



Functional traits influence local plant distributions and spatial patterns of diversity within a heterogeneous bedrock glade

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Abstract

Functional traits influence plant distributions along broad environmental gradients leading species to occupy communities where their traits enable them to successfully establish and compete for resources. Trait differences are also expected to influence plant distributions and diversity at finer spatial scales within communities. However, relatively few empirical studies have examined the extent to which interspecific trait variation predicts local species-environment distributions. We surveyed herbaceous plants within a heterogeneous acid bedrock glade in south-central Wisconsin to elucidate how traits influence local plant distributions and diversity. Using quadrat-scale environmental covariates (soil depth, canopy openness, and neighborhood tree phenology) and species functional trait means (SLA, vegetative height, and seed mass), we modeled variation in local species distributions as well as plant diversity across 361 quadrats distributed evenly in a 1 ha study plot. Functional traits predictably mediated individualistic species distributions along local gradients in soil depth and canopy openness as well as differential plant responses to variation in canopy leaf phenology. Small-seeded herbs occurred in shallow soil microsites while the prevalence of large-statured plants increased with canopy openness. Local species richness and functional trait dispersion were greatest in microsites near canopy gaps where sun-adapted and shade-adapted plant species co-occur and in microsites surrounded by later-leafing trees. Interspecific trait differences influence local species distributions and shape spatial patterns of diversity within heterogeneous plant communities like bedrock glades. The parallels between local plant distributions within this heterogeneous community and regional plant distributions across the landscape suggest trait-mediated ecological sorting influences plant distributions along environmental gradients similarly across spatial scales.

Keywords Bedrock glade · Canopy openness · Community assembly · Environmental filtering · Soil depth · Tree phenology · Wisconsin

Introduction

Environmental variation plays a fundamental role in determining plant distributions and diversity (Shmida and Wilson 1985; Stein et al. 2014). At landscape and continental scales, species distributions often track variation in climate,

topography, and edaphic conditions. Classic studies of plant distributions at broad spatial scales reveal how species sort individually along environmental gradients to form local communities (Whittaker 1956; Curtis 1959). These differential species distributions often reflect interspecific trait variation (Weiher and Keddy 1999; HilleRisLambers et al. 2012; Kraft et al. 2015). Plant traits thus link classical debates and concepts in plant ecology with modern approaches to the study of plant distributions and community patterns (Clements 1916; Gleason 1926; Curtis 1959; Beck et al. 2022). Morphological and physiological characteristics determine which species can successfully establish and compete for resources within a given environment. By examining trait-environment associations, ecologists can infer the importance of ecological sorting in community assembly and determine which traits structure plant communities (McGill et al. 2006; Violle et al. 2007; HilleRisLambers

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et al. 2012; Kraft et al. 2015). Predictable trait-environment associations across a variety of systems point to the general importance of trait-mediated ecological sorting in shaping broad-scale plant distributions (Ordoñez et al. 2009; Pollock et al. 2012; Jamil et al. 2013; Amatangelo et al. 2014; Bañares-de-Dios et al. 2020; Beck et al. 2022).

Plant distributions also respond to environmental variation at finer spatial scales (Struik and Curtis 1962; Leach and Givnish 1999; Burton et al. 2011; Beatty 2014). In temperate forests and savannas, local species distributions often track variation in light availability (Leach and Givnish 1999), soil depth (Bratton 1976; Beck and Givnish 2021), moisture availability (Beatty 1984), and soil fertility (Crozier and Boerner 1984; Vellend et al. 2000). Most studies examining the potential role of trait differences in mediating these local species-environment distributions focus on a small group of representative species (Bratton 1976; Pruka 1994; Leach and Givnish 1999; Burton et al. 2011; Beck and Givnish 2021). However, community-wide analyses of local trait-environment associations within heterogeneous plant communities remain scarce (Bergholz et al. 2017; Blonder et al. 2018). More comprehensive trait-based analyses of local species-environment distributions and diversity are needed to discern the strength of local trait-environment associations as well as the spatial scales at which trait-mediated ecological sorting shapes local plant distributions and spatial patterns of plant diversity (Silvertown et al. 2006; Kraft and Ackerly 2010; Chase and Myers 2011; HilleRisLambers et al. 2012; Chase 2014; Kraft et al. 2015; Blonder et al. 2018; Beck et al. 2022).

Environmentally heterogeneous plant communities present excellent systems for evaluating the potential importance of trait-mediated ecological sorting at finer spatial scales. In such communities, we expect species to occupy environmental microsites where their traits confer a competitive advantage leading to predictable trait-environment associations *within* the community. However, high rates of dispersal between adjacent but environmentally divergent microsites could weaken trait-environment associations at local scales if competitive differences are small relative to the rate of dispersal among microsites (Leach and Givnish 1999; Beck and Givnish 2021). Previous empirical studies in heterogeneous North American oak savannas reveal how trait differences can influence plant distributions along local variation in canopy cover and understory light availability (Pruka 1994; Leach and Givnish 1999). Like these oak savannas, bedrock glades are spatially heterogeneous and biologically diverse plant communities that exhibit patchy tree cover (Will-Wolf and Stearns 2010).

Bedrock glades are characterized by non-vertical bedrock exposures and thin, discontinuous soils that limit tree growth and result in highly heterogeneous environmental conditions (Armstrong 1994; Lange 1998; Ware 2002; Will-Wolf and

Stearns 2010). Soil depth can vary considerably from pockets of deep soil in rock crevices to exposed bedrock within the span of a meter. The sparse and spatially variable tree cover creates highly heterogeneous understory light conditions that can vary from full sun to full shade in the span of several meters. Moreover, the leaf phenology of different tree species can result in temporally heterogeneous light regimes. Characteristic plants include taxa variously associated with tallgrass prairie, oak savanna, dry to dry-mesic forests, and rock outcrops. This eclectic assemblage of species represents numerous functional strategies and presumably reflects the mosaic of spatially heterogeneous microsites varying in soil depth, canopy openness, and canopy tree phenology (Lange 1998; Epstein 2017). However, the assembly processes structuring local plant distributions remain poorly understood (Ware 2002; Epstein 2017). Trait-based analyses of local plant distributions in relation to fine-scale environmental heterogeneity will provide valuable insights into the ecological processes structuring local plant distributions and diversity in bedrock glades.

Here we examined local plant distributions and spatial patterns of plant diversity within a heterogeneous quartzite glade in south-central Wisconsin (USA). We sought to address the following questions: (1) How do functional traits influence local species-environment distributions? And, (2) are spatial patterns of taxonomic and functional diversity associated with soil depth and/or spatial and temporal variation in understory light availability? We predicted that local species-environment associations would reflect trait-mediated ecological sorting. Specifically, we expected shallow soil microsites would favor small-seeded and short-statured plant species. Shallow soils constrain the size and density of plants which should allow small-seeded seedlings to establish and access light despite having limited energy reserves for growth at the time of germination (Gross 1984; Westoby 1998). Similarly, shorter-statured plants are expected to occur in environments where the density of competitors is low and the structural costs incurred by taller species are not balanced by relatively higher rates of carbon assimilation (Givnish 1982). We expected large-statured plants to dominate in sunlit microsites where the density of herbaceous competitors is high. As herbaceous plant density increases, greater height allows taller plants to overtop neighbors, providing greater energetic returns on the structural costs associated with growing taller (Givnish 1982; Keddy and Shipley 1989; Keddy et al. 2002; Falster and Westoby 2003; Cahill et al. 2008). We predicted microsites with greater canopy cover and earlier-leaving trees would favor species with high specific leaf area (SLA) reflecting the photosynthetic advantages experienced by species with broad, thin leaves in shaded environments (Givnish 1988; Westoby 1998). Conversely, later canopy closure could support the persistence of early-emerging but shorter-statured plant species that

actively photosynthesize prior to canopy closure or leaf out among taller herbaceous plants (Taylor and Pearcy 1976; Givnish 1987; Kudo et al. 2008). Finally, we expected species richness and functional diversity to peak in microsites where sun- and shade-adapted herbs co-occur.

Methods

Study site

Our study focused on an acid bedrock glade located in the Baraboo Hills (Wisconsin, USA). The Baraboo Hills encompass a 580 km² region in south-central Wisconsin delineated by remnants of an ancient mountain range composed of uplifted Precambrian quartzite that rises approximately 200 m above the surrounding landscape. The Baraboo Hills and surrounding landscape comprise a regional biodiversity hotspot, supporting more than 1200 plant species. While acid bedrock glades represent just 0.13% of this landscape's total area, they support a disproportionate number of rare and threatened plant species (Lange 1998). Historically, these glades were maintained by a combination of shallow soils and periodic ground fires that restricted the establishment and growth of woody vegetation (Epstein 2017). Reduced fire frequency has contributed to the spread of trees and woody shrubs, but rates of canopy closure remain relatively slow. As a result, bedrock glades serve as refugia for light-adapted herbaceous plants that were historically more widespread across the open oak woodlands and savannas of the Baraboo Hills (Lange 1990, 1998; Armstrong 1994).

We conducted our study at a preserve owned and managed by the Nature Conservancy that encompasses the largest complex of acid bedrock glades in the Baraboo Hills. Our study focused on a relatively large (> 1 ha) quartzite glade situated atop a southeast-facing quartzite outcrop. The study plot spanned a conspicuous gradient from the semi-open glade dominated by shagbark hickory (*Carya ovata*), spreading vegetatively over bedrock via stolons, to a closed canopy forest dominated by sugar maple (*Acer saccharum*) and northern red oak (*Quercus rubra*). The glade is characterized by terraced quartzite bedrock exposures; a patchy, savanna-like canopy creating a mosaic of shaded and sunlit microsites; and dense cover of Pennsylvania sedge (*Carex pensylvanica*). Soils are classified as moderately well-drained and moderately fertile Baraboo stony silt loam.

Field methods

We established a 100 × 100 m plot (1 ha) spanning the transition from bedrock glade with patchy tree cover to closed canopy forest (Fig. S1). This transition followed a generally northwest to southeast direction perpendicular to the

somewhat gentle (10–15 percent) southeast slope gradient. In June–August of 2019, we identified, mapped, and measured diameter at breast height (DBH) of every tree stem greater than 1 cm DBH (Fig. S1; Table S1). In 2020, we established 361 1 × 1 m quadrats spaced evenly at 5 m intervals across the plot. We conducted two rounds of vegetation surveys to capture early- and later-leaving species, in May 19–25, 2020, and July 10–23, 2020, respectively, recording the presence or absence of all vascular plant species within each quadrat. During both survey periods, we also performed systematic walk-through surveys to obtain a complete list of plant species within the 1 ha plot. In total, we observed 139 vascular plant species during walk-through surveys within the 1 ha study plot. Of these, 108 occurred in at least 1 quadrat (Fig. 1f). Many tree and herbaceous plant distributions generally follow a northwest to southeast gradient which parallels the underlying bedrock terraces (Figs. S1 and S2).

Environmental variables

To characterize local environmental conditions, we measured soil depth and canopy openness in each quadrat and calculated the leafing phenology of neighboring trees adjacent to the quadrat. We measured soil depth at four locations (recorded to the nearest cm up to a maximum of 50 cm) within each quadrat by probing the soil with a metal wire 2.6 mm in diameter. The four measurements were averaged to obtain the mean soil depth for each quadrat (Fig. 1a). Average depth to bedrock was 17.6 cm, with 10.5% of our sampling locations having a soil depth of ≤ 1 cm. To quantify canopy openness, a measure of light availability in the understory, we took hemispherical photographs using a camera mounted with a leveled 180° fisheye lens at a height of 1 m positioned in the center of each quadrat. Photos were taken under overcast conditions between July 30 and August 3, 2020. We processed the photos using the Hemispherical 2.0 plug-in (Beckschäfer 2015) in ImageJ (Rueden et al. 2017) to obtain a measure of gap fraction for each quadrat (Fig. 1b). The timing of tree leaf out can also influence the amount of light available to plants over the course of a growing season and may be especially important to species that complete the majority of their photosynthesis before canopy closure (Givnish 1987). To quantify leaf phenology of overstory trees, we obtained leaf out dates for tree species measured at the Arnold Arboretum (Boston, MA, USA) in 2011 and 2012 (Panchen et al. 2014). We averaged the Julian date for each species between years to derive a mean leaf out date. Although these dates will not exactly correspond to the slightly colder climate at our study site, the relative timing of leaf out among species is consistent with our observations at the study site in 2019 and 2020. Data were available for all tree species in our plot from both

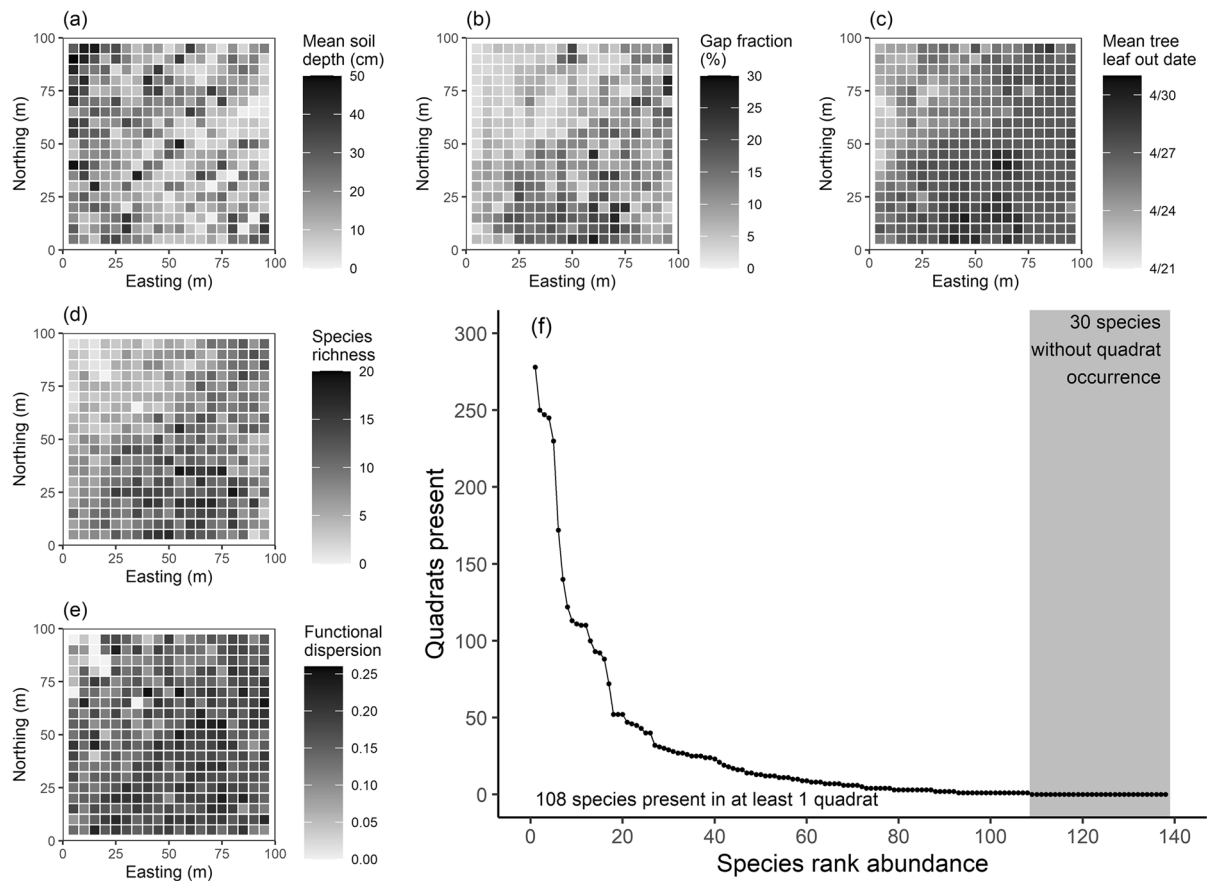


Fig. 1 Maps illustrating spatial variation in **a** mean soil depth, **b** canopy openness (gap fraction), **c** neighborhood tree phenology (average tree leaf out date), **d** species richness, and **e** functional disper-

sion as well as **f** rank-abundance curve for understory plant species within the 1 ha study plot. Squares depict the location of 361 quadrats spaced evenly at 5 m intervals across the 100×100 m study plot

years except *Juglans cinerea*, which only had a date listed for 2012. We assigned a mean date for that species based on the mean dates for *Carya cordiformis* and *C. ovata*, both of which leafed out on the same day as *J. cinerea* in 2012. We then derived a community-weighted leaf out date for each quadrat by weighting the mean leaf out date of neighboring trees by their DBH (Fig. 1c). We included all small trees (> 5 cm DBH) within 1.5 m of the quadrat center point, all medium trees (5–20 cm DBH) within 3.5 m, and all large trees (> 20 cm DBH) within 8 m to capture the tree canopy influencing each quadrat.

Functional traits

We quantified interspecific differences in specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness, seed (propagule) mass, and vegetative height using published trait values for Wisconsin plant species (Waller et al., 2021). To supplement this data set, we queried the TRY Plant Traits Database (Kattge et al., 2019) to obtain SLA, LDMC,

vegetative height (E. Weiher, unpublished data), and seed mass (Moles et al. 2004; Royal Botanic Gardens Kew 2020) for *Ranunculus fascicularis* as well as spore mass for *Dryopteris* spp. (J. Cornelissen, unpublished data). Seed mass for six additional species came from the Seed Information Database (Royal Botanic Gardens Kew 2020) and for 11 species from Prairie Moon Nursery (Winona, Minnesota, USA). Categorical traits for functional group, bloom season, longevity, and woodiness were assigned based on species descriptions (Voss and Reznicek 2012). We calculated functional diversity for each quadrat using the R package ‘FD’ (Laliberté and Legendre 2010; Laliberté et al. 2014). These diversity calculations included all continuous and categorical traits for each species. Our analysis of local plant distributions included three quantitative traits (SLA, vegetative height, and propagule mass) expected to influence plant distributions (see a priori predictions in Introduction). There was no correlation between vegetative height and seed mass ($r=0.01$, $N=60$, $P=0.916$) or vegetative height and SLA ($r=0.03$, $N=60$, $P=0.791$). SLA and seed mass were

weakly correlated ($r=0.32$, $N=60$, $P=0.014$). LDMC and leaf thickness were excluded in these models because these traits were strongly correlated with SLA.

Data analysis: local species-environment distributions

Our analysis of understory plant distributions focused on 60 herbaceous plant species present in at least 5 quadrats. These represented 92.8% of the quadrat occurrences among herbaceous species. We modeled local plant distributions using a Bayesian multilevel model (Jackson et al. 2012). This statistical approach is analogous to fitting a logistic regression for each species to characterize their environmental distributions but multilevel models allow us to simultaneously model the environmental distribution of all species (Jackson et al. 2012), assess the extent to which these local species-environment relationships depend on functional traits (Pollock et al. 2012; Jamil et al. 2013; Miller et al. 2019), and account for spatial non-independence in local plant distributions (Li and Ives 2017; Li et al. 2020; Ives 2022). We modeled the probability of quadrat-scale plant occurrences as a function of environmental conditions (soil depth, canopy openness, & neighborhood tree phenology), functional traits (SLA, seed mass, & vegetative height), and trait-environment interactions while accounting for residual spatial dependence in the distribution of individual species. Our multilevel model followed the general form:

$$P(Y_i = 1) = \text{logit}^{-1}(\mu_i)$$

$$\mu_i = \beta_0 + a_{spp[i]} + \beta_1 * \text{trait}_{spp[i]} + (\beta_2 + b_{spp[i]}) * \text{environment}_{quad[i]} + (\beta_3 + c_{spp[i]}) * \text{environment}_{quad[i]}^2 + \beta_4 * \text{trait}_{spp[i]} * \text{environment}_{quad[i]} + \tau,$$

where a specifies a random intercept allowing the probability of occurrence to vary among species and deviate from the global mean (β_0), b specifies a random slope allowing monotonic species' distributions to vary with local environmental conditions (average response to environmental variation given by β_2), and c is a random slope that allows for variation in unimodal species' responses to environmental predictors via a quadratic term (β_3 provides average unimodal response across species). The fixed effect β_1 quantifies the effect of a functional trait on species incidence (overall probability of occurrence) while the term β_4 quantifies a trait-environment interaction that allows us to quantify whether interspecific trait differences influence how species respond to local environmental distributions. Graphical exploration and examination of residuals suggested trait-environment associations were monotonic so we did not include a quadratic interaction term between environmental variables and traits. In the fitted model, we included separate terms for each trait (SLA,

vegetative height, seed mass) and environmental predictor (soil depth, canopy openness, neighborhood tree phenology) as well as interaction terms for each trait-environment combination.

To account for potential spatial autocorrelation in local species' distributions, we included an $nm \times nm$ spatial covariance matrix (where n is the number of species and m is the number of quadrats), τ . We parameterized spatial dependency using an exponential model of spatial correlation: $-\exp(d/\phi)$, where d denotes the pairwise distance between quadrats (in meters) and ϕ denotes the spatial range (scale of spatial dependence in meters). To obtain the spatial covariance matrix used in the multilevel model, we converted the exponential correlation matrix into an $m \times m$ covariance matrix and scaled the covariance matrix such that its determinant was equal to 1. This scaling improves computational efficiency. We then calculated the Kronecker product of the scaled spatial covariance matrix and an $n \times n$ diagonal species matrix to obtain the $nm \times nm$ spatial covariance matrix (τ). This large covariance matrix accounts for spatial autocorrelation in the distribution of each species (see Ives and Helmus 2011). This approach for modeling spatial covariance applies methods utilized in phylogenetic generalized linear mixed-effects models to model phylogenetic covariance among species (Ives and Zhu 2006; Ives and Helmus 2011; Ives 2022). To define a suitable range (ϕ), we fit a non-spatial version of the model and examined empirical semivariograms describing residual spatial dependence for each species. After fitting multilevel models specifying ranges of $\phi=5, 7.5, 10, 12.5$, and 15 m respectively, we compared WAIC scores to identify the best-fitting model ($\phi=10$ m range offered the best performance and was used in all subsequent analyses).

We evaluated the importance of both fixed effects (e.g., trait and environment predictors) and random effects (e.g., residual species-environment relationships) using 95% credible intervals. Spatial covariance matrices were created using the 'geoR' package (Ribeiro et al. 2020). These Bayesian multilevel models were fit using INLA (Rue et al. 2009) via the `communityPGLMM` function in the 'phyr' package (Li et al. 2020).

Data analysis: local variation in taxonomic and functional diversity

In addition to our analyses of local plant distributions, we also examined how environmental conditions influence local taxonomic and functional diversity. We analyzed patterns of species richness using a regression model. We modeled quadrat-scale species richness as a function of soil depth, canopy openness, and neighborhood tree leaf phenology. This model also included a term to account for spatial non-independence (using the same approach described above but

the spatial covariance matrix was not blocked by species). In addition to analyses of local species richness, we also modeled quadrat-scale functional trait diversity using the same regression model structure and predictors. We quantified the variation in functional characteristics of non-woody plant species in each quadrat using functional dispersion (F_{dis} , sensu Laliberté and Legendre 2010). This metric averages the multivariate distance in trait space between each species and the centroid for all species present within the quadrat. Graphical exploration and examination of residuals suggests all environment–diversity associations were linear. All analyses were conducted using R 4.0.2 (R Core Team 2021) and figures were generated using ‘ggplot2’ (Wickham 2016).

Results

Local plant distributions within our 1 ha study plot were highly heterogeneous (Fig. S2) and often varied individually in response to environmental predictors (Fig. 2; Figs. S3–S5). For most species, occurrence probabilities declined as soil depth increased, but there was considerable variation among species in soil depth associations (Table 1; residual standard deviation in differential species’ responses to soil depth [95% credible interval]: $\sigma = 0.14$ [0.08, 0.29]). Several species were strongly associated with shallow soils, including *Antennaria plantaginifolia*, *Taraxacum officinale*,

Danthonia spicata, *Dodecatheon meadia*, and *Symphyotrichum lateriflorum* (Fig. S3). Most plant species were unimodally distributed relative to gap fraction, reaching their modal abundance in microsites with greater-than-average light availability (Fig. S4). However, the distribution of plants relative to gap fraction varied considerably among species (residual standard deviation in differential species’ responses to gap fraction: $\sigma = 0.28$ [0.19, 0.45]). *Helianthus strumosus*, *Monarda fistulosa*, *Vicia caroliniana*, *Fragaria virginiana*, and *Elymus hystrix* were the species most strongly associated with greater canopy openness (Fig. S4). Plant species also varied in their distribution relative to the phenology of neighboring trees (residual standard deviation in differential species’ responses to gap fraction: $\sigma = 0.44$ [0.30, 0.67]). Most species exhibited unimodal distributions skewed towards greater abundance in microsites surrounded by later-leafing trees. The species most strongly associated with microsites surrounded by late-leafing trees included *Fragaria virginiana*, *Monarda fistulosa*, *Helianthus strumosus*, *Ranunculus fascicularis*, and *Heuchera richardsonii* (Fig. S5).

Our model revealed that functional traits mediated these differential plant responses to soil depth and canopy openness (Fig. 2a). Large-seeded plant species were more likely to occur in microsites with deeper soils while small-seeded plants reached peak abundance in shallow soil microsites (Fig. 2e; estimated coefficient for seed mass $\times$ soil depth

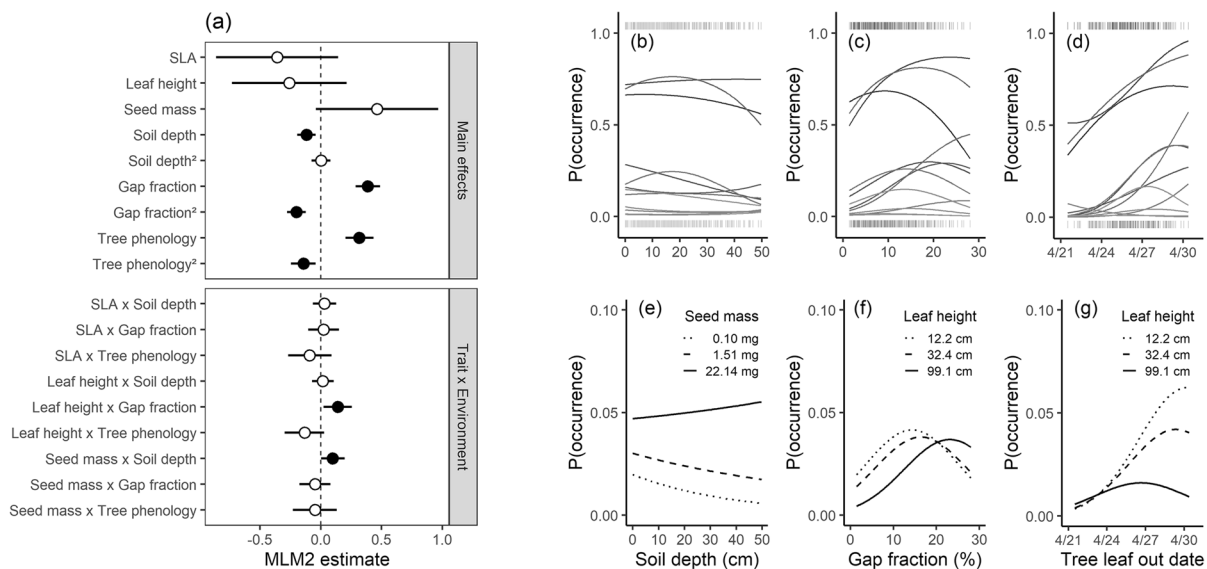


Fig. 2 Traits mediate local species–environment relationships. In (a), points and 95% credible intervals depict estimated coefficients from our multilevel model quantifying how trait values, environmental covariates, and trait–environment interactions influence the probability of plant species occurrence. Solid points represent estimates for which 95 percent confidence intervals do not overlap with zero. In (b–d), graphical depictions of modeled species–environment associations for 20 representative species illustrate how species respond

to local environmental variation. Note the individualistic species’ distributions along gradients in soil depth (b) and canopy openness (c). In panels (e–g), marginal predictions from the multilevel model illustrate how functional traits influence local species–environment distributions. For each important trait–environment association, we depict the predicted environmental distribution of understory plant species with low, intermediate, and high trait values (corresponding with the 5th, 50th, and 95th percentile of observed species trait values)

Table 1 Random effect summary from multilevel models characterizing understory plant responses to local environmental variation

Random effects term	Biological interpretation	σ (CrI)
Species abundance	Plant species vary in abundance	1.74 (1.43, 2.13)
Species $\times$ Mean soil depth	Plant species vary in their responses to soil depth	0.14 (0.08, 0.29)
Species $\times$ (Mean soil depth) ²	Plant species vary in unimodal responses to soil depth	0.14 (0.08, 0.30)
Species $\times$ Gap fraction	Plant species vary in their responses to canopy openness	0.28 (0.19, 0.45)
Species $\times$ (Gap fraction) ²	Plant species vary in unimodal responses to canopy openness	0.03 (0.01, 0.18)
Species $\times$ Tree leaf phenology	Plant species vary in their responses to tree phenology	0.44 (0.30, 0.67)
Species $\times$ (Tree leaf phenology) ²	Plant species vary in unimodal responses to tree phenology	0.18 (0.10, 0.35)
<i>Spatial autocorrelation in species' distributions</i>	<i>Plant species exhibit residual spatial aggregation</i>	<i>1.17 (1.09, 1.27)</i>

We included random effects allowing the probability of occurrence (abundance) to vary among the 60 focal understory species as well as random effects terms allowing species to respond differently to soil depth, canopy openness (gap fraction), and neighbor tree phenology. These species-environment random effects included terms accounting for variation in unimodal species' distributions. We also included a covariance matrix specifying spatial autocorrelation in the distribution of each species. For each random effects term, we report the standard deviation and credible interval. See Figs. S3–S5 for graphical depiction of the variation in estimated species-environment relationships. The italicized line of text summarizes model components characterizing residual spatial variation

interaction [95% credible interval]: 0.099 [0.002, 0.196]). Meanwhile, short-statured plant species reached modal occurrence in microsites with lower gap fractions while taller species were most likely to occur in microsites with greater canopy openness (Fig. 2f; estimate for vegetative height $\times$ gap fraction: 0.140 [0.022, 0.256]). Finally, there was some evidence that shorter-statured plants occurred more frequently under stress with later leaf out dates, but credible intervals overlapped slightly with zero (Fig. 2g;

estimate for vegetative height $\times$ mean tree leaf out date: -0.133 [$-0.297, 0.028$]). Notably, functional trait differences partially explain the observed individualistic species-environment associations (compare modeled species-environment relationships in Fig. 3b, c to predicted relationships based on functional traits in Fig. 2e, f). Comparing spatial and non-spatial models confirmed that accounting for spatial autocorrelation in species' distributions improved model performance ($\sigma = 1.17$, $\Delta\text{WAIC} = 2089.71$; Table 1).

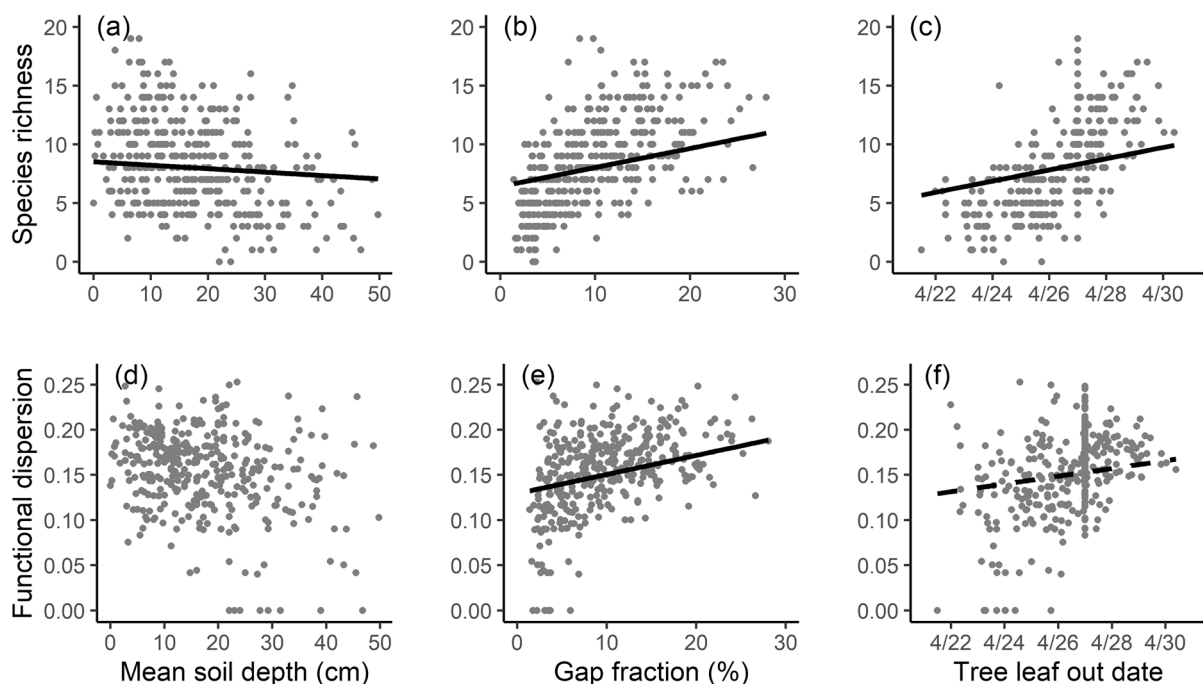


Fig. 3 Associations of soil depth, canopy openness (gap fraction), and neighborhood tree phenology (tree leaf out date) with herbaceous plant species richness (a–c) and functional dispersion (d–f). Lines

illustrate marginal predictions from spatial regression models when relationships are statistically significant (see [Methods](#) and [Table 2](#) for statistical summary of spatial regression models)

Spatial patterns of taxonomic and functional diversity reflected local environmental heterogeneity (Table 2; Fig. 1d, e). Herbaceous species richness declined with quadrat mean soil depth ($Z = -2.106$, $P = 0.035$; Fig. 3a) and increased with the canopy openness of microsites ($Z = 5.214$, $P < 0.001$; Fig. 3b). Understory species richness also increased in microsites where neighboring trees leaf out later in the spring ($Z = 3.246$, $P = 0.001$; Fig. 3c). The functional dispersion of understory plant species within microsites was positively associated with greater canopy openness ($Z = 4.406$, $P < 0.001$; Fig. 3e) but unrelated to the soil depth of microsites ($Z = -1.066$, $P = 0.286$; Fig. 3d). Functional dispersion also tended to increase in microsites where neighboring trees leaf out later ($Z = 1.933$, $P = 0.053$; Fig. 3f). Accounting for residual spatial covariance improved model performance for both models of local taxonomic diversity ($\Delta AIC = 80.59$) and functional dispersion ($\Delta AIC = 11.32$).

Discussion

Herbaceous plant distributions varied along local gradients in soil depth, canopy openness, and tree leafing phenology within this heterogeneous bedrock glade. These local species-environment distributions were mediated by functional traits and mirror trait-environment associations observed at broader spatial scales, providing strong evidence that ecological sorting shapes local plant distributions. Trait-mediated ecological sorting within this highly heterogeneous habitat also influenced spatial patterns of plant diversity. Both species richness and functional dispersion increased in microsites near canopy gaps where herb species with divergent environmental distributions co-occur. Taken together, these findings provide new insights into the ecological processes shaping local plant distributions and diversity within bedrock glades and certainly have relevance for other spatially heterogeneous plant communities.

Functional traits mediated differential species distributions along local environmental gradients. This finding provides strong evidence that trait-mediated ecological

sorting shapes local herb distributions. Small-seeded plants occurred most frequently in shallow soil microsites while larger-seeded plants were more prevalent in microsites with deeper soils (Fig. 3e). Theory predicts small-seeded plants should be favored in environments with little competition for light (Gross 1984; Westoby 1998), as is the case in shallow soil microsites in bedrock glades where the density of competing plants is low. We also found large-statured species occurred most frequently in microsites with greater canopy openness (Fig. 3f). Greater vegetative height is expected to provide a competitive advantage in environments with greater herb coverage and competition for light (Givnish 1982). Observationally, microsites near canopy gaps were characterized by dense coverage of herbaceous plants whereas microsites with dense tree canopies were sparsely vegetated. Although we expected herbs with high SLA to occur in shady microsites, reflecting advantages of broad, thin leaves for capturing light in shady environments, interspecific variation in SLA did not mediate herb responses to canopy openness. It is possible our analysis of trait means averaged over relevant intraspecific variation in SLA. Future studies investigating intraspecific variation in SLA, leaf inclination, and other traits associated with light availability among savanna and woodland herbs would be informative (Givnish 1987; Pruka 1994; Leach and Givnish 1999). Additionally, SLA can influence plant responses to variation in other environmental conditions that we did not measure, namely variation in soil nutrient availability. It may be difficult to detect SLA patterns if this trait influences plant distributions along multiple, interacting environmental gradients.

This work adds to a growing collection of studies documenting the importance of trait-mediated ecological sorting across spatial scales (Ordoñez et al. 2009; Kraft and Ackerly 2010; Pollock et al. 2012; Jamil et al. 2013; Amatangelo et al. 2014; Scherrer et al. 2019; Beck et al. 2022). Moreover, it provides further insights into the role of trait-mediated ecological sorting in driving individualistic plant responses to environmental variation. The individualistic plant distributions we observed along local gradients in soil depth and

Table 2 Summary of regression models examining the relationship between environmental variables and quadrat-scale taxonomic and functional diversity

Model term	Species richness		Functional dispersion	
	Estimate	P-value	Estimate	P-value
Soil depth	− 0.307	0.035	− 0.002	0.286
Canopy openness (gap fraction)	0.917	< 0.001	0.012	< 0.001
Neighborhood tree phenology	0.745	0.001	0.007	0.053
<i>Residual spatial autocorrelation</i>	<i>$\sigma = 1.28$</i>	<i>$\Delta AIC = 80.59$</i>	<i>$\sigma = 0.02$</i>	<i>$\Delta AIC = 11.32$</i>

We report estimated slope and P-value for environmental predictors as well as the residual variation (σ) attributed to environmental variation. We compared the difference in AIC values (ΔAIC) from spatial and non-spatial regression models to assess the importance of quantifying residual spatial autocorrelation. The italicized line of text summarizes model components characterizing residual spatial variation

canopy openness echo historical debates about whether plant communities represent tightly integrated entities composed of species responding in concert to environmental variation (Clements 1916) or loose affiliations of species formed as they respond individually to environmental variation (Gleason 1926). Curtis's (1959) and Whittaker's (1956) classic studies provided unequivocal support for the Gleasonian model of plant communities at broad scales by showing how regional species' distributions varied individually along environmental gradients. Our work suggests similar individualistic species-environment distributions can occur at local spatial scales within environmentally heterogeneous plant communities.

In many ways, bedrock glades epitomize Gleason's (1926) original notion of plant communities as loose associations of species responding individually to continuous environmental variation. These glades support an eclectic assemblage of plant species variously affiliated with woodlands, savannas, prairies, and rock outcrops. Moreover, we show here how plant distributions vary individually in response to local variation in soil depth and understory light availability. This study, in combination with previous landscape-scale studies of plant distributions (Whittaker 1956; Curtis 1959) and paleoecological research illustrating the individualistic post-glacial migration of North American tree species (Davis 1976, 1981), provides compelling evidence that Gleason's original insight has relevance across spatial and temporal scales. Our study also demonstrates how trait differences influence individualistic plant distributions along local environmental gradients *within* a heterogeneous community. Directly paralleling our findings at local scales, a recent study of herbaceous plant distributions across Wisconsin forests revealed how the additive effects of trait-environment associations contribute to individualistic herb distributions at broad spatial scales (Beck et al. 2022). These studies provide an important link between foundational work in plant community ecology (Gleason 1926; Whittaker 1956; Curtis 1959), plant physiological ecology (Givnish 1982, 1988), and modern trait-based approaches to community ecology (Westoby and Wright 2006; McGill et al. 2006; Funk et al. 2017).

Spatial patterns of local plant diversity provide further insights into how fine-scale environmental variation and functional trait differences influence locally heterogeneous plant communities. Herbaceous plant species richness increased in microsites surrounded by later-leafing tree species. This association may reflect temporal resource partitioning. The added window for early-leafing herbs to photosynthesize in the spring beneath late-leafing trees may facilitate co-occurrence of herbaceous species with divergent leaf phenology and elevate diversity (Givnish 1987; Kudo et al. 2008). However, inferences about tree leaf phenology at this site warrant caution. Spatial variation in the timing

of tree leaf out likely parallels other environmental gradients as well as the directional spread of woody vegetation. Both species richness and functional dispersion increased with canopy openness (Fig. 3a, d). In our study plot, microsites with high gap fraction (20–30%) are those with patchy canopy cover where shade-tolerant understory plants and shade-intolerant species co-occur. In previous studies of structurally similar midwestern oak savannas, Leach and Givnish (1999) noted the close proximity of environmentally divergent microsites could elevate local plant diversity if high rates of dispersal between adjacent microsites prevent species from being competitively excluded in microsites where they experience a competitive disadvantage. These 'mass effects' driven by source-sink dynamics have often been studied in the context of broader-scale metacommunities (Cottenie 2005; Chase and Myers 2011; Logue et al. 2011), though the concepts are clearly applicable at finer spatial scales (Shmida and Wilson 1985; Leach and Givnish 1999; Leibold et al. 2004; Holyoak et al. 2005). The residual spatial autocorrelation in species distributions and spatial patterns of diversity we observed in this study are consistent with mass effects. Nevertheless, future analyses of community dynamics—especially spatial patterns of microsite-scale colonization and extinction—over time would be instrumental for elucidating the potential role of mass effects in bedrock glades and other heterogeneous plant communities.

Finally, this study provides new insights into the ecological processes structuring bedrock glade plant communities. Fine-scale heterogeneity and ecological sorting have been presumed to structure local plant distributions in bedrock glades and contribute to their high species diversity, but few quantitative analyses exist (Ware 2002). Bedrock glades have been most extensively studied in the Ozark region of central North America (limestone and dolomite glades) with some additional work in the cedar glades of the southeastern United States, granitic glades in the Piedmont region, and a handful of other regions in North America (Anderson et al. 1999). These previous studies largely focus on characterizing plant composition and diversity (Kucera and Martin 1957; Anderson et al. 1999), comparing bedrock glades to related plant communities (Baskin and Baskin 2000; Ware 2002), and describing the functional characteristics of resident species (Van Zandt 2007; Miller et al. 2018). Our results largely parallel findings from other locally heterogeneous communities, linking assembly processes in bedrock glades to savannas and other better-studied plant communities.

Early work in Midwestern oak savannas revealed the important role of understory light availability in structuring local plant distributions (Bray 1958). Subsequent work by Leach and Givnish (1999) found plant distributions along gradients in understory light availability and soil texture reflected interspecific differences in leaf morphology and stature. Most similar to our own work, Pruksa's (1994) study

in a dry oak savanna documented individualistic species' distributions along local gradients in soil depth and light availability. Interspecific and intraspecific variation in traits such as leaf inclination, plant stature, and modes of seed dispersal were associated with these local plant distributions. The similarities between our study and previous work in midwestern oak savannas are unsurprising given that bedrock glades are structurally and compositionally similar to dry savannas (Will-Wolf and Stearns 2010). The most conspicuous compositional difference between our study site and oak savannas is the absence of warm season grasses. These grasses often dominate sunlit microsites in oak savannas and occur in some bedrock glades, including numerous acid bedrock glades in the study region. Given the similar inferences provided by this study and previous work, we expect our findings have relevance to other locally heterogeneous plant communities regardless of species composition.

Conclusion

Our study of local plant distributions and diversity provides new inferences about fine-scale community assembly in locally heterogeneous plant communities and advances our understanding of bedrock glades. Although trait-environment frameworks are most often applied at broader spatial scales, we found that functional traits predictably shape local plant distributions and contribute to the diverse plant assemblage found in bedrock glades. This study also extends the individualistic concept of plant distributions and plant communities to finer spatial scales and reveals how trait differences drive individualistic species responses to environmental variation. These insights will contribute to our understanding of plant community assembly across spatial scales.

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Author contributions JB conceived of the research idea, JB and JR collected and analyzed data, JB led efforts to write the paper with substantial input from JR.

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Data availability Upon acceptance, all data and code necessary to replicate analyses will be made publicly accessible on Figshare.

Declarations

Competing interests The authors declare that they have no conflict of interest.

Ethical Approval Not applicable.

References

- Amatangelo K, Johnson S, Rogers D, Waller DM (2014) Trait-environment relationships remain strong despite 50 years of trait compositional change in temperate forests. *Ecology* 95:1780–1791. <https://doi.org/10.1890/13-0757.1>
- Anderson RC, Fralish JS, Baskin JM (eds) (1999) Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, New York
- Armstrong PK (1994) Vegetation survey of a quartzite glade in Sauk County, Wisconsin. In: Fralish JS, Anderson RC, Ebinger JE, Szafoni R (eds) Proceedings of the North American Conferences on Savannas and Barrens. U.S. Environmental Protection Agency, Great Lakes National Program Office, Chicago, Illinois, pp 355–363
- Bañares-de-Dios G, Macía MJ, Granzow-de la Cerda Í, Arnelas I, Martins de Carvalho G, Espinosa CI, Salinas N, Swenson NG, Cayuela L (2020) Linking patterns and processes of tree community assembly across spatial scales in tropical montane forests. *Ecology* 101:e03058. <https://doi.org/10.1002/ecy.3058>
- Baskin JM, Baskin CC (2000) Vegetation of limestone and dolomite glades in the Ozarks and midwest regions of the United States. *Ann Missouri Bot Gard* 87:286–294. <https://doi.org/10.2307/2666165>
- Beatty SW (1984) Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65:1406–1419. <https://doi.org/10.2307/1939121>
- Beatty SW (2014) Habitat Heterogeneity and the Maintenance of Species in Understory Communities. In: Gilliam FS (ed) The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, New York, NY, USA, pp 215–232
- Beck JJ, Givnish TJ (2021) Fine-scale environmental heterogeneity and spatial niche partitioning among spring-flowering forest herbs. *Am J Bot* 108:63–73. <https://doi.org/10.1002/ajb2.1593>
- Beck JJ, Li D, Johnson SE, Rogers DA, Cameron KM, Sytsma KJ, Givnish TJ, Waller DM (2022) Functional traits mediate individualistic species-environment distributions at broad spatial scales while fine-scale species' associations remain unpredictable. *Am J Bot* 109:1991–2005. <https://doi.org/10.1002/ajb2.16085>
- Beckschäfer P (2015) Hemispherical_2.0 - Batch processing hemispherical and canopy photographs with ImageJ – User Manual.
- Bergholz K, May F, Giladi I, Ristow M, Ziv Y, Jeltsch F (2017) Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment. *Perspect Plant Ecol Evol Syst* 24:138–146. <https://doi.org/10.1016/j.ppees.2017.01.001>

- Bratton SP (1976) Resource division in an understory herb community: Responses to temporal and microtopographic gradients. *Am Nat* 110:679–693. <https://doi.org/10.1086/283097>
- Bray JR (1958) The distribution of savanna species in relation to light intensity. *Can J Bot* 36:671–681. <https://doi.org/10.1139/b58-061>
- Burton JJ, Mladenoff DJ, Clayton MK, Forrester JA (2011) The roles of environmental filtering and colonization in the fine-scale spatial patterning of ground-layer plant communities in north temperate deciduous forests. *J Ecol* 99:764–776. <https://doi.org/10.1111/j.1365-2745.2011.01807.x>
- Cahill JF, Kembel SW, Lamb EG, Keddy PA (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspect Plant Ecol Evol Syst* 10:41–50. <https://doi.org/10.1016/j.ppees.2007.10.001>
- Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. *Philos Trans R Soc London* 366:2351–2363. <https://doi.org/10.1098/rstb.2011.0063>
- Clements FE (1916) *Plant succession: An analysis of the development of vegetation*. Carnegie Institution of Washington, Washington D.C.
- Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecol Lett* 8:1175–1182. <https://doi.org/10.1111/j.1461-0248.2005.00820.x>
- Crozier CR, Boerner REJ (1984) Correlation of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. *Oecologia* 62:337–343. <https://doi.org/10.1007/BF00384265>
- Curtis JT (1959) *The Vegetation of Wisconsin: An Ordination of Plant Communities*. The University of Wisconsin Press, Madison, WI
- Davis MB (1976) Pleistocene biogeography of temperate deciduous forests. *Geosci Man* 13:13–26
- Davis MB (1981) Quaternary History and the Stability of Forest Communities. In: West DC, Shugart HH, Botkin DB (eds) *Forest Succession: Concepts and Application*. Springer-Verlag, New York, pp 132–153
- Epstein E (2017) Natural communities, aquatic features, and selected habitats of Wisconsin. The ecological landscapes of Wisconsin: An assessment of ecological resources and a guide to planning sustainable management. Wisconsin Department of Natural Resources, Madison
- Falster DS, Westoby M (2003) Plant height and evolutionary games. *Trends Ecol Evol* 18:337–343. [https://doi.org/10.1016/S0169-5347\(03\)00061-2](https://doi.org/10.1016/S0169-5347(03)00061-2)
- Funk JL, Larson JE, Ames GM, Butterfield BJ, Cavender-Bares J, Firn J, Laughlin DC, Sutton-Grier AE, Williams L, Wright J (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biol Rev* 92:1156–1173. <https://doi.org/10.1111/brv.12275>
- Givnish TJ (1982) On the adaptive significance of leaf height in forest herbs. *Am Nat* 120:353–381. https://doi.org/10.1007/978-1-349-04627-0_17
- Givnish TJ (1987) Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytol* 106:131–160. <https://doi.org/10.1111/j.1469-8137.1987.tb04687.x>
- Givnish TJ (1988) Adaptation to sun and shade: a whole-plant perspective. *Aust J Plant Physiol* 15:63–92. <https://doi.org/10.1071/PP9880063>
- Gleason H (1926) The individualistic concept of the plant association. *Bull Torrey Bot Club* 53:7–26
- Gross KL (1984) Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J Ecol* 72:369. <https://doi.org/10.2307/2260053>
- HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. *Annu Rev Ecol Evol Syst* 43:227–248. <https://doi.org/10.1146/annurev-ecolsys-110411-160411>
- Holyoak M, Leibold MA, Holt RD (eds) (2005) *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago
- Ives AR (2022) Random errors are neither: on the interpretation of correlated data. *Methods Ecol Evol* 13:2092–2105. <https://doi.org/10.1111/2041-210X.13971>
- Ives A, Helmus M (2011) Generalized linear mixed models for phylogenetic analyses of community structure. *Ecol Monogr* 81:511–525. <https://doi.org/10.1890/10-1264.1>
- Ives AR, Zhu J (2006) Statistics for correlated data: phylogenies, space, and time. *Ecol Appl* 16:20–32. <https://doi.org/10.1890/04-0702>
- Jackson MM, Turner MG, Pearson SM, Ives AR (2012) Seeing the forest and the trees: multilevel models reveal both species and community patterns. *Ecosphere*. <https://doi.org/10.1890/ES12-00116.1>
- Jamil T, Ozinga WA, Kleyer M, Ter Braak CJF (2013) Selecting traits that explain species-environment relationships: a generalized linear mixed model approach. *J Veg Sci* 24:988–1000. <https://doi.org/10.1111/j.1654-1103.2012.12036.x>
- Keddy P, Shipley B (1989) Competitive hierarchies in herbaceous plant communities. *Oikos* 54:234–241. <https://doi.org/10.2307/356527>
- Keddy P, Nielsen K, Weiher E, Lawson R (2002) Relative competitive performance of 63 species of terrestrial herbaceous plants. *J Veg Sci* 13:5–16. <https://doi.org/10.1111/j.1654-1103.2002.tb02018.x>
- Kraft NJB, Ackerly DD (2010) Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecol Monogr* 80:401–422. <https://doi.org/10.1890/09-1672.1>
- Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. *Funct Ecol* 29:592–599. <https://doi.org/10.1111/1365-2435.12345>
- Kucera CL, Martin SC (1957) Vegetation and soil relationships in the glade region of the southwestern Missouri Ozarks. *Ecology* 38:285. <https://doi.org/10.2307/1931687>
- Kudo G, Ida TY, Tani T (2008) Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. *Ecology* 89:321–331. <https://doi.org/10.1890/06-2131.1>
- E Laliberté P, Legendre B, Shipley 2014 FD: Measuring functional diversity from multiple traits, and other tools for functional ecology R Package FD
- Laliberte E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305. <https://doi.org/10.1890/08-2244.1>
- KI Lange 1990 A postglacial vegetational history of Sauk County and Caledonia Township, Columbia County, south central Wisconsin. Dept Nat Res
- Lange KI (1998) *Flora of sauk county and caledonia township, Columbia County, south central wisconsin*. Madison
- Leach MK, Givnish TJ (1999) Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. *Ecol Monogr* 69:353–374. [https://doi.org/10.1890/0012-9615\(1999\)069\[0353:GITCSA\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0353:GITCSA]2.0.CO;2)
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Li D, Dinnage R, Nell LA, Helmus MR, Ives AR (2020) phyr: An R package for phylogenetic species-distribution modelling in ecological communities. *Methods Ecol Evol* 11:1455–1463. <https://doi.org/10.1111/2041-210X.13471>

- Logue JB, Mouquet N, Peter H, Hillebrand H (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol Evol* 26:482–491. <https://doi.org/10.1016/j.tree.2011.04.009>
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Miller JED, Ives AR, Harrison SP, Damschen EI (2018) Early- and late-flowering guilds respond differently to landscape spatial structure. *J Ecol* 106:1033–1045. <https://doi.org/10.1111/1365-2745.12849>
- Miller JED, Damschen EI, Ives AR (2019) Functional traits and community composition: a comparison among community-weighted means, weighted correlations, and multilevel models. *Methods Ecol Evol* 10:415–425. <https://doi.org/10.1111/2041-210X.13119>
- Ordoñez JC, Van Bodegom PM, Witte JPM, Wright IJ, Reich PB, Aerts R (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Glob Ecol Biogeogr* 18:137–149. <https://doi.org/10.1111/j.1466-8238.2008.00441.x>
- Panchen ZA, Primack RB, Nordt B, Ellwood ER, Stevens AD, Renner SS, Willis CG, Fahey R, Whittmore A, Du Y, Davis CC (2014) Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytol* 203:1208–1219. <https://doi.org/10.1111/nph.12892>
- Pollock LJ, Morris WK, Vesk PA (2012) The role of functional traits in species distributions revealed through a hierarchical model. *Ecography* (cop) 35:716–725. <https://doi.org/10.1111/j.1600-0587.2011.07085.x>
- Pruka BW (1994) Distribution of understory plant species along light and soil depth gradients in an upland oak savanna remnant in southern Wisconsin. In: *Proceedings of the North American Conference on Savannas and Barrens*
- R Core Team (2021) A language and environment for statistical computing
- Ribeiro P, Diggle PJ, Christensen O, Schlather M, Bivand RS, Ripley B (2020) *geoR: Analysis of geostatistical data*
- Royal Botanic Gardens Kew (2020) Seed Information Database (SID). Version 7.1. Available from: <http://data.kew.org/sid/> (Accessed December 2020)
- Rue H, Martino S, Chopin N (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *J R Stat Soc Ser B Stat Methodol* 71:319–392. <https://doi.org/10.1111/j.1467-9868.2008.00700.x>
- Rueden CT, Schindelin J, Hiner MC, DeZonia BE, Walter AE, Arena ET, Eliceiri KW (2017) ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics* 18:1–26. <https://doi.org/10.1186/s12859-017-1934-z>
- Scherrer D, Mod HK, Pottier J, Litsios-Dubuis A, Pellissier L, Vittoz P, Götzenberger L, Zobel M, Guisan A (2019) Disentangling the processes driving plant assemblages in mountain grasslands across spatial scales and environmental gradients. *J Ecol* 107:265–278. <https://doi.org/10.1111/1365-2745.13037>
- Shmida A, Wilson MV (1985) Biological determinants of species diversity. *J Biogeogr* 12:1–20. <https://doi.org/10.2307/2845026>
- Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol Lett* 17:866–880. <https://doi.org/10.1111/ele.12277>
- Struik GJ, Curtis JT (1962) Herb distributions in an *Acer saccharum* forest. *Am Midl Nat* 68:285–296. <https://doi.org/10.2307/2422734>
- Taylor RJ, Pearcy RW (1976) Season patterns of the CO₂ exchange characteristics of understory plants from a deciduous forest. *Can J Bot* 54:1094–1103. <https://doi.org/10.1139/b76-117>
- Vellend M, Lechowicz MJ, Waterway MJ (2000) Environmental distribution of four *Carex* species (Cyperaceae) in an old-growth forest. *Am J Bot* 87:1507–1516. <https://doi.org/10.2307/2656877>
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! *Oikos* 116:882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Voss EG, Reznicek AA (2012) *Field Manual of Michigan Flora*. The University of Michigan Press, Ann Arbor, MI
- Waller DM, Paulson AK, Richards JH, Alverson WS, Amatangelo KL, Bai C, Johnson SE, Li D, Sonnier G, Toczydlowski RH (2021) Functional trait data for vascular plant species from Northeastern North America. *Ecology* 103:e03527. <https://doi.org/10.1002/ecy.3527>
- Ware S (2002) Rock outcrop plant communities (glades) in the Ozarks: A synthesis. *Southwest Nat* 47:585–597. <https://doi.org/10.2307/3672662>
- Weiher E, Keddy PA (eds) (1999) *Ecological assembly rules: perspectives, advances*. Cambridge University Press, Cambridge
- Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199:213–227. <https://doi.org/10.1023/A:1004327224729>
- Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. *Trends Ecol Evol* 21:261–268. <https://doi.org/10.1016/j.tree.2006.02.004>
- Whittaker RH (1956) Vegetation of the Great Smoky Mountains. *Ecol Monogr* 26:1–80. <https://doi.org/10.2307/1943577>
- Wickham H (2016) *ggplot2: Elegant graphics for data analysis*. Springer, NY
- Will-Wolf S, Stearns F (2010) Dry Soil Oak Savanna in the Great Lakes Region. In: Anderson RC, Fralish JS, Baskin JM (eds) *Savannas, Barrens, and Rock Outcrop plant communities of North America*. Cambridge University Press, pp 135–154
- Van Zandt PA (2007) Plant defense, growth, and habitat: A comparative assessment of constitutive and induced resistance. *Ecology* 88:1984–1993. <https://doi.org/10.1890/06-1329.1>

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