

RESEARCH ARTICLE

Early- and late-flowering guilds respond differently to landscape spatial structure

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Abstract

1. Species with unique phenologies have distinct trait syndromes and environmental affinities, yet there has been little exploration of whether community assembly processes differ for plants with different phenologies. In this study, we ask whether early- and late-blooming species differ in the ways that dispersal, persistence and resource acquisition traits shape plant occurrence patterns in patchy habitats.
2. We sampled plant communities in 51 Ozark dolomite glade grasslands, which range in size from <1 ha to >100 ha. We modelled the occurrence of 71 spring- and 43 summer-blooming grassland species in these patches, using as predictors both environmental variables (landscape structure, soil resources) and plant traits related to dispersal, longevity and resource acquisition. We were especially interested in how the environmental variables and plant traits interacted to determine the occurrence of phenological strategies in habitats that vary in size and isolation.
3. Summer-blooming species with better persistence and dispersal abilities had higher relative frequencies in smaller, more isolated habitat patches, and summer-blooming species with higher specific leaf area—suggesting fast growth and low stress tolerance—were more likely to occur in patches with greater soil organic matter and clay content. However, spring-blooming species showed much weaker interactions between functional traits and environmental gradients, perhaps because environmental conditions are less harsh in spring than in summer.
4. *Synthesis.* Several axes of plant life-history variation may simultaneously influence community responses to habitat connectivity. In this case, explicitly considering plant phenology helped identify generalizable relationships between functional traits and landscape spatial structure.

KEYWORDS

biodiversity, dispersal, fragmentation, functional traits, habitat connectivity, multilevel models, patch quality, persistence, plant diversity, resource acquisition strategies

1 | INTRODUCTION

Studies from diverse biomes have identified phenology—most commonly classified based on first flowering date—as one of the most important axes of functional trait variation for community assembly (Frenette-Dussault, Shipley, Meziane, & Hingrat, 2013; Merow, Latimer, & Silander, 2011; Sonnier, Navas, Fayolle, & Shipley, 2012).

Early- vs. late-blooming plant species, for example, may have different suites of functional traits, suggesting that they may have distinct responses to environmental gradients (Craine, Wolkovich, Towne, & Kembel, 2011; Wolkovich & Cleland, 2014). However, there has been little investigation into mechanisms by which phenology could mediate species occurrences along ecological gradients, making it difficult to make general predictions about how phenology will affect community

composition. Because phenology can be related to multiple axes of plant life-history traits, such as resource acquisition strategies, dispersal modes and longevity, considering phenology in trait analyses may help untangle factors that drive plant distributions (Laughlin, 2014).

Understanding how plants respond to habitat patch size and connectivity is a long-standing area of inquiry in ecology (Haddad et al., 2015), and species guilds with different phenology may have different mechanistic responses to fragmented landscapes. For example, early- and late-blooming species often vary in stress tolerance traits (Craine et al., 2011; Laughlin, 2014), and these guilds might have different abilities to persist and disperse in fragmented landscapes. Traits related to persistence and stress tolerance could be particularly important for species that grow during an environmentally stressful season (e.g. hot, dry summers), while traits related to mobility (or dispersal) could be more important for species that grow during a more environmentally benign season. In this study, we test how three functional trait axes—dispersal, persistence (or longevity) and resource acquisition traits—drive species occurrences along gradients of habitat connectivity and soil resource availability for two plant guilds with distinct phenologies.

Plant dispersal traits may influence species occurrences in patchy habitats because the distance propagules can travel may determine whether they can reach isolated habitat patches (MacArthur & Wilson, 1967). If dispersal among patches is a key determinant of community composition, species that are poor dispersers would be expected to occur only in more connected habitat patches, while isolated patches would be expected to contain a greater proportion of species that are good dispersers. There is some empirical evidence that plant communities in isolated patches have a higher proportion of species with long-distance dispersal adaptations, such as structures for wind or animal dispersal (Marini et al., 2012; May, Giladi, Ristow, Ziv, & Jeltsch, 2013; Schleicher, Biedermann, & Kleyer, 2011; Schmucki, Reimark, Lindborg, & Cousins, 2012). However, other studies have found that habitat isolation can favour poor dispersers, in part because species that invest heavily in long-distance dispersal may be at a disadvantage in small, isolated patches if most of their propagules will fall into the inhospitable matrix (Bonte, Hovestadt, & Poethke, 2010; Negoita et al., 2016; Purschke, Sykes, Reitalu, Poschlod, & Prentice, 2012; Riba et al., 2009). Poor dispersers can also be favoured in isolated patches if traits associated with stress tolerance are correlated with dispersal traits via phylogenetic relationships (Spasojevic, Damschen, & Harrison, 2014). Although explanations for associations between dispersal traits and patch isolation remain incomplete, mathematical models suggest that contingencies such as disturbance and plant life span could cause plants with better dispersal abilities to have either positive or negative responses to habitat fragmentation (Büchi & Vuilleumier, 2012). The importance of dispersal for community assembly could also be contingent upon phenology; for example, the availability of dispersal vectors, environmental conditions favouring establishment and granivore pressure could all vary between different seasons.

The ability of species to persist through environmentally stressful years by, for example, being long lived or producing a seed bank may also influence the composition of communities in different landscapes, and some studies have concluded that traits that confer persistence are

better predictors of plant occurrences in isolated habitat patches than traits that affect dispersal. Long-lived species may be favoured in small patches that are isolated from other populations because these plants are less sensitive to stochastic factors that could cause local extinctions; for example, poor germination conditions during a dry year could eliminate annual species from an isolated patch where recolonization is unlikely (Dupré & Ehrlén, 2002; Maurer, Durka, & Stöcklin, 2003). Persistence ability in isolated populations could be particularly important for species that reproduce during an environmentally harsh season when the risk of local extinctions could be greater. Although there is evidence that long-persisting species fare better than shorter-lived species in isolated habitats (Auffret, Aggemyr, Plue, & Cousins, 2016; Evju, Blumentrath, Skarpaas, Stabbeborg, & Sverdrup-Thygeson, 2015; Maurer et al., 2003; Purschke et al., 2013), some studies from anthropogenically fragmented grasslands have found non-significant or even the opposite relationship (Hemrová & Münzbergová, 2015; Lindborg et al., 2012). Grasslands that are more recently fragmented and heavily influenced by human land use could exhibit different trait–environment relationships than naturally fragmented grasslands. Because community assembly processes may vary substantially along anthropogenic disturbance gradients, land-use history is an important covariate that could explain discrepancies in previous studies (Veldman et al., 2015). For example, anthropogenic fragmentation could select for short-lived species with high investment in dispersal, while natural fragmentation could select for long-lived species (Lindborg et al., 2012).

Because resource acquisition life-history strategies and other plant functional traits may simultaneously affect community assembly (Pollock, Morris, & Veski, 2012), multiple axes of trait variation should be considered in tests of the relative importance of dispersal or persistence. Here, we ask whether species phenology affects the importance of environmental and spatial drivers of plant community composition in a naturally fragmented grassland system. Specifically, using gradients of habitat connectivity and soil resource availability, we test whether patch-level species occurrences (presence/absence) are predicted by traits representing three major plant life-history axes: dispersal ability, persistence (or longevity) and resource acquisition strategies. We expected that summer-flowering species would be more sensitive to environmental gradients, particularly soil resource availability, than spring-flowering species, because the harsher environmental conditions of hot summer months may cause plants to be more stressed. This would result in stronger trait–environment interactions for summer-flowering species than spring-flowering species (Figure 1). We tested two specific hypotheses for spring- and summer-flowering species as separate groups. (1) Isolated sites have more long-lived, slow growing, stress-adapted species; we expected this result because species with faster life cycles that depend on frequent reproduction and dispersal may be less suited to persistence in isolated habitats. (2) Seed size increases with patch isolation; we expected this result because producing many small seeds that can travel far may be disadvantageous when propagules cannot reach other habitat patches, and large seeds may be more formidable competitors within patches.

Integrating numerous community predictors and functional traits into a coherent analytical framework has historically posed statistical

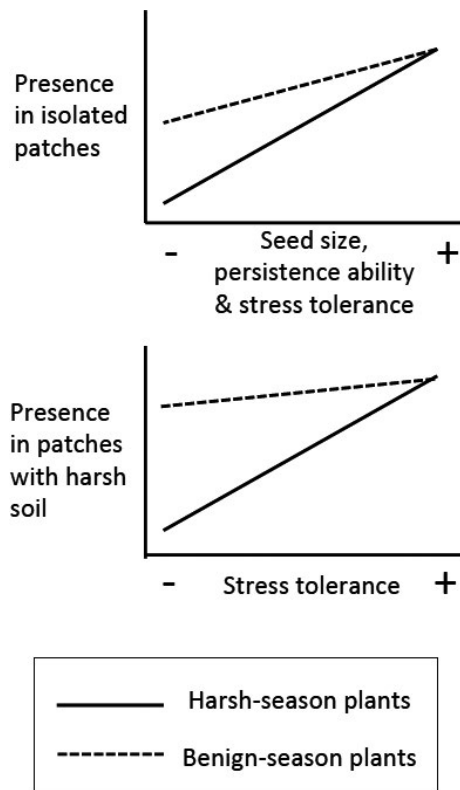


FIGURE 1 Conceptual diagram illustrating hypothesized differences in responses to environmental gradients in species growing during harsh and benign seasons. In this study, summer-blooming species equate to the harsh-season plants and spring-blooming species equate to the benign-season plants above

challenges. Previous studies have generally utilized three different approaches. The first approach involves two-step analyses, in which species responses to environmental gradients are analysed first, and then the influence of traits on these relationships responses is considered (Hemrová & Münzbergová, 2015; Lindborg et al., 2012). The second approach uses ordination and permutation tests to solve the “fourth corner” problem, solving for associations between traits and environmental variables (Legendre, Galzin & Harmelin-Vivien, 1997; Dray & Legendre, 2008). A third approach averages trait values at the community level, and then regresses these community-weighted means against environmental variables (Ricotta & Moretti, 2011); this approach, however, can suffer badly from Type I errors in some cases, falsely identifying statistically significant patterns when in fact none exist (Miller, Ives, & Damschen, in review). Multilevel models (mixed models) offer a promising and adaptable alternative to these approaches, in which the influences of multiple trait–environment interactions can be evaluated in a single model that provides information about both the presence and absence of individual species and the composition of the community as a whole; thus, multilevel models allow the simultaneous analyses at both the species and community levels (Jamil, Ozinga, Kleyer, & Ter Braak, 2013; Miller et al., in review; Pollock et al., 2012). Multilevel models also make it possible to include phylogenies to account for phylogenetic relatedness among species (Li, Ives, & Waller, 2017), since phylogenetic non-independence can

be a confounding factor in trait analyses (Li & Ives, 2017) and closely related species may exhibit trait syndromes (correlated traits across different life-history axes; Spasojevic et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Study system

We sampled plant communities and measured plant functional traits in dolomite glades in the Ozark highlands of Missouri (36.5°–38.4° latitude and –90.5° to –93.4° longitude). Glades are dry, rocky grasslands that usually occur on south-facing slopes, where intense solar radiation and shallow soils create a harsh growing environment for plants (Nelson, 2005). Glades usually occur as spatially discrete openings in the oak woodlands that make up the dominant land cover in upland areas of the Ozark region. Glades range in size from <1 ha to >100 ha (Figures S1 and S2), and glade size is related to habitat connectivity, with smaller glades being more isolated from other glades (Nelson, 2005). The substantial variation in glade size and isolation makes them an appropriate system for testing the effects of landscape spatial structure on plant communities (Miller, Damschen, Harrison, & Grace, 2015).

The glade flora can be divided into two relatively distinct groups based on phenology (Figure 2). A group of early-flowering species (hereafter “spring-blooming species”) begin blooming between March and May and include both ephemerals that go dormant by early summer and small-statured, hardy perennials often with inconspicuous flowers that persist for much of the growing season. A group of later-flowering species (hereafter “summer-blooming species”), which are often taller-statured plants with showy flowers, begins blooming between late June and August and continues into early fall. This bimodal distribution of flowering dates (Figure 2) is likely a response to the environmental stress that plants experience in the glade environment (Craine, Wolkovich, & Towne, 2012). Ozark summers are hot and characterized by dry periods, and water stress for glade plants is exacerbated by shallow, rocky glade soils. Plants ameliorate stressful conditions by either blooming in the spring and then going dormant, blooming in the late summer and into the cooler weather of fall, or by having physiological adaptations to environmental stress if they bloom during the heat of summer (Craine et al., 2011).

Glades are a fire-adapted ecosystem that historically burned on c. 2- to 10-year fire return intervals (Guyette & McGinnes, 1982; Nelson, 2005). In the 1940s, widespread fire exclusion was implemented in the region. Beginning in the 1980s and 1990s, however, agencies began reintroducing prescribed fire in glades on public lands in response to recognition that fire is an integral process for maintaining the biodiversity and vegetation structure of the system (Nelson, 2005).

2.2 | Site selection and community sampling

We selected 51 dolomite glades across the Ozark region for study (Figure 3). We limited our study to sites that are currently managed

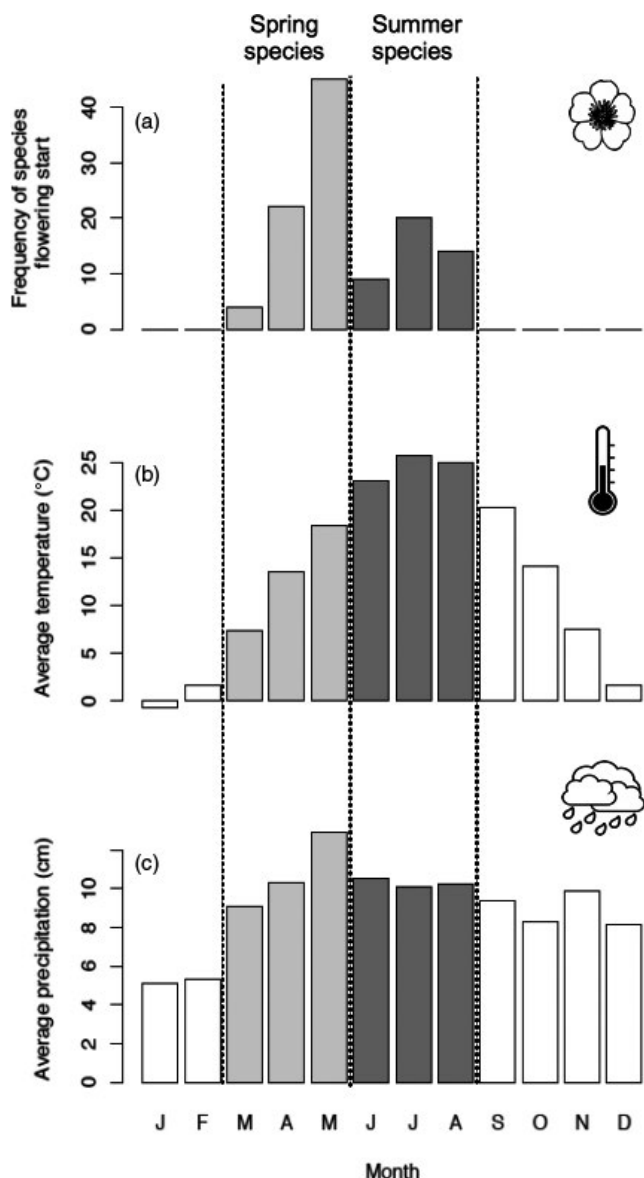


FIGURE 2 (a) Histogram of flowering start times for all species analysed in this study. June represents a low point in flowering initiation between peaks in the spring and summer. (b) Average monthly temperature and (c) average monthly precipitation illustrate the greater environmental stress experienced by summer-blooming species

with prescribed fire to avoid confounding influences of comparing burned and unburned sites. We selected sites that managers believe have been relatively undisturbed by historical land uses, in particular intensive grazing. Within selected glades, we randomly located study plots, but required that they be located >5 m from glade edges and in areas with <10% woody cover to avoid confounding effects of edges and dense shade.

To sample glade plant communities, we established one study plot in each glade. Study plots were 100 m² (50 × 2 m) with a centre transect containing 20 evenly spaced 0.25 m² quadrats. Within each quadrat, we recorded the presence of all plant species, and we also recorded all plant species that occurred in the larger plot but outside



FIGURE 3 Map of study sites in the Missouri Ozarks

of the quadrats. We conducted sampling from May to August of 2012 and May to September of 2013. We visited each plot twice during the growing season of either 2012 or 2013 to detect both spring- and summer-blooming species. To analyse variation in soils among study sites, at each site we collected six soil samples from the top 15 cm of soil using a trowel, and we combined the six samples for analysis. Soil texture and organic matter content were analysed by Brookside Labs (New Knoxville, OH, USA).

2.3 | Trait collection

To test how plant functional traits are associated with plant responses to habitat connectivity and the soil resource availability, we measured functional traits related to dispersal (seed mass, dispersal mode, terminal velocity), persistence (persistence index) and resource acquisition (specific leaf area [SLA], leaf dry matter content [LDMC], carbon to nitrogen ratio [CN] and plant height). Data for all continuous traits (SLA, LDMC, CN, seed mass and plant height) were collected in the field during the 2013, 2014 and 2015 seasons following methods described by Cornelissen et al. (2003). We collected plant tissue and made field measurements on plants growing in glade complexes where our study plots were located. Individuals of each species were measured and collected at ≥2 sites.

We assigned plant dispersal modes using the Kew Gardens database (Kew Royal Botanic Gardens 2016) and primary botanical literature. In cases where information could not be found, we assigned species to the most likely category based on seed morphology. We assigned plants to three dispersal mode categories: unassisted (no specialized dispersal structures), wind dispersed (with pappuses), and vertebrate dispersed (with fleshy fruits or adhesive dispersal structures). Ant

dispersed and ballistic species were assigned to the unassisted category because they disperse relatively short distances, and we did not have specific hypotheses about how these modes would affect community responses differently from unassisted species. Species with very small seeds without pappuses that dispersed independently and were positioned on plants such that they could become airborne were also assigned to the wind-dispersed category since such “dust-like” seeds can travel long distances (Kew Royal Botanic Gardens, 2016). For wind-dispersed species with pappuses (but not “dust-like” seeds, which were too small to measure), we measured seed terminal velocity using a high-speed video camera. We averaged measurements of terminal velocity from 15 seeds of each species.

To quantify plant persistence ability (or longevity; Marini et al., 2012; Weiher et al., 1999), we classified species into five groups based on descriptions of underground structures from Yatskievych (1999, 2006, 2013): (1) annual and biennial species; (2) perennials without root storage structures or rhizomes; (3) perennials with storage structures such as tubers, taproots, corms or bulbs; (4) species with short rhizomes; and (5) species with long rhizomes. To simplify interpretation of the effects of persistence, for the main models (Tables S2–S5), we simplified this index into a binary persistence variable following the method recommended by Weiher et al. (1999). For the binary persistence variable, we considered perennial species with rhizomes or underground storage structures (groups 3–5) to be longer persisting species. Annual, biennial and perennial plants without storage structures or rhizomes (groups 1–2) were classified as shorter persisting species. We also present a model for summer-blooming species that analyses persistence using the five-level factor to show how each category responds to habitat connectivity and soil resource availability (Table S6).

To measure the percent of foliar C and N, leaf tissue was analysed using Micro-Dumas combustion for total carbon and total nitrogen at the Center for Applied Isotope Studies at the University of Georgia.

We averaged quantitative traits at the species level and analysed only interspecific trait variation. Although intraspecific variation can be substantial, there is evidence that most of the community-level trait responses to environmental gradients are associated with species turnover (e.g. interspecific variation) rather than intraspecific trait variation (Cornwell & Ackerly, 2015). Accordingly, intraspecific variation has been shown to be inconsequential in systems where there is high species turnover among sites (Spasojevic, Turner, & Myers, 2016). Because species-level and community-level functional traits are expected to shift in the same direction along environmental gradients, considering intraspecific variation would probably only strengthen the patterns we observed (Ackerly & Cornwell, 2007).

2.4 | Model variable selection

2.4.1 | Trait axes and correlations

Several of the traits we measured were correlated with each other in the overall dataset (i.e. across both spring- and summer-blooming

species; Table S1). For analysis, we selected one or two functional traits to represent each of the three major axes of trait variation related to our hypotheses, avoiding selection of highly correlated traits. We used seed mass to represent dispersal; increasing seed mass was correlated with a dispersal mode gradient from unassisted species (large seeds) to wind-dispersed species (small seeds; Table S1). We also used terminal velocity to represent dispersal ability for wind-dispersed species. We used the binary index (described above) to represent persistence. We used SLA and plant height, which were correlated with LDMC and CN, to represent plant resource acquisition strategies. We only included species for which we had measured all four traits; these species represented >80% of species-by-quadrat occurrences in all plots (range 81%–98%, $M = 90\%$; data available on online). We analysed terminal velocity in a separate model from the other traits because fewer spring-blooming species were wind-dispersed than summer-blooming species. Therefore, we ran the terminal velocity model only for summer-blooming species.

2.4.2 | Landscape spatial structure

We represented landscape spatial structure with the proximity index, a metric that is based on both habitat area and configuration (Gustafson & Parker, 1994). Proximity index values increase with increasing habitat cover within the focal landscape and with decreasing distances among habitat patches. The proximity index may have greater ecological significance than simpler metrics of connectivity, such as nearest neighbour distance, which does not account for area (Kupfer, 2012). The proximity index was previously shown to be a predictor of the richness of specialist plant species in Ozark glades (Miller et al., 2015).

To characterize glade spatial structure, we used Nelson's (2014) glade maps, which were developed by hand using landscape imagery. We converted the glade maps to rasters in ArcGIS (ESRI, 2011) and used Fragstats (McGarigal, Cushman, & Ene, 2012) to calculate the proximity index for 1-km buffers surrounding our study sites. The 1-km buffer distance was chosen because previous research has shown that grassland plant communities often respond to the landscape at this scale, and most grassland plants disperse distances of 1 km or less (Kinlan & Gaines, 2003). Habitat connectivity has also previously been shown to influence dolomite glade plant species richness at this scale (Miller et al., 2015).

2.4.3 | Soil resource availability

To develop a single soil resource availability variable, we conducted a principal components analysis in the Vegan package (Oksanen et al., 2012) in R (R Core Team, 2016) of soil organic matter and clay content, which are typically correlated with nitrogen availability and soil water holding capacity (Laughlin, Abella, Covington, & Grace, 2007). We used the first principal components axis for all subsequent analyses. Previous research in Ozark dolomite glades has found that this metric is a strong predictor of species richness (Miller et al., 2015).

2.5 | Analysis

To analyse the influence of trait–environment interactions on species occurrences for spring- and summer-blooming species, we used generalized linear mixed models (GLMMs, Gelman & Hill, 2007). In this approach, the environmental variables and functional traits that correspond to each potential species–site combination are used to predict species occurrence. A significant interaction between a functional trait and an environmental variable indicates that the trait modulates species responses to that environmental variable. We used the significance and the sign of the trait–environment interaction terms in the models to evaluate whether the models supported our hypotheses about how traits structure community responses to environmental gradients. Species identity was included in the model as a random effect, allowing individual species to have varying responses (unique slopes and intercepts) to the environmental variables (soil resource availability and habitat connectivity). Specific model formulations that test our hypotheses are described below. To improve variable distributional properties and better meet model assumptions, we log transformed SLA, seed mass and proximity index, and square-root transformed plant height in all models.

A formal description of the presence/absence model for the case of one trait and one environmental variable is as follows:

$$\begin{aligned} \Pr(Y_i = 1) &= \text{logit}^{-1}(y_i) \\ y_i &= \alpha + a_{\text{spp}[i]} + b_{\text{site}[i]} + (\beta_X + c_{\text{spp}[i]})X_{\text{site}[i]} + \beta_T T_{\text{spp}[i]} + \beta_{XT} X_{\text{site}[i]} T_{\text{spp}[i]} \\ a &\sim \text{Gaussian}(\mathbf{0}, \sigma_a^2 \mathbf{I}_n) \\ b &\sim \text{Gaussian}(\mathbf{0}, \sigma_b^2 \mathbf{I}_m) \\ c &\sim \text{Gaussian}(\mathbf{0}, \sigma_c^2 \mathbf{I}_n) \end{aligned} \quad (1)$$

Here, we use the convention of multilevel models (Gelman & Hill, 2007), with fixed and random effects given by Greek and Latin letters, respectively, and functions $\text{spp}[i]$ and $\text{site}[i]$ mapping observation i to the identity of the n species and m sites. Y_i represents presence/absence for each species–site combination whose probability is given by the inverse-logit of the random variable y_i . The random effect $a_{\text{spp}[i]}$ represents variation in species-specific intercepts, while the random effect $b_{\text{site}[i]}$ represents variation in site-specific intercepts. The environmental variable $X_{\text{site}[i]}$ (habitat connectivity or soil resource availability) has a mean slope of β_X across all species, with species-specific variation given by the random effect $c_{\text{spp}[i]}$. Species traits $T_{\text{spp}[i]}$ affect presence/absence with slope β_T . Our main objective is to test for trait by environment interactions given by the coefficient β_{XT} . Our approach is similar to the methods used by Pollock et al. (2012), except that we include traits as main effects (in addition to allowing them to interact with environmental variables) to reduce the risk of inflated type I errors (Miller et al., in review). We ran the models using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) in R (R Core Team, 2016), and we used the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2015) to calculate denominator degrees of freedom and p -values based on Satterthwaite's approximations. Because <15%

of species had non-monotonic relationships with landscape spatial structure and soil resource availability, and none of these were significant after multiple comparisons corrections, we did not include quadratic terms in the models. Finally, the p -values were confirmed using a bootstrap test in which 2,000 datasets were simulated using the model fitted to the data, and each simulated dataset was then fitted with the same model; the resulting 2,000 bootstrap estimates of β_{XT} give the approximate distribution of its estimator from which p -values were derived. The bootstrap test confirmed the Satterthwaite's approximations.

We used several formulations of the basic model described above to test our hypotheses. First, to test whether species had varying responses to landscape spatial structure and soil resource availability, we used likelihood ratio tests to assess whether species-level random effects were significant for models that contained only environmental variables but not traits. We ran separate models for spring-blooming species (first blooming in May or earlier) and summer-blooming species (first blooming in June or later). We then ran models containing four traits (SLA, plant height, binary persistence and seed mass) and the two environmental variables for both spring- and summer-blooming species to test our hypothesis that species with different phenologies would exhibit different trait–environment interactions, β_{XT} . We ran a separate model for summer-blooming species with terminal velocity as the only trait, since terminal velocity was measured for a subset of the community. We also ran a model for summer-blooming species where the binary persistence variable was replaced by the persistence index (with five levels), representing a higher resolution analysis of how underground structure traits interacted with habitat connectivity to influence species occurrences. To facilitate comparison between the responses of spring- and summer-blooming plants, we present the results of full models (without removing non-significant variables, Tables S2–S3), although reduced models showed similar results.

Phylogenetic relatedness among species can lead to type I errors in statistical tests (false positives) with in community analyses of trait–environment interactions (Li & Ives, 2017). This occurs because phylogenetically related species are more likely to show similar trait values, leading to correlated residuals. Therefore, we tested whether accounting for phylogenetic non-independence among species improved the models for spring- and summer-blooming plants using binary PGLMM (Ives & Helmus, 2011; Ives & Garland, 2010) in the ape package in R (Paradis, Claude, & Strimmer, 2004; Appendices S1, S4, and S5). Because the phylogenetic GLMMs gave the same statistical conclusions as the non-phylogenetic GLMMs (Tables S2–S3), we present only the non-phylogenetic GLMMs in the main text.

3 | RESULTS

3.1 | Traits and environmental responses of spring- and summer-blooming species

Spring- and summer-blooming species differed substantially in traits related to stress tolerance and resource acquisition (e.g. as indicated by the leaf economic spectrum; Figure 4). Spring-blooming species had

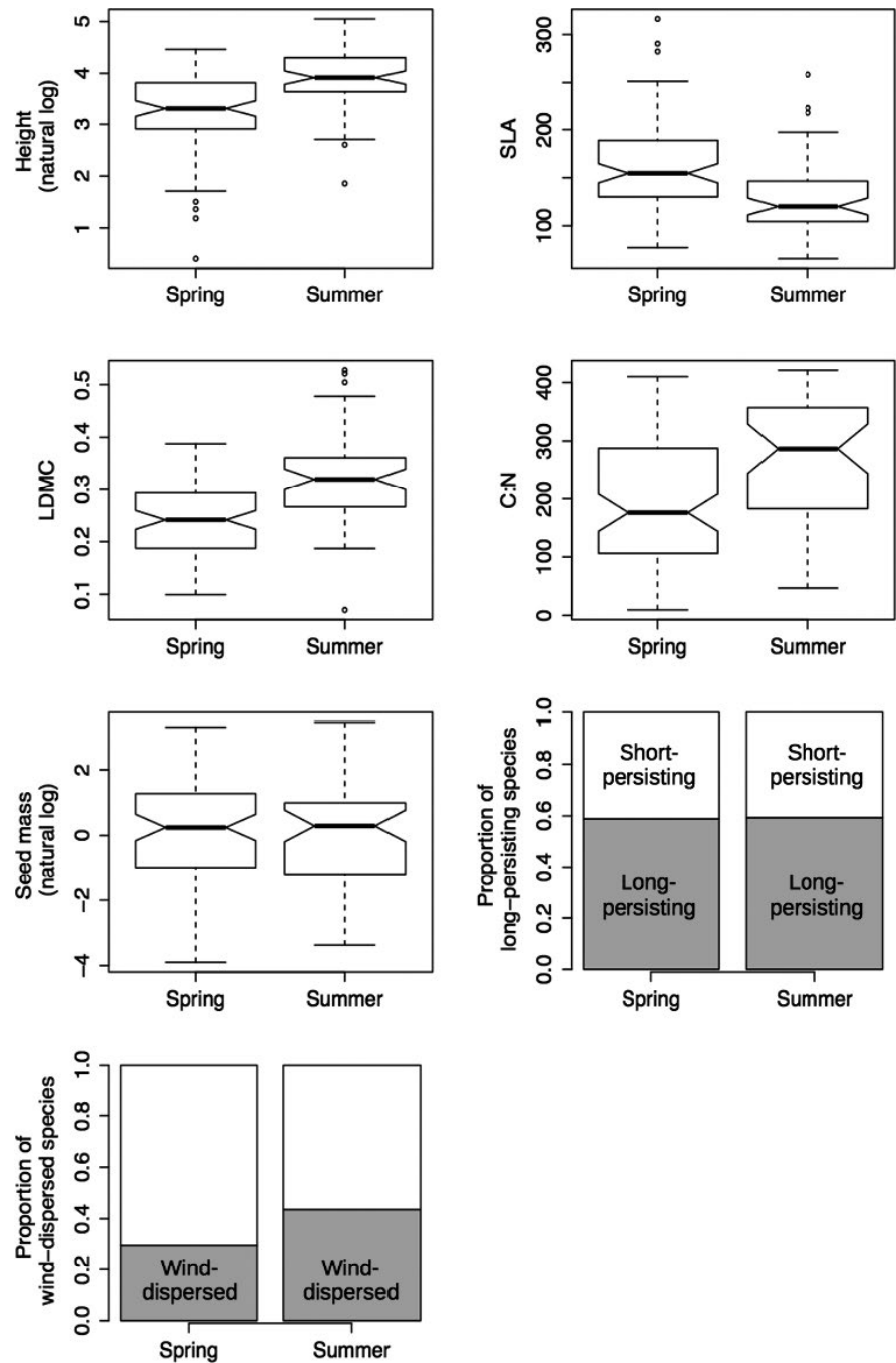


FIGURE 4 Comparison of functional trait distributions for spring- and summer-blooming species. Summer-blooming plants have traits suggesting greater adaptations to environmental stress. SLA, specific leaf area; LDMC, leaf dry matter content; C:N, carbon to nitrogen ratio

lower specific leaf area, lower leaf dry matter content and were shorter statured. However, spring-blooming species and summer-blooming species had similar ranges of seed mass, and similar proportions of spring- and summer-blooming species were long persisters. Phenology was also related to dispersal mode: most spring-blooming species did not have long-distance dispersal adaptations (most had unassisted dispersal modes), while more summer-blooming species were wind dispersed.

Both spring- and summer-blooming species varied significantly in their responses to landscape spatial structure and the environment. Occurrences of spring-blooming species responded to habitat connectivity ($\sigma^2 = 1.039$, $\chi^2 = 44.153$, $df = 3$, $p < .001$) and soil resource availability ($\sigma^2 = 1.010$, $\chi^2 = 57.371$, $df = 3$, $p < .001$). Summer-blooming

species occurrences also responded to habitat connectivity ($\sigma^2 = 3.733$, $\chi^2 = 114.09$, $df = 3$, $p < .001$) and soil resource availability ($\sigma^2 = 0.721$, $\chi^2 = 18.71$, $df = 3$, $p < .001$).

3.2 | Trait–environment interactions

Few functional traits predicted how spring-blooming species responded to spatial and edaphic heterogeneity, while several traits predicted the responses of summer-blooming species to these gradients (Figures 5 and 6, Tables S2–S7). This was not a simple consequence of sample sizes in the analyses, since more spring-blooming species (71) were analysed than summer-blooming species (43). The

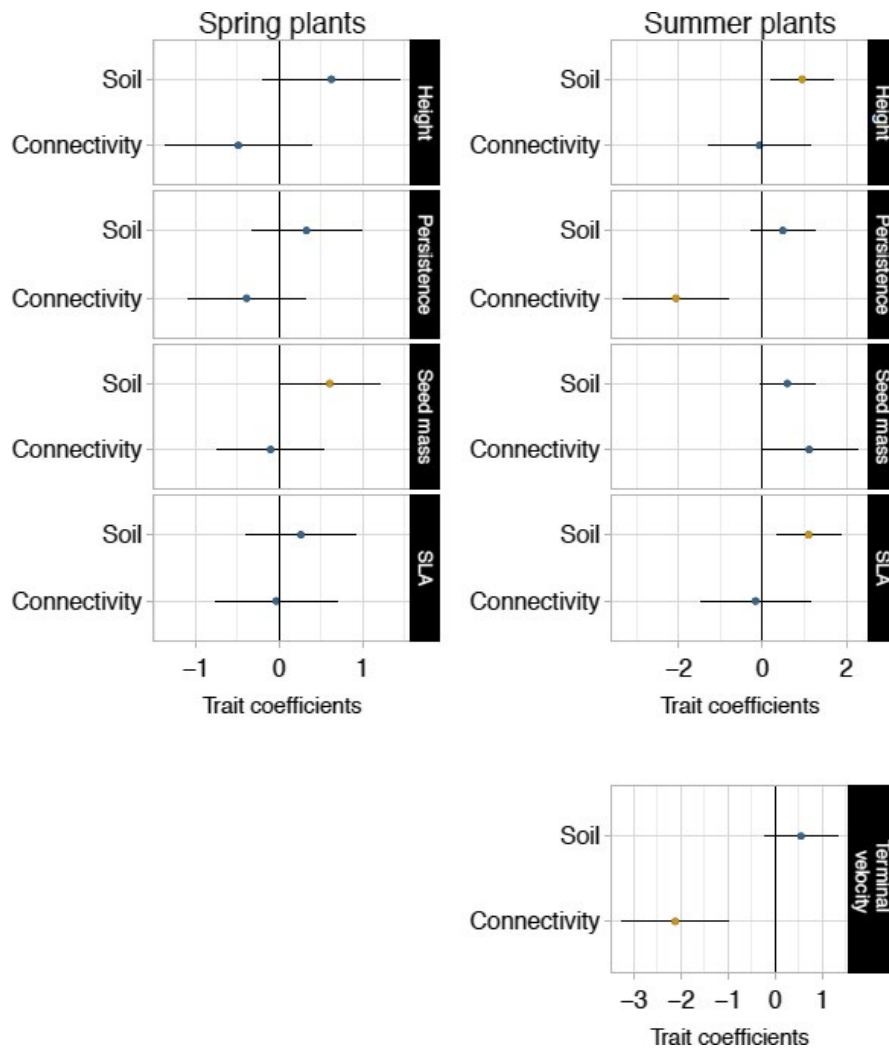


FIGURE 5 Coefficients for trait-environment interactions for spring and summer models with lines giving the approximate standard errors of the estimates. Statistically significant coefficients are shown with yellow dots, while non-significant coefficients are shown with blue dots; see Tables S2 and S3

model for spring-blooming species contained only one significant trait-environment interaction between seed mass and soil resource availability ($p = .045$, Table S2). For summer-blooming species, however, several trait-environment interactions were significant (Table S3). Of these, the interaction between persistence and habitat connectivity was the strongest ($p = .001$), with long-persisting species becoming more likely to occur in more isolated glades. Seed mass also had a marginally significant ($p = .056$) interaction with habitat connectivity; species with smaller seeds occurred more frequently in smaller, less connected glades. There was no significant interaction between either SLA or plant height and habitat connectivity.

For summer-blooming species, there were also significant or marginally significant interactions between soil resource availability and functional traits (Figures 5 and 6). The relationship between SLA and soil was significant ($p = .011$): high SLA species (with less stress-adapted leaves) had a greater probability of occurrence on soils with higher clay and organic matter content than low SLA species did. Taller plants were more likely to occur on sites with high soil resource availability ($p = .010$). Seed mass exhibited a positive interaction trend with soil resource availability ($p = .074$), with larger seeds occurring on richer soils. There was no significant interaction between persistence and soil resource availability.

The terminal velocity model for 31 summer-blooming species showed that terminal velocity responded significantly to landscape spatial structure ($p < .001$; Table S7). Species with slower falling seeds were more likely to occur in smaller, more isolated glades.

The model for summer-blooming species that divided persistence into five rather than two categories showed that species with rhizomes and storage structures had a stronger affinity for more isolated habitats relative to annual, biennial and perennial species without storage structures and rhizomes (Figure S3). Annual plants, which were the base factor level in the model, differed significantly in response to landscape spatial structure from species with storage structures ($p = .013$) and species with short rhizomes ($p = .006$), but not perennials without persistence structures (rhizomes or storage structures; $p = .718$) or species with long rhizomes ($p = .381$; Table S6).

4 | DISCUSSION

Plant distributions within the glade landscape respond to both landscape spatial structure (habitat patch size and connectivity) and soil resource availability, and functional traits play a role in determining species responses to these environmental gradients. Our main result

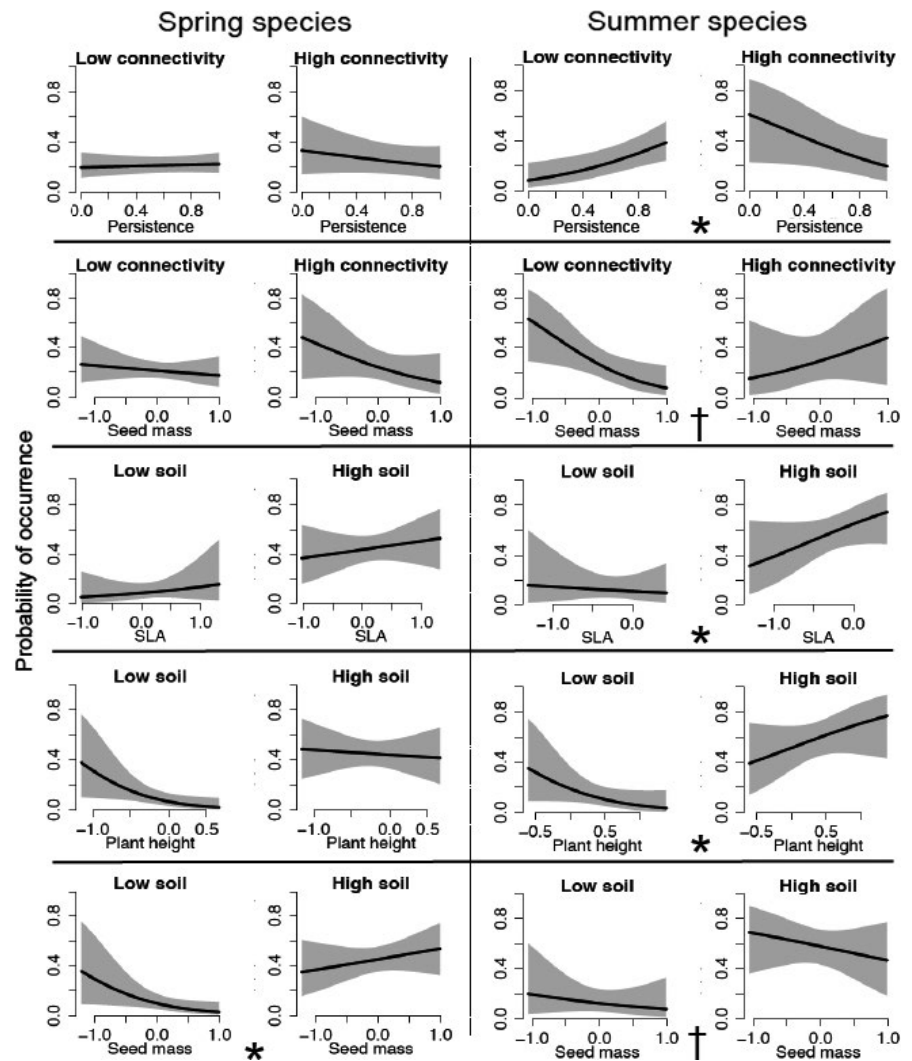


FIGURE 6 Trait–environment interactions at high and low points along environmental gradients for spring-blooming species (left column) and summer-blooming species (right column). Trait–environment interactions that were analysed for both seasons and were significant or marginally significant ($p < .1$) for at least one season are shown. Significant interactions are marked with an asterisk ($*p < .05$). Marginally significant interactions are marked with a dagger ($†p < .1$)

is that functional traits have a stronger influence on the occurrence of plants that grow during the environmentally harsh summer season than on those that grow during the more benign spring season. For example, summer-blooming species without strong adaptations to environmental stress (e.g. species with high SLA) are unlikely to occur in areas of harsher soils, while traits such as SLA do not influence responses to soil variation for species that bloom during the cooler, wetter spring. Dispersal and persistence traits also mediate the responses to landscape spatial structure only for summer-blooming species and not spring-blooming species. The stronger role of trait–environment interactions in determining species occurrences during harsher conditions could be caused by more frequent local extinctions during the summer, while spring-blooming species might be more likely to persist when growing at the margins of their environmental tolerances. Many of the differences in functional traits between spring- and summer-blooming species documented here resemble patterns that have been observed in other communities (e.g. earlier flowering species with traits associated with faster growth and reduced stress tolerance; Wolkovich & Cleland, 2014), suggesting that phenology could be similarly important in other systems.

Summer-blooming species with smaller and slower falling seeds occur more frequently in isolated patches, contrary to our hypothesis, while dispersal traits are not related to the occurrence of spring-blooming species along the habitat connectivity gradient. Summer-blooming species may be more responsive to landscape spatial structure in part because wind dispersal is more common in summer-blooming species than in spring-blooming species. These results suggest that better dispersers may more readily colonize and occupy isolated habitat patches, as theory and some empirical evidence suggests (Leibold et al., 2004; Marini et al., 2012; May et al., 2013; Schmucki et al., 2012). However, other research has found that species with larger seeds are more abundant in isolated patches. Studies with such findings have often taken place in highly fragmented habitats with strong habitat contrast between habitat patches and the surrounding matrix, such as European semi-natural grasslands, urban green patches and oceanic islands (Negoita et al., 2016; Saar, Takkis, Pärtel, & Helm, 2012; Schleicher et al., 2011). Average habitat connectivity in the glade system is likely greater than that in such highly fragmented systems; glade cover approaches 50% of the landscape in some areas of the Ozarks (Nelson, 2005). Thus, seeds might travel

among patches more readily in the glade system than in systems where spatial isolation has appeared to favour poor dispersers.

Nonetheless, long-distance propagule exchange among the more isolated glades we studied is undoubtedly a rare event, and it is possible that other factors that correlate with dispersal ability could explain the apparent interaction between dispersal and glade isolation. For example, species with smaller seeds that we categorized as better dispersers in our dataset also persist longer in soil seed banks than species with larger seeds (Thompson, Band, & Hodgson, 1993). Seed-banking species may be favoured in isolated habitats, since a “temporal rescue effect” may prevent stochastic extinctions during times of environmental stress (Buoro & Carlson, 2014; Marini et al., 2012). Research in another patchy edaphic system has shown that dispersal traits can also come “along for the ride” by being correlated with other traits, such as stress tolerance, that have a greater role in shaping community composition along environmental and spatial gradients (Spasojevic et al., 2014).

Long-lived summer-blooming species are prevalent in isolated glades, while short-lived summer-blooming species are prevalent in connected glades. This suggests that long-lived species can tolerate spatial isolation better than short-lived species, at least during the season of harsh environmental conditions, perhaps because stochastic local extinctions are less likely for long-lived species. Although several studies have reached similar conclusions (Evju et al., 2015; Lindborg, 2007; Maurer et al., 2003; Purschke et al., 2012), others have found contrasting patterns. For example, Lindborg et al. (2012) and Dupré and Ehrlén (2002) found that species with shorter life spans tolerated spatial isolation better in semi-natural grasslands in Europe. Both authors suggest that this pattern was caused by clonal species having poorer dispersal ability, making them unable to seek habitat refuges during fragmentation. This suggests that the ability of species to “escape” via dispersal to undisturbed habitats may be important in settings characterized by rapid anthropogenic fragmentation (Dupré & Ehrlén, 2002; Lindborg et al., 2012; Marini et al., 2012). In the naturally fragmented glade system where there have not been rapid landscape changes, investing in vegetative reproduction even at the cost of long-distance dispersal could be beneficial, since propagules dispersed long distances in patchy habitats are likely to be lost into the matrix (Purschke et al., 2012). The correlation between our categorical persistence variable and seed mass in our dataset is weak ($r = -.012$, Table S1), but quantitative measurements (such as the relative biomass allocations for roots and propagules) could comprehensively assess such a trade-off (Poorter et al., 2011).

Plant persistence may have a strong influence on species responses to habitat patch size and connectivity, and there is growing awareness that perennial grassland plants can be very long-lived (Ehrlén & Lehtilä, 2002; Veldman et al., 2015). Persistence is often analysed as a binary trait (often called “clonality”), but our findings suggest that classifying plant persistence into a multilevel index provides greater insight into community assembly processes. We found that species with storage organs (e.g. bulbs and tubers) exhibit responses that correspond to often-observed responses of rhizomatous clonal species (Figure S3). However, no categorical

classification can fully capture variation in plant life spans (Weiher et al., 1999), and functional ecology is ripe for studies that measure plant life spans on a continuous scale (e.g. following methods described by Ehrlén & Lehtilä, 2002; Schweingruber & Poschold, 2005). This would allow for more-nuanced study of the relative importance of persistence and dispersal traits along gradients of habitat connectivity. Similarly, more detailed quantitative studies of resource allocation (e.g. underground vs. aerial biomass) could help tease apart life-history trade-offs between competition, colonization and other functional dimensions.

Our results suggest that some community assembly processes in relatively undisturbed, remnant “old-growth grasslands” may differ from those in more anthropogenically modified habitats (Veldman et al., 2015). Numerous studies of how functional traits mediate community responses to habitat connectivity have taken place in intensely human-influenced, recently fragmented habitats, and functional community composition in these study systems may vary considerably from that in naturally fragmented habitats (Lindborg et al., 2012). For example, ruderal species become more dominant in isolated patches in European semi-natural grasslands (Husáková & Münzbergová, 2016), while glades studied here contain relatively few ruderal species. In addition, anthropogenic fragmentation may select for species with dispersal adaptations for “escaping” from disturbed areas (Lindborg et al., 2012; Marini et al., 2012), but such species do not seem to be favoured in naturally fragmented systems (e.g. Auffret et al., 2016). Community assembly processes that we observed in Ozark glades may be similar to those that occur in other global old-growth grasslands (Veldman et al., 2015). Explicitly considering land-use history could help ecology move towards a generalizable framework for community assembly processes in patchy habitats.

From a methodological perspective, our analyses show the simplicity and effectiveness of multilevel models in community analyses (Ives & Helmus, 2011; Jamil et al., 2013; Pollock et al., 2012). Testing interaction terms in GLMMs can potentially be problematic, because GLMMs are necessarily nonlinear, with the nonlinearity occurring in the “link function” that must be included for non-Gaussian data (Gelman & Hill, 2007). When relationships between dependent and independent variables are nonlinear, slopes will change with mean values of the independent variables, and these can lead to false detection of interaction effects. Nonetheless, our bootstrap calculations of p -values confirmed the standard outputs of p -values from the GLMMs. A particular advantage of multilevel models is that they can incorporate phylogenetic relationships among species (Ives & Helmus, 2011; Li et al., 2017), and Li and Ives (2017) show that phylogenetic correlations can lead to false positives in statistical tests. We found for our data, however, that this was not the case, since phylogenetic GLMMs produced the same statistical conclusions as the non-phylogenetic GLMMs.

4.1 | Implications for management and conservation

Understanding how communities in fragmented habitats will respond to climate change is an issue of critical conservation importance,

since shifts in mean temperature and precipitation as well as more extreme weather events (e.g. drought) could further stress populations already under spatial constraints. Species in fragmented habitats may be especially vulnerable to climate change, since they could be unable to undergo range shifts as their climate niches shift unless they can “leap” across the inhospitable matrix to other habitat patches (Harrison, Damschen, & Grace, 2010). However, there is also evidence that communities in harsh, edaphic habitats where plants are already well-adapted to environmental stress may be more resilient to the effects of climate change than species growing on more fertile soils (Harrison, Damschen, Fernandez-Goñi, Eskelinen, & Copeland, 2014). Glades on the low end of the soil resource-availability spectrum are comparable to harsh, edaphic soils like serpentine where such resilience to climate change has been documented; in contrast, glades with higher soil resource availability are much more productive (Miller et al., 2015). Therefore, communities on high-resource soils may be most vulnerable to increased environmental stress from climate change; this is particularly concerning, because glades with high-resource soils have the highest plant diversity. Within these communities, summer-blooming species may be particularly vulnerable to increased temperature or drought, since they already appear to be limited by an environmental harshness gradient. Communities on high-resource availability soils and summer-blooming species may be especially vulnerable when they occur in small, isolated patches. The relative importance of habitat isolation and pre-existing community adaptations to harsh conditions for community trajectories under climate change is an area that is ripe for future research.

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AUTHORS' CONTRIBUTIONS

Authorship was determined using a first-last-author-emphasis approach; J.E.D.M. and E.I.D. led conceptualization of the project; J.E.D.M. conducted fieldwork; J.E.D.M. and E.I.D. led lab data collection; J.E.D.M. and A.R.I. led the development of the analytical approach and conducted analyses; J.E.D.M., E.I.D., S.P.H. and A.R.I. contributed to writing.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.7fq07> (Miller, Ives, Harrison, & Damschen, 2017).

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