



Little evidence of native and non-native species influencing one another's abundance and distribution in the herb layer of an oak woodland

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Introduction

Plant species abundance and composition can vary among sites due to differences in climate, macro-habitat differences (including disturbance regimes), regional species pools and history among the sites (Peet et al. 2014b). Within sites, environmental heterogeneity, including both biotic and abiotic factors, can cause spatial variation in species abundance and composition (Stein et al. 2014). The abiotic factors can include micro-disturbances (Beatty

Abstract

Question: To what extent are species, including native and non-native species, influencing one another's distribution and abundance in the herb layer of a Minnesota oak woodland?

Location: Oak woodland succeeding into a more mesic forest, on bluffland of the Mississippi River, east-central Minnesota.

Methods: We collected plant composition and species cover data in 182 1.0 × 0.5 m quadrats regularly spaced on a 6-ha study grid in the oak woodland. We also recorded slope, slope position, aspect, elevation and photosynthetically active radiation (PAR) at each quadrat.

Results: Presence and abundance of other plant species, topographic variables and light availability explained only a small portion of the variation (5–19%) in the distribution and abundance of individual species. The most common strongest predictor of cover for the ten most common species was species richness, with the association being positive. The non-native species, garlic mustard (*Alliaria petiolata*) exhibited the strongest positive association with species richness. Only one of the 45 pair-wise comparisons of the ten species resulted in a negative relationship between the species. Abundance and distribution of two species were associated with topographic features, but this accounted for much less of the variation in abundance than did species richness.

Conclusion: We found little evidence that competition or any other interactions among common herb layer species, including the non-native *Alliaria petiolata*, play an important role in determining the abundance and the distribution of herb layer species in this oak woodland. Topographic factors may explain a small amount of the distribution and abundance patterns of a few species. But, for the most part, species are more likely to be present when other species are present, suggesting that they are simply establishing in microsites favourable to plants in general.

2014), heterogeneity in topography (Cantlon 1953), light availability (Pearcy et al. 1987) and a variety of edaphic factors, such as pH, moisture and soil nutrients (Peet et al. 2014a) some of which, e.g. light, water and nutrient availability can, in turn, be influenced by biotic interactions such as competition (Tilman 1982).

In the 1980s, interspecific competition, grounded in niche theory, was believed to be a primary driver of community structure in general (MacArthur 1972) and in plant communities in particular (Tilman 1982, 1985;

Lomnicki 1988). Thus, it is perhaps not surprising that ecologists' initial view of non-native forest herbs was as a competitor, and that if the non-natives established and spread widely, they must inevitably exclude some native herbs. For example, during the past several decades, ecologists have typically characterized garlic mustard, *Alliaria petiolata* (M. Bieb.) Cavara & Grande, a perennial herb introduced into North America from Eurasia, as an aggressive invader that is changing the ecology of eastern North American forests and causing a decline in native plant diversity (Rodgers et al. 2008).

More recent assessments have concluded that non-native forest herbs in eastern North American forests are not fundamentally ecologically different from indigenous species (Luken 2014), and some long-term studies have not found them to negatively affect the distributions of native species in any substantial way (Davis et al. 2012, 2014; Beatty 2014). Increasingly, data are showing that other agents and factors are more likely responsible for most of the changes in the abundance and distribution of native herbs in forests and woodlands in eastern North America, including herbivory from white-tailed deer (Tilgham 1989; Eschtruth & Battles 2009), changes to the soil and litter environment by earthworms (Hale et al. 2006; Nuzzo et al. 2009), fragmentation and changes in disturbance histories (Nowacki & Abrams 2008; Eschtruth & Battles 2009), and nitrogen deposition (Gilliam 2014a).

The purpose of the study reported here was to examine the spatial distributions and abundance of the most common species in the herb layer of a single oak woodland in a way that would enable us to evaluate the extent to which the species may be affecting one another's abundances and distributions, as well as to determine the role that topographic factors (elevation, slope, aspect, slope position) and light availability may be playing in structuring the herb layer community. By focusing on species abundances and composition patterns within a single site we tried to assess the importance of within-site environmental heterogeneity, including both biotic and abiotic heterogeneity (Stein et al. 2014), in determining the abundance and distribution of herb layer species within a single oak woodland.

Methods

Study site and study grid

We conducted this study at Macalester College's field station, the Katharine Ordway Natural History Study Area, located in Inver Grove Heights, Dakota County, in eastern Minnesota (44°48'36" N, 93°01'24" W). Situated on the bluffs of the Mississippi River, the field station contains a variety of habitats, including grasslands, several wetlands, riparian habitat, a backwater lake and a woodland, the last

of which was the site of this study. The woodland is dominated by oaks (*Quercus rubra* L., *Q. ellipsoidalis* E.J. Hill, *Q. alba* L., *Q. macrocarpa* Michx.); however, the absence of fire in most of the woodland during the past half century has resulted in the establishment of a number of fire susceptible tree species, which now make up the majority of the understory and mid-storey trees, the most common being *Ulmus americana* L., *U. rubra* Muhl., *Acer negundo* L., *Prunus serotina* Ehrh., *Tilia americana* L. and *Fraxinus pennsylvanica* L. The absence of fire and on-going succession has resulted in a mostly closed tree canopy. Earthworms are abundant in the soil at the study site, and we rated the site as being in stage three of Loss et al.'s (2013) five stage classification scheme of earthworm invasion in northern hardwood forests, which is based on characteristics of the forest floor. Stage three is described as: leaf litter from previous autumn and small fragmented leaves under intact leaves, no humus, mineral soil present, earthworm casting present (<50% of forest floor/mineral soil interface covered), fine plant roots absent. White-tailed deer, *Odocoileus virginianus*, Zimmerman, are abundant in the Mississippi River forest corridor, and at the study site.

In this study, we consider the herb layer as consisting of all vascular plants, both herbaceous and woody, <1 m in height (Gilliam 2014b). Prior studies (Davis et al. 2012, 2014) showed that the ten most common species in the herb layer are: two shrubs – *Ribes missouriense* Nutt. and *Rubus* spp.; one tree – *Rhamnus cathartica* L.; one woody vine – *Parthenocissus quinquefolia* (L.) Planch.; one herbaceous vine – *Amphicarpaea bracteata* (L.) Fernald; and five other herbs – *Desmodium glutinosum* (Muhl. ex Willd.) A.W. Wood, *Geranium maculatum* L., *Ageratina altissima* (L.) King & H.E. Robins., *Circaea lutetiana* L. and *A. petiolata*. *R. cathartica* and *A. petiolata* are non-native species.

In the summers of 2010 and 2011, we set up an irregularly shaped (roughly rectangular) 6.08-ha study grid in the oak woodland, consisting of 152 20 × 20 m cells, with vertices defined by UTM (Universal Transverse Mercator) coordinates. Each vertex was permanently marked with a 1.5 m rebar (iron pole, 1 cm diameter) affixed with a metal tag indicating its coordinates. Situated on the bluff landscape, which, in the area of the grid, faces just south of east (105°) at a macro-scale, the grid includes considerable topographic variation at smaller scales, including slope (1–45°), aspect (2–354°, and all compass directions in between) and nearly 30 m in elevation (212.4–241.7 m a.s.l.).

Data collection

Vegetation

In July 2014, we established a 1.0 × 0.5-m quadrat at each of the 182 rebars that delineated the 6.08-ha study grid.

Since we wanted to focus on the distributions of the most common species, we estimated percentage cover of the ten most common herb layer species described above. In addition, we recorded the number and total percentage cover of other herb layer species in each of three groups: ferns, woody plants (including seedlings) and herbs (including seedlings).

Topography

At each rebar, we recorded the aspect at that point using a compass and the slope using a clinometer. We also recorded slope position of each rebar as one of five categories describing its local topographic position: top (flat area on the top of a hill), shoulder (transition from the top to a downward slope), middle (positioned along the downward slope), ankle (transition from the downward slope to a bottom valley position) and valley (flat low elevation position). We obtained elevation values for each of the rebars from the Dakota County Office of GIS (Geographical Information System).

Light

At each rebar, we recorded photosynthetically active radiation (PAR; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) using a LiCor 250A light meter (LiCor, Lincoln, NE, US). The 1-m long recording rod was positioned at each rebar parallel with the slope 1 m above the ground (above any herb layer vegetation) and facing the aspect direction at that point. Thus, we measured the actual intensity of light received by the herb layer at each location, taking into account slope and aspect. Light readings were recorded during cloudless periods between 11:00 and 13:00 hr from 18 July to 2 Aug 2014. A measurement of full sun PAR (outside of forest canopy cover), with the surface of the rod positioned perpendicular to the sun, was also taken on each measuring day during the 2-hr period so that individual rebar measurements could be converted to percentage maximum PAR.

Data analysis

In order to look at simple relationships between individual species and some community characteristics, we conducted pair-wise non-parametric correlations for the ten target species, as well as correlations between each species and total herb layer species richness and total herb layer cover minus the cover of the target species. To account for the high number of ties due to zero values we used Kendall's tau-b as a measure of correlation, which is adjusted for the presence of ties (Kendall 1970), and generated confidence intervals via bootstrap resampling (1000 replicates) using the bias-corrected option in SPSS 22.0 (SPSS,

Chicago, IL, US). Due to the high number of comparisons (65 correlations) performed, we limited consideration of a correlation as significant only if the 99% confidence intervals did not include zero.

In order to examine more comprehensively how the distribution and abundance of individual species may be associated with both biotic (vegetation cover and species richness) and abiotic (topographic heterogeneity and PAR) factors, we conducted step-wise multiple regression analyses for each of the ten species. We utilized the mixed forward and backward selection procedure in JMP 11.0 (SAS Institute, Cary, NC, US) and selected variables based on *P*-value thresholds (0.25 to enter and leave). The following factors were included at the outset: species richness (of the herbaceous layer for herbaceous dependent variables and all species for woody dependents), total cover minus cover of the target species, elevation, slope, aspect, slope position and percentage maximum summer PAR. Richness was tested as linear and with square, and square root transformations, based on the non-linear relationship between cover and richness in our plots (Fig. 1). Since our interest in aspect involved its role in mediating sunlight intensity, we were interested in where quadrats fell along a north-south aspect gradient. Thus, for analysis purposes, we adjusted all aspects with degree measurements between 180 and 360 to their mirror counterparts, e.g. 190 to 170, 270 to 90, 350 to 10, etc. Dependent variables (percentage cover for the target species) were log-transformed, which stabilized variance but still yielded non-normally distributed residuals for most of the target species, due largely to the presence of thresholds stemming from zero values for dependent variables (Appendix S1). Therefore, final independent variable selection was based on *P*-values obtained via bootstrap resampling (1000 replicates) of a reduced model that began with a subset of explanatory variables found to be promising in the parametric step-wise procedure. Explanatory variables selected by this method were also tested using generalized linear models (GLiM) with exponentially distributed dependent variable and reciprocal link function (JMP 11.2). In all cases GLiMs produced nearly identical results compared to multiple regression models, while removing the threshold effect in residual plots (data not shown). Residuals were checked for the presence of spatial autocorrelation using Moran's *I* (both global and correlogram with ten distance classes) calculated in PASSaGE 2.0 (Rosenberg & Anderson 2011).

Multiple regression models yielded by the step-wise procedure were validated using split sample cross-validation (Neter et al. 1996). Observations were assigned to training and validation sets in alternating order based on spatial position on the sampling grid, yielding data sets that completely overlapped across the sampled area. Models generated by step-wise selection from the training set were

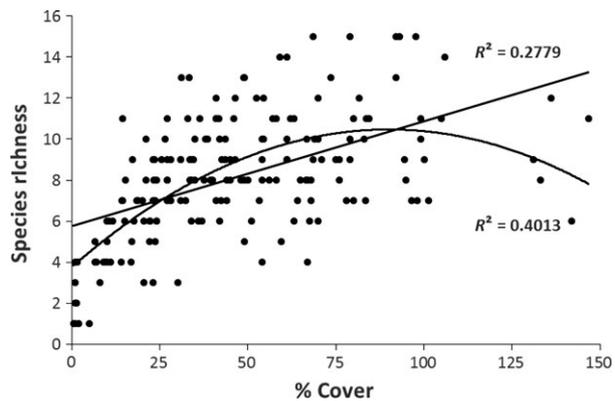


Fig. 1. Species richness shown as a function of total percentage cover of all herb layer species in the 182 quadrats. Shown are both a best linear fit and a best second order polynomial fit.

re-tested in the validation set. Final validation was assessed using three criteria: (1) model strength based on r^2 , for which a difference between training and validation results of <5% was considered validated; (2) retention of explanatory variables in the validation model, which was assessed by examining whether the 95% confidence intervals for bootstrapped (1000 reps) coefficient values of explanatory variables selected in the training set included zero in the validation set; and (3) specific coefficient values for each validated explanatory variable, which were considered validated if there was <5% non-overlap of 95% bootstrap confidence intervals for training and validation models.

Results

Percentage cover by herb layer species in the 182 quadrats ranged from 0.5% to 147% (mean = 46.7%, median = 41.9%). Species richness ranged from one to 15 species (mean = 8.1, median = 8). Herb layer species richness was positively correlated with total percentage cover ($r = 0.53$, $P < 0.0001$; Spearman $P = 0.56$, $P < 0.0001$). While there is a highly significant correlation between total percentage cover and species richness, Fig. 1 shows that the relationship is not linear but hump-shaped, and that a second order polynomial line fits the data better. The mean covers for the individual species ranged from 10.9% (*Desmodium glutinosum*) to 0.69% (*Rhamnus cathartica*), and frequencies (percentage of the 182 quadrats containing each species) ranged from 78.6% (*D. glutinosum*) to 13.7% (*R. cathartica*).

The pair-wise non-parametric analyses of the cover of individual species with one another, with species richness and with cover of all other species in the quadrat revealed 14 significant correlations (Table 1); 13 of these were positive. Half of the positive correlations involved the cover of

Table 1. Significant pair-wise non-parametric (Kendall's Tau-b) correlations between vegetation parameters. 99% confidence intervals were determined by bias-corrected bootstrap resampling (1000 replicates; SPSS 22.0). Bold values are correlations determined for original data.

Variable 1	Variable 2	Kendall's Tau-b
Herbaceous	<i>Alliaria petiolata</i>	0.29 – 0.429 – 0.54
Richness	<i>Ageratina altissima</i>	0.18 – 0.325 – 0.46
	<i>Amphicarpaea bracteata</i>	0.13 – 0.272 – 0.39
	<i>Geranium maculatum</i>	0.09 – 0.249 – 0.37
	<i>Rubus</i> spp.	0.09 – 0.224 – 0.36
	<i>Desmodium glutinosum</i>	0.09 – 0.215 – 0.34
	<i>Circaea lutetiana</i>	0.02 – 0.180 – 0.32
<i>Amphicarpaea bracteata</i>	<i>Rubus</i> spp.	0.04 – 0.212 – 0.38
<i>Parthenocissus quinquefolia</i>	<i>Geranium maculatum</i>	–0.01 to –0.167 to –0.31
<i>Alliaria petiolata</i>	Total cover of other herbs	0.09 – 0.227 – 0.36
<i>Ageratina altissima</i>	Total cover of other herbs	0.03 – 0.178 – 0.33
<i>Amphicarpaea bracteata</i>	Total cover of other herbs	0.03 – 0.157 – 0.28
<i>Rubus</i> spp.	Total cover of other species	0.11 – 0.228 – 0.33
<i>Ageratina altissima</i>	Total cover of other species	0.03 – 0.191 – 0.34

individual species with species richness, with *A. petiolata* being most strongly positively associated with species richness. Over a third of the correlations were positive correlations with total cover of all other herbaceous species. The only negative correlation involved the cover of *Parthenocissus quinquefolia* and *Geranium maculatum*.

Multiple regression models explained little of the variation in any of the ten most common herb species in our plots: model r^2 ranged from non-significant for *R. cathartica* to a maximum of 0.19 for *A. petiolata* (Table 2). By far the most important correlate with cover of target species was richness of the plant community, which was the most significant explanatory variable in eight of the nine significant models, and the only retained variable in seven of them. The only abiotic environmental variable retained in any model was elevation, which was only retained for one target species (*P. quinquefolia*) for which it was the sole explanatory variable. Significant spatial autocorrelation was only detected for two species. For *A. bracteata* significant Moran's I values ranged from 0.09 to 0.16 over distance classes ranging from 100–120 to <55 m, respectively, and from –0.07 to –0.19 over distance classes ranging from 180–210 to >240 m, respectively. For *P. quinquefolia*, Moran's I was only significant at the smallest distance class (<55 m), for which it had a value of 0.11.

Table 2. Results of multiple regression models performed using each of the ten target species as the dependent variable. Models were validated using split-sample cross-validation based on r^2 (<5% difference), presence of explanatory variables and parameter values for each explanatory variable (<5% non-overlap of 95% bootstrap confidence intervals).

Species	Model Statistics (Full Data Set)				Validation Results					Auto-Correlated Residuals?	
	Adj R^2 (Model)	F (Model)	P (Model)	Explanatory Variables	F (Variable)	P (Variable)	Positive or Negative	Strength (Model r^2)	Factor Presence		Factor Coefficient
<i>Desmodium glutinosum</i>	0.13	27.5	<0.0001	Herb	27.5	<0.0001	Positive	No	Yes	Yes	No
<i>Alliaria petiolata</i>	0.19	42.6	<0.0001	Richness ^{^(1/2)}	42.6	<0.0001	Positive	Yes	Yes	Yes	No
				Herb							
<i>Amphicarpaea bracteata</i>	0.08	17.3	<0.0001	Richness ^{^2}	17.3	<0.0001	Positive	Yes	Yes	Yes	Yes
				Herb							
<i>Ageratina altissima</i>	0.13	28.5	<0.0001	Richness ^{^(1/2)}	28.5	<0.0001	Positive	No	Yes	Yes	No
				Herb							
<i>Geranium maculatum</i>	0.10	21.7	<0.0001	Richness ^{^2}	21.7	<0.0001	Positive	No	Yes	Yes	No
				Herb							
<i>Circaea lutetiana</i>	0.05	9.9	0.002	Richness	9.9	0.002	Positive	Yes	Yes	Yes	No
				Herb							
<i>Parthenocissus quinquefolia</i>	0.09	19.7	<0.0001	Richness	19.7	<0.0001	Positive	Yes	Yes	Yes	Yes
				Elevation							
<i>Rhamnus cathartica</i>	NS	–	–	–	–	–	–	–	–	–	–
<i>Ribes missouriense</i>	0.06	11.7	0.0008	Total Richness	11.7	0.0008	Positive	Yes	Yes	Yes	No
<i>Rubus</i> spp.	0.11	12.2	<0.0001	Total Richness	22.2	<0.0001	Positive	Yes	Yes	Yes	No
				Slope							
					6.3	0.01	Positive		No	No	No

Discussion

The combination of possible interactions with other species, topographic heterogeneity and light availability explained only a small amount of the distribution and abundance variation of the ten most common herb layer species at the study site. The range in variation accounted for by the multiple regression models extended from a maximum of 19%, in the case of *Amphicarpaea bracteata*, to a minimum of 5%, in the case of *Circaea lutetiana*.

Factors associated with the abundance and distribution of herb layer species in the study site

In the multiple regression analyses, species richness was strongly positively associated with the abundance of eight of the ten species, and it accounted for a substantial portion of the variation explained by the models.

The positive correlation between most of the species and species richness raises the possibility of strong facilitation of some sort taking place among species. However, past research has found little evidence of such interactions (Peet et al. 2014a). Much more likely is that there are favourable and not so favourable areas in the woodland for herb layer species and different species simply cluster in the favourable areas (Peet et al. 2014b). For an herb layer species, favourableness undoubtedly involves a number of factors, including soil conditions (pH, moisture, nutrients) and light (Peet et al. 2014b). Once multiple species are found in favourable locations, processes such as dispersal (Bazzaz 1996) and clonal growth (Canullo et al. 2011) may serve as positive feedback loops that help to maintain these 'hotspots'.

Although species richness almost certainly is a consequence, not a driver, of species' distributions, topographic factors may be causal agents, contributing to the favourableness of particular microsites, e.g. influencing soil and light conditions. The results show that only two species were associated with some of the topographic heterogeneity at the site, including elevation, aspect, slope and slope position.

Tilgham (1989) concluded that light is the most important factor limiting growth of woodland herbs, and Bazzaz (1996) emphasized that light is the most variable plant resource. Thus, it may seem surprising that summer light was found to be a significant factor for any of the species. The lack of association between summer light and the distributions of the majority of the herb layer species is likely due to the fact that there is not much spatial heterogeneity with respect to summer light in the study site. While occasional tree falls provide sporadic patches of light, most of the site is covered by tree canopy and light availability is low. We recorded less than 5% maximum summer PAR at

130 (74%) of the 182 sampling quadrats, and 88% of the quadrats (160) received <10% maximum PAR. Only five of the quadrats received more than 20% maximum PAR. Thus, there was not much spatial heterogeneity in light availability to which the species could respond.

Little evidence that competition is structuring the herb layer community

We found very little evidence that competition is an important factor in structuring the herb layer community at the scale sampled in this study (0.5 m²). In the bi-variate and multiple regression analyses, all the significant associations between individual species and species richness were positive, as were all but one of the significant pair-wise species associations. It is known that neighbouring woodland plants can reduce interspecific competition by spatially and/or temporally segregating the root and shoot environments (Balandier et al. 2006), and it is possible this may partly account for our findings.

The inverse correlation between *Parthenocissus quinquefolia* and *Geranium maculatum* suggests the possibility that competition could be occurring between these two species. However, as Silvertown & Charlesworth (2001) pointed out, such an inverse correlation could have nothing to do with interactions between the species, and instead could be due to the respective species responding differently to other factors. Additional research with respect to these two species is needed to distinguish between these two possibilities.

One can always demonstrate competition among plants by making the observed spatial scale small enough, e.g. competition will always be exhibited when the observed scale is so small that there is room for just one plant. But we found little evidence for competition in the 0.5-m² quadrats in this study. In a similar study, Duncan et al. (1998) found no evidence that competition limited the number of species in 0.2-m² quadrats, and Rogers (1983) found little evidence of competition among forest herbs even at scales as small as 0.02 m² (10 × 20 cm quadrats). This is not to say that no competition is occurring, just that it is not playing much of a role in community assembly at the scale of the quadrats. Rogers (1983) came to the same conclusion, acknowledging that the herbs may compete with one another but not to an extent that influences community organization. Likewise, Peet et al. (2014a) concluded that competition among mature herbaceous forest plants might be limited in its explanatory power, suggesting instead that current patterns of abundance and distribution might, in large part, be due to history.

Most studies of herb layer species have documented a monotonic increasing relationship between species richness and productivity (Peet et al. 2014b). If cover is

used as a surrogate for annual productivity, the same pattern holds true in our study up to about 75% cover, when species richness levels off up to about 100% cover (Fig. 1). Beyond 100% cover, species richness declines, which is consistent with Grime's (1973) proposed humped-back relationship between productivity and species richness (assuming that cover is an adequate substitute for productivity). This suggests that competition may be influencing community composition at the quadrat scale in very high cover areas. However, only eight of the 182 quadrats (4%) contained herb layer cover exceeding 100%, meaning that this is not likely a common occurrence.

Little evidence that *Alliaria petiolata* negatively affects native herb layer species

We were unable to find evidence that *A. petiolata* is negatively affecting the other common herb layer species, a finding that is consistent with recent conclusions of others that *A. petiolata* is not a significant driver of change in eastern North American forests (Nuzzo et al. 2009). Five years of monitoring of *A. petiolata* in the study site have shown that the population has not increased during this time and may be beginning to decline in abundance (Davis et al. 2014). Declining abundance of *A. petiolata* as the oak woodland is succeeding to a more mesic forest with a more closed canopy would be consistent with *A. petiolata* being light-sensitive (Eschtruth & Battles 2009), as well other findings and observations that non-native plant species in general, which typically are quite light-dependent, decline during succession (Vankat & Snyder 1991; Luken 2014).

Summary

We found little evidence that competition or any other interactions between common herb layer species are influencing their abundance and distribution in this particular oak woodland. With respect to *Alliaria petiolata* in particular, we found no evidence that it is negatively affecting the common native herb layer species. The strongest predictor for the presence and abundance of most of the species, including *A. petiolata*, was the presence of other species. Essentially, certain areas seem to be quite favourable for most of the herb layer species to grow, while other areas are less favourable. One might argue that dispersal limitation is a primary reason why species are not found in some areas, and hence that areas with few species are not necessarily unfavourable. However, the fact that all the species seem to be able to disperse to apparently favourable locations throughout the study grid seems to undermine the dispersal limitation hypothesis.

Conceivably, history and stochasticity could have been responsible for the establishment of groups of species at

particular locations in the study grid and not in others. However, while perhaps theoretically possible, it seems unlikely that entire groups of species would have stochastically established themselves at particular locations and not in others. The simplest explanation for our findings is that species in the herb layer at this study site are distributing themselves mostly independent of one another. For some of the species, topographic factors may partly explain their distribution and abundance patterns. However, these are quite weak associations and they explain only a very small part of the distribution of these species. It is possible that heterogeneity in edaphic factors such as soil texture, pH and nutrient availability may be more important determinants at this site. Levels of soil base cations and pH exhibit considerable spatial variability throughout the study site: pH (5.3–7.6), Ca (830–3300 ppm), Mg (180–540 ppm) and Mn (40–215 ppm) (Michael D. Anderson, unpubl. data). In other studies of eastern deciduous forests, both pH and soil cations were found to be highly correlated with herb layer species richness (Peet & Christensen 1988; Peet et al. 2014a). More research is needed to determine the importance of edaphic factors in contributing to microsite favourability at this site.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Diagnostic statistics and plots for multiple regression models.

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main.



We found little evidence that competition among common herb layer species, including the non-native and reputed invasive *Alliaria petiolata*, significantly affects their respective abundances and distributions in a Minnesota oak forest. For the most part, species are more likely to be present when other species are present, suggesting that they are simply establishing in microsites favorable to plants in general.