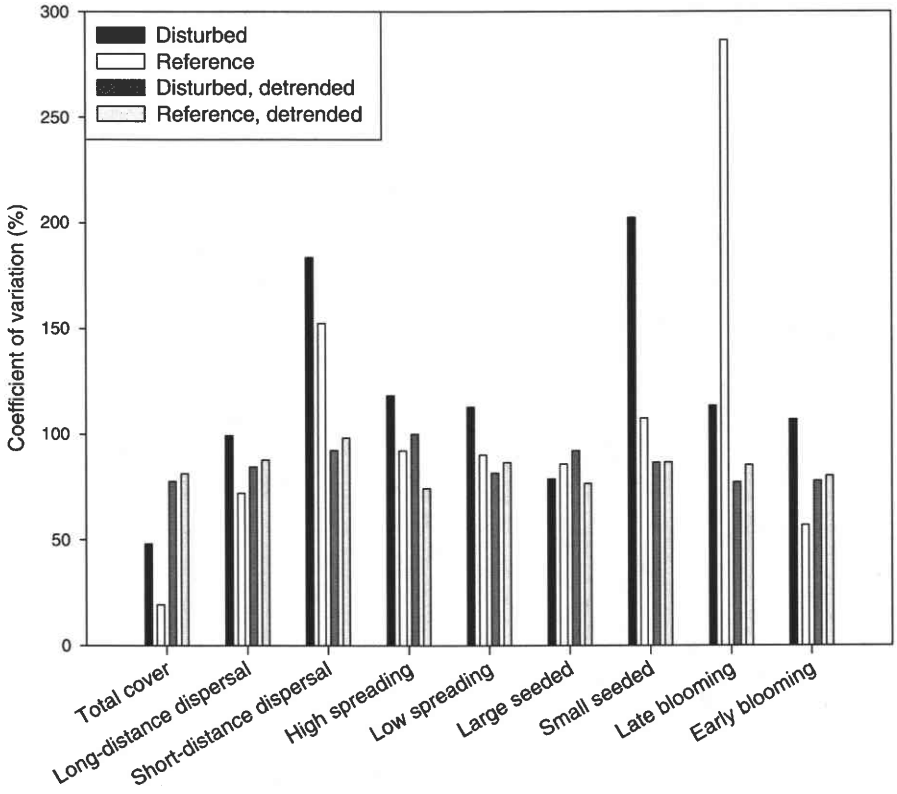

Figure 2. Mean coefficient of variation by past land use for total herbaceous cover and the cover of focal species and genera grouped by life-history characteristics (Table 1). Values represent within-stand variability in plant abundance before and after differences in soil nutrient availability were accounted for by detrending.

how former practices affect vegetation patterns. We addressed two interrelated hypotheses around which the following discussion is organized.

Hypothesis 1: Because past land use alters the distribution of soil nutrients, we hypothesized that the within-stand heterogeneity of herbaceous plants would be greater in reference areas than disturbed areas, while among-stand heterogeneity would be greater in disturbed areas than reference areas. Ancillary to these hypotheses was that plant heterogeneity would be similar in historically altered and reference stands if differences in nutrient availability were taken into account.

Previous work suggested that past land use would homogenize nutrient distributions (Fraterrigo et al. 2005), yet in this study we found that within-stand nutrient variability was generally greater in disturbed areas than in reference areas. The contradictory conclusions of these studies may be due to fact that only a subset of the original data were used in the current study. Nonetheless, patterns of plant variability were consistent with soil nutrient distributions: disturbed areas showed more within-stand variability than reference areas. Presumably patterns of plant abundance reflected differences in the microhabitats of disturbed stands and their capacity to support plant productivity. Soil cation concentrations, especially calcium, have frequently been shown to influence herbaceous species distributions (Palmer 1990; Gilliam and Turrill 1993; Kolb and Diekmann 2004), and the variability of cations were somewhat more variable in disturbed stands. Indeed, removing the effect of nutrient availability minimized within-stand differences in plant heterogeneity between disturbed and reference areas, suggesting that past land use influenced

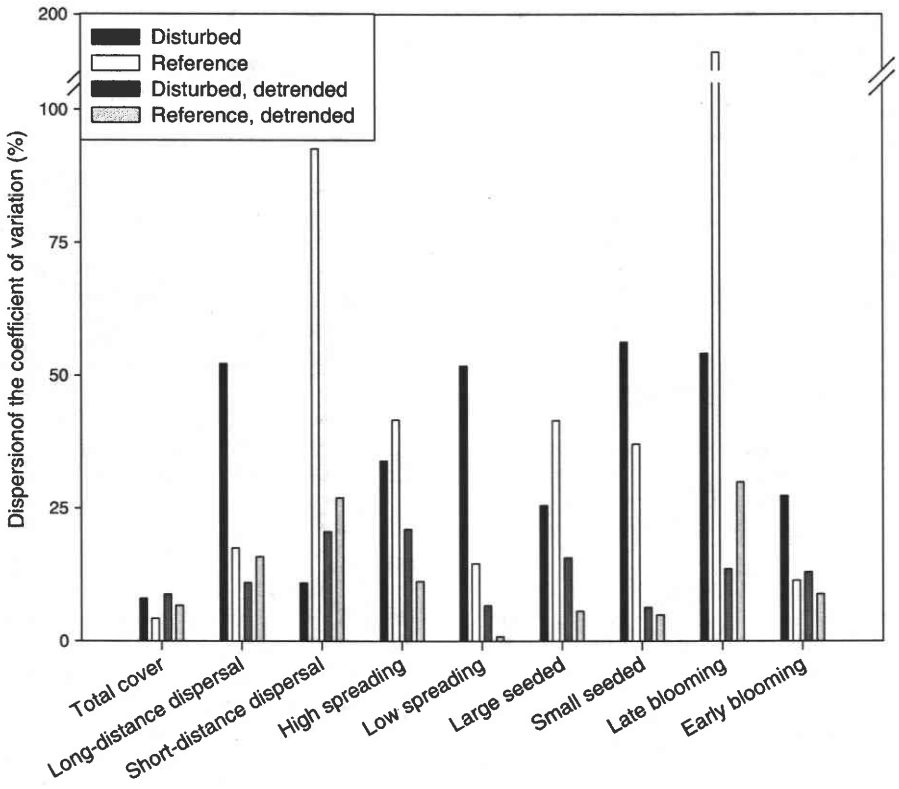

Figure 3. Mean dispersion of the coefficient of variation by past land use for total herbaceous cover and the cover of focal species and genera grouped by life-history characteristics (Table 1). Values represent among-stand variability in plant abundance before and after differences in soil nutrient availability were accounted for by detrending.

vegetation patterns by altering the distribution of soil resources at fine scales. However, among-stands we found no relationship between past land use and vegetation patterns regardless of whether soil resources were considered. Among-stand nutrient variability was generally greater between disturbed stands, but differences were not significant for calcium. Thus, plant abundance may not have varied at this scale because plants experienced a relatively similar environment among stands with respect to the soil resources that were most important for determining productivity. Another possibility is that there was a high degree of scale dependency in the relationships between vegetation patterns and their governing factors.

Scale dependency has been attributed to changes in the processes that dominate at different scales (Greig-Smith 1979; Reed et al. 1993). For example, Reed et al. (1993) proposed that correlations between compositional variation and the environment should be weak at fine scales because they are moderated by plant–plant interactions, whereas correlations should be strong at coarse scales because spatially extensive sampling is likely to capture a larger portion of the range of variation in the environment and vegetation. Although our results demonstrate scale dependent soil–plant associations, they do not corroborate the hypotheses advanced by Reed et al. (1993). Instead, our results support the findings of others who show that, in human-modified areas, abiotic factors dictate fine-grained vegetation patterns, while habitat isolation and biotic factors (such as dispersal limitation and seed size) are more important in determining landscape-scale patterns of contemporary vegetation (Butaye et al. 2002; Jacquemyn et al. 2003; King et al. 2004; Seabloom et al. 2005). In the present study, successional dynamics

may thus partly explain the differences in relationships occurring at fine and coarse scales.

Christensen and Peet (1984) were among the first to propose that the determinants of herbaceous communities change along successional gradients. They suggested that chance arrival (*sensu* Chesson and Warner 1981) may be more important relative to site characteristics in determining plant composition as a result of founder effects. This pattern has since been confirmed by studies conducted in historically altered landscapes, which show that past land use can alter the composition of understory communities by providing the chance for opportunistic species to colonize and persist for a considerable time (Motzkin et al. 1996; Eberhardt et al. 2003). More recently, Christensen and Gilliam (2003) argued that soil chemistry accounts for much of the variation in herbaceous species composition at nearly every stage of succession. If spatial scale is taken into account, our findings are consistent with both models, as well as with Ehrlén and Eriksson's (2000) conclusion that the distribution of species is the result of processes operating both among and within patches.

Aside from soil nutrient distributions, various other factors may contribute to understory heterogeneity in forest stands. Scheller and Mladenoff (2002) observed that variation in coarse woody debris was positively correlated with the heterogeneity of herb richness and abundance in northern Wisconsin, USA. However, the amount of coarse woody debris did not vary with land use in this study (personal observation, J. Fraterrigo) and differences in organic matter content were statistically removed. Other studies have shown that litter and light can influence seedling recruitment and thereby alter plant distributions through their effects on microsite availability for germination (Eriksson 1995; Dzwonko and Gawronski 2002), yet we found no differences in litter depth or canopy closure that would indicate these factors were responsible for the patterns we observed. Shrub cover differed significantly with past land use, and community composition is widely known to vary between forests with different histories (Peterken and Game 1984; Motzkin et al. 1996; Flinn and Vellend 2005). Both of these factors could have affected the competitive environment in the study areas and thereby influenced our results. Muller (1990) found that the spatial patterns of understory herbs were not affected by competition with other plants in the understory, while Miller et al. (2002) showed that sapling density altered herb distributions in hardwood forests. Thus, it appears that additional research is needed to identify the role of competition in determining herbaceous variability.

Hypothesis 2: We hypothesized that plant life-history traits would modulate the effects of past land use on the heterogeneity of plant abundance. Specifically, we expected that dispersal, vegetative spread, seed size, and phenology would influence the abundance of plants through their effects on plant recruitment and establishment.

Our findings suggest that dispersal, seed size, and phenology may have an effect on the within-stand variability of plant abundance in understory communities. The abundance of plants whose seeds are dispersed by gravity or ants should be heavily influenced by the dispersal process, which would enhance differences in their spatial distribution and produce greater variability at the within-stand scale. Previous research has shown that poorly dispersed species are autocorrelated for longer distances than well dispersed species, and thus demonstrates the strong spatial patterning that dispersal processes can impose on plant distributions (Miller et al. 2002; Svenning and Skov 2002). In contrast, enhanced variability in the abundance of small-seeded and late-blooming plants may reflect the influence of these traits on plant recruitment and establishment. Small seeds have been associated with low rates of establishment and high rates of incidence (Ehrlén and Eriksson 2000), although the later relationship is confounded with the large seed output of small-seeded plants (Westoby et al. 2002; Mabry 2004). If small seeds have a lesser chance of successfully establishing, their distribution may be more random than that of large-seeded plants. A similar argument may be made for late-blooming plants, which may have smaller odds of establishing than early-blooming plants because of the heterogeneous environment they face in terms of sunlight and soil moisture upon becoming active (Anderson et al. 1969). However, many traits exhibit some level of correlation (e.g., may large-seeded species are poorly dispersed), so associations between traits and the variability of plant abundance should be considered carefully and with respect to potential tradeoffs.

Interestingly, although past land use was not generally related to patterns of variability when plants were grouped by life history, accounting for differences in nutrient availability absorbed the effects of traits on within-stand heterogeneity. One possible explanation for this is that the patterns of abundance imposed by life history initially masked the effects of differences in soil availability caused by past land use. Using path analysis, Verheyen et al. (2003) demonstrated that both life history and soil resources could affect the distribution of understory plants in post-agricultural forests. Others have observed that correlations between herbaceous species distributions and soil chemistry vary with life history (Bossuyt et al. 1999; Verheyen and Hermy 2001a; Dupré and Ehrlén 2002). Weak interactions between past land use and seed size, and past land use and phenology may additionally indicate that the effects of management history and traits on abundance variability do not completely overlap. In either case, a lack of statistical power limited our ability to assess these patterns fully and necessitates further investigation.

Among-stand variability of abundance showed greater sensitivity to past land use than within-stand patterns. The abundances of plants that disperse short distances or bloom late in the growing season were more variable among reference stands than among disturbed stands. Time lags may constrain the expression of some traits and restrict the degree to which they can impose patterns of abundance during the early stages of succession. Halpern (1989) showed that temporal trends in the abundance of herbaceous species could be explained by interactions between life-history traits and disturbance. Yet in the present study, soil nutrient availability accounted for differences in variability, again suggesting some overlap in the effects of management history and traits on abundance patterns. The one exception was plants with a low potential for vegetative spreading; the abundance of these was more variable among disturbed stands than among reference stands after nutrient differences had been considered. Species that do not spread vegetatively have a high probability for sexual reproduction by seed, so differences in variability may be related to differences in recruitment and establishment success and linked to other life-history characteristics, such as seed size and phenology. Moreover, these patterns may have been more evident only among disturbed stands because the energetic payoffs of sexual reproduction are greater than those of vegetative reproduction following disturbance (Jurik 1985), and herbaceous plants tend to invest more energy in seed production following disturbance (Newell and Tramer 1978). Differences in the timing of recolonization of disturbed stands may also have enhanced among-stand variability in sexually reproducing plants through similar mechanisms.

Conclusions

Collectively, our results suggest that nutrient availability may play an important role in determining the variability of herbaceous plant abundance in human altered forests. Others have observed that herb layer development is linked with soil characteristics in early successional forests but that it declines with stand age (Gilliam et al. 1995). We found no indication that the influence of soil nutrient availability declines with age in our >50 year old stands. This apparent inconsistency may be due to the greater heterogeneity of soil nutrients in the stands we studied. Our low sample size and power limit the inference space of the current study. Thus, broad conclusions about the drivers of plant heterogeneity in altered forests should be made with caution pending the replication of this work in other areas. Additionally, more detailed studies of the spatial distribution of abiotic factors (e.g., litter, light) and their effects may be necessary to understand their relative contribution to plant abundance patterns and to anticipate the long-term influence of land-use change.

Other studies have documented how past land uses interact with the biotic characteristics of plants to alter their abundance, but few have done so with respect to plant heterogeneity. Changes in the spatial heterogeneity of plants may affect the distribution of higher organisms. They may also influence the competitive dynamics of forest stands, particularly among understory species. Effects of heterogeneity are poorly understood, however, and will likely be scale dependent. Future research should address the implications of changes in the spatial heterogeneity of plant communities for other organisms at multiple scales.

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