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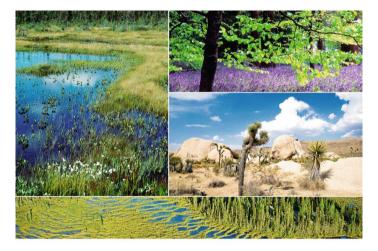*Marshall University*, gilliam@marshall.edu

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Spatial heterogeneity of soil nutrients and plant species in herb-dominated communities of contrasting land use

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Abstract Recent interest in spatial pattern in terrestrial ecosystems has come from an awareness of the intimate relationship between spatial heterogeneity of soil resources and maintenance of plant species diversity. Soil and vegetation can vary spatially in response to several state factors of the system. In this study, we examined fine-scale spatial variability of soil nutrients and vascular plant species in contrasting herb-dominated communities (a pasture and an old field) to determine degree of spatial dependence among soil variables and plant community characteristics within these communities by sampling at 1-m intervals. Each site was divided into 25 1-m^2 plots. Mineral soil was sampled (2-cm diameter, 5-cm depth) from each of four 0.25-m^2 quarters and combined into a single composite sample per plot. Soil organic matter was measured as loss-on-ignition. Extractable NH_4 and NO_3 were determined before and after laboratory incubation (28 days at 27°C) to determine potential net N mineralization and nitrification. Cations were analyzed using inductively coupled plasma emission spectrometry. Vegetation was assessed using estimated percent cover. Most soil and plant variables exhibited sharp contrasts between pasture and old-field sites, with the old field having significantly higher net N mineralization/nitrification, pH, Ca, Mg, Al, plant cover, and species diversity, richness, and evenness. Multiple regressions revealed that all plant variables (species diversity, richness, evenness, and cover) were significantly related to soil characteristics (available nitrogen, organic matter, moisture, pH, Ca, and Mg) in the pasture; in the old field only cover was significantly related to soil characteristics (organic matter and moisture). Both sites contrasted sharply with respect to spatial pattern of soil variables, with the old field exhibiting a higher degree of spatial dependence. These results demonstrate that land-use practices can exert profound influence on spatial heterogeneity of both soil properties and vegetation in herb-dominated communities.

Keywords Herbaceous communities · Soil nutrients · Land-use history · Spatial pattern · Geostatistics

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Introduction

Although temporal patterns of ecosystem processes, such as ecological succession and response to disturbance, have long served as a cornerstone of ecological research, there is considerable current interest in characterizing spatial heterogeneity in

terrestrial ecosystems (Lovett et al. 2005). Much of this has arisen from an awareness of the intimate relationship between spatial heterogeneity of soil resources and maintenance of plant species diversity (Ricklefs 1977; Beatty 2003). Working with 144 0.18 m^2 plots on limestone pavements of southern Ontario, Canada, Lundholm and Larson (2003) found that peaks in species richness correlated most closely with maximum soil heterogeneity. Hutchings et al. (2003) suggested that the mechanism for such relationships arises from the alteration of interspecific competition brought about by spatial heterogeneity in soil resources. Significant responses of plant diversity to soil resource heterogeneity have been observed in studies that span virtually all spatial scales, from the plot (e.g., 1-m^2) (Palmer 1990; Dick and Gilliam 2007), to the landscape (Dufour et al. 2006), and even on a global scale (Kreft and Jetz 2007). Loss of plant biodiversity in some terrestrial ecosystems has been linked to decreases in spatial heterogeneity of soil nutrients, such as nitrogen (N) (Gilliam 2006).

Indeed, although it has long been the bane of designs for field experiments (Dutilleul 1993), spatial heterogeneity is increasingly being considered an important, integral facet of terrestrial ecosystems (McClain et al. 2003; Lovett et al. 2005). The cycling of nutrients, particularly N, in soils of terrestrial ecosystems is controlled by processes, such as microbial activity and vegetation dynamics, which often are quite spatially heterogeneous (Robertson et al. 1988; Parkin 1993; Schlesinger et al. 1996; Thompson et al. 2006; Housman et al. 2007). Relatively undisturbed terrestrial ecosystems typically display a high degree of spatial heterogeneity, with spatially discrete areas of high N mineralization rates in soils.

Spatial variability can be altered by a variety of disturbances (Fraterrigo and Rusak 2008; Xi et al. 2008). In particular, land-use practices can directly alter spatial heterogeneity of both soil resources and plant species of herb-dominated plant communities. For example, activities such as plowing and fertilizer application can influence the spatial pattern of soil organic matter and nutrients, especially N. Furthermore, harvesting and herbicide use can affect plant species composition, and grazing can simultaneously alter spatial heterogeneity of both soil resources and vegetation. Thus, variation in land use can exert a profound impact on soil–plant interactions, and do so in a way that can influence plant community composition (Eskelinen et al. 2009).

The purpose of this study was to examine fine-scale spatial variability of soil nutrients and vascular plant species in herb-dominated communities that vary in land-use: a pasture and an old field. More specifically, we wanted to determine the degree of spatial dependence of soil variables (N dynamics, pH, organic matter, and extractable soil nutrients) and plant community characteristics (cover, species richness, evenness, and diversity) within these communities by sampling at 1-m intervals.

Methods

Site description

This study was done at the Mill Creek mitigation area, a site that will become a constructed wetland to offset wetland losses incurred during road construction. It is located in a 3rd-order stream floodplain in Wayne County, West Virginia (38°31′ N, 82°42′ W). Both pasture and old field comprise an approximately 1-ha area surrounded by uplands dominated by mixed deciduous forest. Long-term (30-year) mean precipitation is 107 cm year^{-1}; for the two years of study, precipitation was 93.1 and 117.1 cm in 2001 and 2002, respectively. Elevation within the floodplain is ~195–200 m.

The study site was dominated by soils of the Kanawha series: fine-loamy, mixed, active, mesic Typic Hapludalfs, and very deep (100–180 cm). They are well-drained, moderately permeable, and formed in alluvium derived from interbedded shale, siltstone, and sandstone. Kanawha soils are found on high bottoms and low stream terraces with slope ranges from 0 to 15%, typical of slopes of our study.

Evans et al. (2004) recognized these site types as two of nine cover types in the general Mill Creek area. The pasture site experiences regular grazing by domestic cattle, but does not undergo haying. The old-field site, abandoned at least 20 year prior to this study, exhibits few remaining characteristics of earlier agriculture (Evans et al. 2004), with grain crops commonly planted and harvested (Slagle et al. 2004).

Field sampling

One 5-m × 5-m sample site was established in each of two community types—an old field and a pasture—approximately 50 m apart. Each site was divided into 25 contiguous 1-m^2 plots, with each plot being quartered with a 1-m^2 PVC frame with center cross. One sample of mineral soil was taken from the center of each 0.25-m^2 quarter of each 1-m^2 plot to a depth of 5 cm with a 2-cm diameter soil corer. This depth was chosen to represent maximum root distribution for this vegetation type (Schenk and Jackson 2002).

The four soil samples (one per quarter) were combined in a single sterile polyethylene Whirl–Pak® bag to create a composite sample for each 1-m^2 plot, a total of 25 mineral soil samples per site (Fig. 1). Samples were kept as intact cores in bags and placed
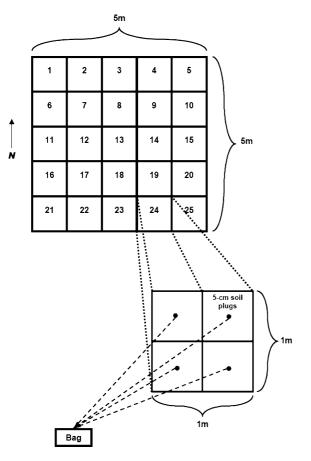
immediately on ice for transport to the laboratory. Soils were collected in August 2001.

Above-ground plant cover was estimated within each 1-m^2 plot at pasture and old-field sites using percent cover estimation in October 2002 (Gilliam and Turrill 1993). Botanical nomenclature follows Strasbaugh and Core (1977).

Laboratory analyses

Upon transport to the Marshall University Weeds and Dirt Laboratory, samples were manually homogenized in original collection bags prior to extraction and analysis. Organic matter was determined from oven-dried sub-samples of soil using a loss-on-ignition method (mass lost over 7 h at 500°C). Soils were also sub-sampled for extraction and pre-incubation analysis of KCl-extractable NO_3, NH_4, Al, Ca, Mg, and pH. Extraction was performed on moist soil using 1 N KCl at an extract:soil ratio of 10:1 (v:w). Extracts were analyzed for NH_4 and NO_3 colorimetrically with a Bran + Luebbe TrAAcs 2000 automatic analysis system. Extractable Al, Ca, and Mg were analyzed using inductively coupled plasma emission spectrometry (ICP) with a Varian Liberty 110 ICP Emission Spectrometer. Remaining soil samples were then incubated in their original polyethylene bags at 27°C for 28 days in a Fisher Scientific Low Temperature Incubator (Model 146E). Post-incubation extraction and analyses were conducted as above.

Extractable N pools were determined as the pre-incubation levels of NH_4 and NO_3. Net N mineralization was calculated as post-incubation NH_4 plus NO_3 minus pre-incubation NH_4 plus NO_3; net nitrification was calculated as post-incubation NO_3 minus pre-incubation NO_3. Because these are based on laboratory incubations, results reflect N mineralization and nitrification potentials, rather than field (i.e., in situ) rates.

Data analysis

Species diversity was calculated using the Shannon–Wiener Index (H′), based on cover estimates and using ln-transformed p_i values. The Pielou Index was used to determine species evenness (J) (Barbour et al. 1999). Finally, species richness (i.e., species

Fig. 1 Schematic diagram of sampling design within each of two sites

Table 1 List of all plant species encountered at Mill Creek study site, Wayne County, West Virginia

Scientific name	Common name
Acalypha rhomboidea Raf.	Common three-seeded mercury
Ambrosia artemisiifolia L.	Common ragweed
Andropogon virginicus L.	Broomsedge
Arthraxon hispidus (Thunb.) Makino	Jointheaded arthraxon
Aster pilosus Willd.	White heath aster
Carex vulpinoidea Michx.	Foxtail sedge
Cinna arundinacea L.	Wood reed-grass
Cirsium vulgare (Savi) Tenore	Common thistle
Cyperus strigosus L.	Strawcolored Flatsedge
Daucus carota L.	Queen Anne's lace
Digitaria sanguinalis (L.) Scop.	Crabgrass
Elephantopus carolinianus Willd.	Elephant's-foot
Erigeron canadensis L.	Horseweed
Eragrostis spectabilis (Pursh) Steud.	Purple lovegrass
Eupatorium coelestinum L.	Mistflower
Eupatorium serotinum Michx.	Late-flowering thoroughwort
Festuca elatior L.	Meadow fescue
Glechoma hederacea L.	Ground-ivy
Holcus lanatus L.	Velvet grass
Juncus effusus L.	Common rush
Juncus tenuis Willd.	Path rush, wiregrass
Lespedeza cuneata (Dumont) G. Don	Sericea
Lespedeza sp.	
Medicago sp.	
Muhlenbergia sp.	
Oxalis stricta L.	Upright yellow wood sorrel
Panicum sp.	
Panicum anceps Michx.	Flat-stemmed panic grass
Panicum clandestinum L.	Deertongue grass
Paspalum laeve Michx.	Smooth paspalum, beadgrass
Phaseolus polystachios (L.) BSP.	Wild kidney bean
Plantago sp.	Plantain
Potentilla simplex Michx.	Common cinqufoil
Poa sp.	Bluegrass
Ruellia caroliniensis (Walt.) Steud.	Wild-petunia
Setaria glauca (L.) Beauv.	Yellow foxtail
Setaria viridis (L.) Beauv.	Green foxtail
Solanum carolinense L.	Horse-nettle

Table 1 continued

Scientific name	Common name
Taraxacum officinale Weber.	Common dandelion
Triodia flava (L.) Smyth	Purpletop
Trifolium pratense L.	Red clover
Verbesina alternifolia (L.) Britton ex Kearney	Wing-stem
Vernonia altissima Nutt.	Tall ironweed

density—S) was determined as number of species per 1-m^2 plot.

All response variables were tested for normality using Shapiro–Wilk test in Statistix 9.0 (Analytical Software 2008) prior to statistical analysis. Because all variables were normally distributed, they were used as untransformed data. Means were compared between pasture and old-field sites using *t*-tests (Zar 2009; Analytical Software 2008). Relationships among variables, sites, and vegetation were assessed with canonical correspondence analysis using CANOCO version 4.5.

Backward stepwise regression was used to identify soil factors as independent variables that more significantly correlate with plant variables—cover and species richness, evenness, and diversity. This technique sequentially eliminates variables from an original model with all soil variables until all the variables remaining in the model produce *F* statistics significant at $P < 0.05$ (Analytical Software 2008).

Degree of spatial dependence of soil and vegetation variables (as well as that of three individual species at each site) and its variation between sites was determined with geostatistics (Robertson 1987; Schlesinger et al. 1996; Iqbal et al. 2005). Using a spherical model, a semi-variogram was constructed for each variable with VESPER, version 1.62 (Minasny et al. 2005). Three possible patterns can arise from these analyses: spatial dependence, randomness, and linearity. Spatial dependence comprises four values relevant to spatial pattern: (1) nugget, which is microvariability (i.e., variability at distance 0), (2) the structural component, which describes spatially correlated variability, (3) sill, which is total variability, or sample variance, and (4) lag distance, which is the distance within which the variable is spatially dependent and beyond which is spatially

independent. Randomness results when the nugget effect is high enough to closely approach the sill (i.e., ratio of nugget to sill is unity). Linearity occurs when there is spatial dependence at scales at least as great as the extent sampled.

Expected species–accumulation curves (sample-based rarefaction, *sensu* Gotelli and Colwell 2001) were created for each site using the EstimateS software (Colwell et al. 2004). Of particular interest was the calculation of 95% confidence intervals using formulas from Colwell et al. (2004) to estimate minimum plot number required to characterize representative species richness for each site. We defined minimum plot number as the number of plots yielding an upper 95% confidence interval that most closely approximated the total species richness of the site (Small and McCarthy 2002).

Our sampling represents a non-replicated study which employed a single intensively sampled area within each land-use site, an approach common in studies that focus on fine-scale spatial heterogeneity (e.g., Schlesinger et al. 1996); thus, interpretation of results should be made with that in mind.

Results

A total of 42 vascular plant species were encountered in all 50 1-m^2 plots from both pasture and old-field sites (Table 1). These sites differed significantly for most soil and plant variables. In particular, the old field had significantly higher net N mineralization/ nitrification, extractable NO_3, pH, Ca, Mg, Al, plant cover, and species diversity, richness, and evenness (Table 2). Note that cover for pasture and old field was greater than 100%. This is the result of overlapping foliar biomass and indicates that leaf area index was greater than 1 for both sites. There were also sharp contrasts between sites for correlations among most soil variables (Table 3).

Multiple regression using backwards stepwise analysis revealed that plant cover and all variables associated with plant biodiversity (species diversity, richness, and evenness) were significantly related to varying combinations of soil characteristics in the pasture, including available N, organic matter, moisture, pH, Ca, and Mg. By contrast, only cover was significantly related to soil characteristics (organic matter and moisture) in the old field (Table 4).

Pasture and old-field sites were dominated by contrasting plant species. *Poa* spp. dominated the old field, representing just over 25% of the total cover of the site; the top three species (*Poa* spp., *Ambrosia artemisiifolia*, and *Verbesina alternifolia*) combined to represent slightly less than 50% of total old-field cover (Table 5). The pasture was dominated by *Festuca elatior*, which was just under 40% of total cover, with the top two species (*Festuca elatior* and *Aster pilosus*) combining for nearly 70% total cover for the pasture (Table 6).

Geostatistics showed that pasture and old-field sites contrasted with respect to spatial pattern of soils and plant cover. The old field exhibited significant spatial dependence for all soil variables except Mg

Table 2 Soil and vegetation variables (mean ± 1 standard error of mean) in 1-m^2 plots ($n = 25$) within pasture and old-field sites

Significant differences between means determined by *t*-tests (Zar 2009). Significant differences between sites at $P < 0.05$, $P < 0.01$, and $P < 0.001$ indicated by *, **, and ***, respectively. Note that cover exceeds 100%, indicating leaf area index >1

Variable	Pasture	Old field	t
Net N mineralization rate (μg N/g soil/day)	0.5 ± 0.2	1.4 ± 0.2	3.1**
Net nitrification (μg NO_3-N/g soil/day)	0.7 ± 0.2	1.6 ± 0.2	3.1**
NH_4 pool (μg NH_4-N/g soil)	5.7 ± 1.3	8.5 ± 0.9	1.8
NO_3 pool (μg NO_3-N/g soil)	9.8 ± 0.7	6.6 ± 0.5	3.8***
Organic matter (%)	8.3 ± 0.1	8.1 ± 0.2	0.8
pH	4.43 ± 0.05	4.56 ± 0.03	2.4*
Ca (μg/g soil)	769 ± 129	1036 ± 43	2.0
Mg (μg/g soil)	122 ± 24	335 ± 11	8.0***
Al (μg/g soil)	0.5 ± 0.3	4.8 ± 1.6	2.7*
Species diversity (H')	1.38 ± 0.03	2.21 ± 0.05	13.6***
Species evenness (J)	0.78 ± 0.01	0.86 ± 0.01	4.3***
Species richness (S—species/m^2)	5.9 ± 0.2	13.4 ± 0.5	13.5***
Cover (%)	180 ± 6	256 ± 12	5.6***

Table 3 Correlation matrix for aluminum (Al), magnesium (Mg), calcium (Ca), soil moisture (Moist), NH_4 and NO_3 pools, net nitrification and N-mineralization rates (Nit and N-min, respectively), organic matter (OM), and pH at old field and pasture sites of Mill Creek study area Wayne County, West Virginia

	Al	Ca	Mg	Moist	NH_4	Nit	N-min	NO_3	OM
Old field									
Ca	−0.54‡								
Mg	–	–							
Moist	–	–	0.51‡						
NH_4	–	–	–	–					
Nit	–	–	–	–	–				
N-min	–	–	–	–	–	0.99‡			
NO_3	–	–	–	–	–	–	–		
OM	–	–	0.58‡	0.84‡	–	–	–	–	
pH	–	0.62‡	–	0.63‡	–	–	–	–	0.64‡
Pasture									
Ca	–								
Mg	0.41†	0.95‡							
Moist	–	–	–						
NH_4	–	–	–	–					
Nit	–	–	–	–	0.62‡				
N-min	–	–	–	–	0.43†	0.97‡			
NO_3	–	–	–	–	0.84‡	0.64‡	0.50†		
OM	–	–	–	0.72‡	–	–	–	–	
pH	–	–	0.50†	–	–	–	–	–	–

Dashes (–) indicate no significant correlation. $N = 25$ for both matrices

† $P < 0.05$, ‡ $P < 0.01$

and Al, whereas pasture soils lacked spatial dependence for net nitrification, NH_4, organic matter, and Al (Table 7). The two sites were similar in exhibiting a high degree of spatial dependence for all plant variables, except that plant cover was not spatially dependent in the old field (Table 7).

Geostatistics further demonstrated variation among dominant species for each site with respect to patterns of spatial dependence. For the pasture, with *Festuca elatior*, *Aster pilosus*, and *Poa* sp. as the top three species based on cover, only *A. pilosus* exhibited spatial dependence. For the top three old-field species, *Poa* sp. and *Verbesina alternifolia* were spatially dependent, whereas *Ambrosia artemisiifolia* was not (Table 8).

Canonical correspondence analysis revealed a wide scatter of sample plots for both sites, based on cover-weighted species composition, despite the contiguous nature of the sample design. For the old-field site, extractable soil Al was the most important factor explaining similarities and differences in composition among plots (Fig. 2), whereas soil organic matter was the most important factor in the pasture (Fig. 3).

Expected species–accumulation curves showed that 95% confidence intervals most closely approximated total species richness at 14 and 15 plots for pasture and old-field sites, respectively. This close similarity in minimum plots number was in spite of sharp contrasts in species richness, with mean plot richness and total site richness for the old field being 13.2 ± 3.7 species/plot and 35 species, respectively, and 7.2 ± 2.9 species/plot and 18 species, respectively, for the pasture (Fig. 4).

Discussion

Not surprisingly, these two sites with contrasting land use differed greatly with respect to community

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Table 4 Multiple regression, using backward stepwise procedure, for vegetation variables at pasture and old-field sites

Species diversity

Old field

  Not significant at $P < 0.05$

Pasture

  $H' = 2.46 - 0.25(\text{pH})$, $r^2 = 0.16$

Species richness

Old field

  Not significant at $P < 0.05$

Pasture

  $S = 5.93 + 0.002(\text{Ca}) - 0.02(\text{Mg})$, $r^2 = 0.32$

Species evenness

Old field

  Not significant at $P < 0.05$

Pasture

  $J = 1.06 + 0.10(\text{organic matter}) - 0.03(\text{moisture})$,
  $r^2 = 0.50$

Cover

Old field

  $\text{Cover} = 376 + 100(\text{organic matter}) - 36(\text{moisture})$,
  $r^2 = 0.52$

Pasture

  $\text{Cover} = 536 - 5(\text{NH}_4) + 9(\text{NO}_3) - 12(\text{moisture})$,
  $r^2 = 0.52$

Variables significantly accounting for variability in the model at P < 0.05 are listed with their coefficients. See Methods for further details

Original models:

$H' = \text{Al} + \text{Ca} + \text{Mg} + \text{NH}_4 + \text{NO}_3 + \text{N}$ mineralization + nitrification + organic matter + pH + moisture

$S = \text{Al} + \text{Ca} + \text{Mg} + \text{NH}_4 + \text{NO}_3 + \text{N}$ mineralization + nitrification + organic matter + pH + moisture

$J = \text{Al} + \text{Ca} + \text{Mg} + \text{NH}_4 + \text{NO}_3 + \text{N}$ mineralization + nitrification + organic matter + pH + moisture

$\text{Cover} = \text{Al} + \text{Ca} + \text{Mg} + \text{NH}_4 + \text{NO}_3 + \text{N}$ mineralization + nitrification + organic matter + pH + moisture

Table 5 Species encountered within a 5-m × 5-m site located within an old field in Wayne County, WV

Species	Mean cover (%)
Poa sp.	64.6
Ambrosia artemisiifolia	29.4
Verbesina alternifolia	24.0
Panicum anceps	16.8
Setaria viridis	12.4
Elephantopus carolinianus	12.2
Lespedeza cuneata	12.0
Glechoma hederacea	10.0
Potentilla simplex	8.8
Aster pilosus	8.0
Panicum sp.	7.8
Oxalis stricta	7.4
Eupatorium coelestinum	6.2
Ruellia caroliniensis	6.0
Triodia flava	4.8
Andropogon virginicus	4.0
Festuca elatior	3.4
Cirsium vulgare	2.2
Paspalum leave	2.2
Holcus lanatus	1.8
Lespedeza sp.	1.8
Eragrostis spectabilis	1.6
Acalypha rhomboidea	1.2
Panicum clandestinum	1.2
Juncus tenuis	1.0
Muhlenbergia sp.	1.0
Erigeron canadensis	0.8
Trifolium pratense	0.8
Daucus carota	0.6
Plantago sp.	0.4
Taraxacum officinale	0.4
Vernonia altissima	0.4
Eupatorium serotinum	0.2
Medicago sp.	0.2

Order based on mean percent cover for $n = 25$ 1-m^2 plots

structure and composition. The old field had >40% more plant cover than did the pasture and twofold higher species richness, which, along with higher evenness, resulted in higher species diversity (Table 2). The pasture was overwhelmingly dominated by *Festuca elatior* (Table 5), one of the most commonly planted pasture species (Smith 1995). With a mean cover of >70%, *F. elatior* exhibited a

degree of dominance in the pasture not seen in the old field. Its single-species relative cover of >40% was similar to the sum of relative cover of the top three old-field taxa (*Poa* spp., *Ambrosia artemisiifolia*, and *Verbesina alternifolia*)—all of which are common constituents of fields following agricultural abandonment (Raynal and Bazzaz 1975; DeSteven 1991; USDA 2004) (Table 6).

Table 6 Species encountered within a 5-m × 5-m site located within an abandoned pasture in Wayne County, WV

Species	Mean cover (%)
Festuca elatior	71.0
Aster pilosus	58.4
Poa sp.	23.0
Solanum carolinense	7.2
Cinna arundinacea	7.0
Vernonia altissima	5.8
Setaria glauca	3.2
Digitaria sanguinalis	2.8
Arthraxon hispidus	2.6
Elephantopus carolinianus	1.8
Juncus effusus	1.8
Carex vulpinoidea	1.2
Juncus tenuis	1.2
Phaseolus polystachios	1.2
Glechoma hederacea	0.6
Oxalis stricta	0.6
Panicum anceps	0.6
Cyperus strigosus	0.2
Taraxacum officinale	0.2

Order based on mean percent cover for $n = 25$ 1-m^2 plots

There were also sharp contrasts in soils between the two sites, despite being of the same (Kanawha) series comprising deep alluvial parent materials. More notable differences were in soil N (net N mineralization/nitrification rates of old-field soils being twice that of the pasture) and extractable Mg and Al, both significantly higher in old-field soils (Table 2).

Studies such as ours recall the *circulus vitiosus* first described by Jenny et al. (1969) to characterize the dilemma in distinguishing effects of soil on plants versus effects of plants on soil. Our data suggest that the reciprocating nature of these effects may itself vary with land-use history. Not only did spatial correlations (patterns) of soil constituents vary between pasture and old-field sites (Table 3), but the degree to which soil factors explained plant variables (via backward stepwise regression) was far greater in the pasture than in the old field (Table 4).

Equally clear, however, is the potential for plants to exert direct influences on soil (van der Krift and Berendse 2001). Wedin and Tilman (1990) provided strong evidence for the direct effects plants can have on soil. Focusing on plant-mediated changes in net N

Table 7 Summary of geostatistical analyses of soil and vegetation variables for pasture and old-field sites

Variable	Pasture						Old field					
	Model	Nugget	C1	Sill	N:S	A1	Model	Nugget	C1	Sill	N:S	A1
N mineralization	Spherical	0.57	0.04	0.61	0.93	3.49	Spherical	0.73	6.07	6.81	0.11	1.41
Nitrification	Linear						Spherical	0.00	0.78	0.78	0.00	0.25
NH$_4$	Linear						Spherical	0.06	13.12	13.18	0.00	0.13
NO$_3$	Spherical	0.00	7.68	7.68	0.00	0.39	Spherical	0.00	6.80	6.80	0.00	0.37
Organic matter	Linear						Spherical	0.43	0.15	0.58	0.74	2.16
pH	Spherical	0.03	0.05	0.08	0.34	4.45	Spherical	0.01	0.01	0.02	0.59	0.98
Ca	Random						Spherical	0.00	41757	41757	0.00	1.43
Mg	Spherical	0.00	18147	18147	0.00	3.69	Random					
Al	Linear						Linear					
Cover	Spherical	120.00	580.20	700.20	0.17	1.41	Linear					
Species richness	Spherical	0.18	0.97	1.15	0.16	2.31	Spherical	0.56	0.41	0.97	0.58	4.14
Species evenness	Spherical	0.002	0.001	0.003	0.62	1.23	Spherical	0.0003	0.004	0.004	0.09	2.75
Species diversity (H')	Spherical	0.01	0.01	0.02	0.32	1.31	Spherical	0.01	0.01	0.01	0.42	0.86

"Sill" is calculated as the sum of "nugget" variance and structural variance ("C1"). "N:S" is the ratio of nugget to sill values. "A1" denotes the lag distance (in m) within which a given variable is spatially dependent and beyond which is spatially independent. These statistics are not shown for variables for which the relationship between semi-variance and lag distance was either random or linear

mineralization and nitrification, they grew monocultures of five perennial grass species in identical soil for 3 year and found up to 10-fold differences in rates of N dynamics. They also concluded that strong vegetation/soil feedbacks can exist in herb-dominated communities, such as those in our study, which can mediate processes that control species composition (Wedin and Tilman 1990).

Other studies have shown feedbacks involving plants and soil microbial communities (Bever 1994; Eskelinen et al. 2009). Although we did not characterize microbial communities directly in this study, we did assess microbially mediated processes—net N mineralization and nitrification—that varied substantially between site types (Table 2). It is possible that differences between sites in dominant grasses resulted in variation in soil microbes responsible for soil N dynamics. Bowman et al. (2006) demonstrated that *Festuca* species are capable of taking up essentially 100% of added NH_4 in as short a period as 5 h, precluding its availability to nitrifying bacteria and limiting net nitrification. This control on microbial processes can be maintained by efficient resorption of N by foliage (May et al. 2005), limiting N availability to N-mineralizing microbes. By contrast, Paré et al. (2006) found that *Poa* species are relatively inefficient in taking up available N, allowing more NH_4 for nitrifier populations (increasing nitrification) and creating a positive feedback by resorbing less N and providing more organic N in foliage for N mineralizing microbes.

Evidence for these feedbacks can also be seen in results of geostatistical analyses. Because a nugget:sill ratio (N:S) of 1 indicates a random (rather than spatially dependent) pattern, the degree of spatial dependence is essentially inversely related to N:S. Thus, the N:S for net N mineralization in the pasture of 0.93 (Table 7) suggests that N mineralization in the pasture approached randomness (i.e., was only slightly spatially dependent). That observation, combined with a lack of spatial dependence for net nitrification, is consistent with the lack of spatial dependence for *F. elatior* (Table 8), which was over 40% of total cover for the pasture.

By contrast, both net N mineralization and net nitrification were highly spatially dependent in the old field (N:S = 0.11 and 0.00, respectively), as was *Poa* sp., which dominated the old field (N:S = 0.00). Furthermore, the lag distance (1.41 m) for net N mineralization was similar to that for *Poa* sp. (1.87 m) (Tables 7, 8).

It is further notable that study sites varied in species evenness, with the old field having significantly higher evenness than the pasture (Table 2). Often included primarily as one of a suite of indices to characterize community structure and plant biodiversity (e.g., SHE analysis, Small and McCarthy 2002), evenness has also been shown to have significance at the ecosystem level. Wilsey and Potvin (2000) provided evidence that species evenness can play a direct, mechanistic role in determining and maintaining structure and function of old fields. Experimentally manipulating evenness and identity of dominant species (including *Fragaria virginiana*, *Poa pratensis*, and *Taraxacum officionale*) in an old field of Quebec, they found that total plant biomass increased linearly with species evenness, independent of dominant species. Using cover as a surrogate for biomass

Table 8 Summary of geostatistical analyses for dominant (top three, based on cover) species from pasture and old-field sites

Site/species	Model	Nugget	C1	Sill	N:S	A1
Pasture						
Festuca elatior	Linear					
Aster pilosus	Spherical	59.90	663.90	723.80	0.08	2.86
Poa sp.	Linear					
Old field						
Poa sp.	Spherical	0.00	493.10	493.10	0.00	1.87
Ambrosia artemisiifolia	Linear					
Verbesina alternifolia	Spherical	60.58	455.7	516.28	0.12	4.68

"Sill" is calculated as the sum of "nugget" variance and structural variance ("C1"). "N:S" is the ratio of nugget to sill values. "A1" denotes the lag distance (in m) within which a given variable is spatially dependent and beyond which is spatially independent. These statistics are not shown for variables for which the relationship between semi-variance and lag distance was either random or linear

(Gilliam and Turrill 1993), our results are consistent with their findings, with the old field having >40% higher cover than the pasture (Table 2).

Old field and pasture sites also differed in soil factors that most directly influence species composition. Although canonical correspondence analysis identified plant cover as being of secondary importance at both sites, extractable aluminum (Al) and organic matter (OM) were of primary importance at the old field and pasture, respectively (Figs. 2, 3). This contrast is particularly notable considering the abiotic versus biotic nature of these two soil variables. Soil Al is generally a product of weathering of parent material and, although not commonly analyzed in studies focusing on plant–soil interactions, has been shown to correlate well with plant species' distributions (Gilliam et al. 2005). Variation in OM is generally a function of above- and belowground inputs from vegetation, as well as rates of decomposition (Jackson and Caldwell 1993).
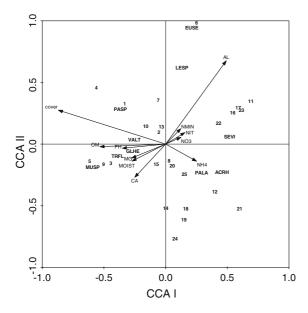

Fig. 2 Canonical correspondence analysis (CCA) ordination plot for the old-field site. Lines radiating from origin represent environmental gradients. Only the top 10 species (based on axis loading) are included: *Eupatorium serotinum* (EUSE), *Lespedeza* sp. (LESP), *Panicum* sp. (PASP), *Vernonia altissima* (VALT), *Glechoma hederacea* (GLHE), *Setaria viridis* (SEVI), *Triodia flava* (TRFL), *Muhlenbergia* sp. (MUSP), *Paspalum laeve* (PALA), *Acalypha rhomboidea* (ACRH). Numbers represent location of each of the 25 sample plots in ordination space (see Fig. 1). Eigenvalues: CCA I—0.222, CCA II—0.101; total inertia: 1.351; species–environment correlations: CCA I—0.94, CCA II—0.78
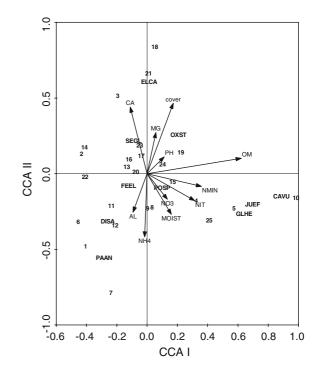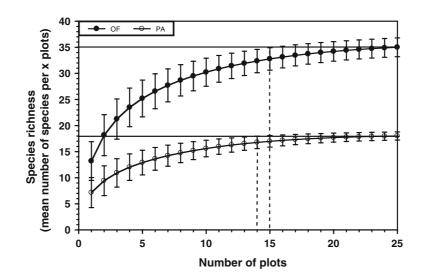

Fig. 3 Canonical correspondence analysis (CCA) ordination plot for the pasture site. Lines radiating from origin represent environmental gradients. Only the top 10 species (based on axis loading) are included: *Elephantopus carolinianus* (ELCA), *Oxalis stricta* (OXST), *Digitaria sanguinalis* (DISA), *Festuca elatior* (FEEL), *Glechoma hederacea* (GLHE), *Setaria glauca* (SEGL), *Carex vulpinoidea* (CAVU), *Poa* sp. (POSP), *Panicum anceps* (PAAN), *Juncus effusus* (JUEF). Numbers represent location of each of the 25 sample plots in ordination space (see Fig. 1). Eigenvalues: CCA I—0.125, CCA II—0.074; total inertia: 0.702; species–environment correlations: CCA I—0.89, CCA II—0.90

Despite the >2-fold higher species richness of the old field versus the pasture (13 and 6 species/m^2, respectively), the minimum number of plots required to adequately characterize community composition was quite similar between the two sites (Fig. 4). Using an approach similar to that of Small and McCarthy (2002), we first created expected species–accumulation curves (which have also been called species–area curves and sample-based rarefaction—Gotelli and Colwell 2001) and then calculated minimum plot number as number of plots resulting in upper 95% confidence intervals closest to total species richness (35 vs. 18 species for old field and pasture, respectively). This method yielded minimum plot numbers of 15 and 14, respectively.

In conclusion, it is clear that two herbaceous-dominated communities of contrasting land-use

Fig. 4 Expected species–accumulation curves for old field (*closed symbols*) and pasture (*open symbols*) sites. Points shown are mean number of species for a given number of 1-m² sample plots; error bars are ±95% confidence interval. Lines parallel to the *x*-axis that intersect the *y*-axis are total richness for each site. The intersection of those lines with the respective upper 95% confidence limit indicates minimum number of plots to characterize species richness representative of each site. The vertical dashed line represents minimum plot number

history are profoundly different in several ways. Not only did they differ with respect to community composition (with *Poa* sp. and *Festuca elatior* clearly dominating old field and pasture sites, respectively) and structure (with the old field having >40% greater plant cover), but they also varied with respect to soil chemistry and fertility. Furthermore, and more to the purpose of this study, these sites also varied in spatial pattern of vegetation, individual plant species, and soil. Fraterrigo and Rusak (2008) concluded that among the more profound influences of disturbance is a direct effect on spatial heterogeneity of ecological properties. Our results are consistent with this contention.

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