Ecology, 96(12), 2015, pp. 3323–3331

Landscape structure affects specialists but not generalists in naturally fragmented grasslands

Jesse E. D. Miller,[1,4] Ellen I. Damschen,[1] Susan P. Harrison,[2] and James B. Grace[3]

[1]*Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA*
[2]*Department of Environmental Science and Policy, University of California, Davis, California 95616 USA*
[3]*U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Boulevard, Lafayette, Louisiana 70506 USA*

Abstract. Understanding how biotic communities respond to landscape spatial structure is critically important for conservation management as natural habitats become increasingly fragmented. However, empirical studies of the effects of spatial structure on plant species richness have found inconsistent results, suggesting that more comprehensive approaches are needed. We asked how landscape structure affects total plant species richness and the richness of a guild of specialized plants in a multivariate context. We sampled herbaceous plant communities at 56 dolomite glades (insular, fire-adapted grasslands) across the Missouri Ozarks, USA, and used structural equation modeling (SEM) to analyze the relative importance of landscape structure, soil resource availability, and fire history for plant communities. We found that landscape spatial structure, defined as the area-weighted proximity of glade habitat surrounding study sites (proximity index), had a significant effect on total plant species richness, but only after we controlled for environmental covariates. Richness of specialist species, but not generalists, was positively related to landscape spatial structure. Our results highlight that local environmental filters must be considered to understand the influence of landscape structure on communities and that unique species guilds may respond differently to landscape structure than the community as a whole. These findings suggest that both local environment and landscape context should be considered when developing management strategies for species of conservation concern in fragmented habitats.

Key words: connectivity; dolomite grasslands; endemics; fire adaptation; fragmentation; glades; Ozarks, Missouri, USA; patch quality; plant diversity; structural equation modeling.

Introduction

Effects of landscape spatial structure on ecological communities have long been of interest to ecologists because habitat fragmentation is one of the greatest threats to global biodiversity (Wilcove et al. 1998). As natural habitats become more fragmented (i.e., smaller and more isolated), ecological communities may undergo homogenization and species loss. Several mechanisms may link landscape spatial structure (i.e., the size and configuration of habitat patches) to ecological communities. Fewer species may be able to colonize small, isolated patches, and small patches may also have higher extinction rates (MacArthur and Wilson 1967). In addition, environmentally mediated community changes may occur with fragmentation; for example, habitat quality may decrease as the edge-to-area ratio increases, leading to species loss (Laurance 2008). Understanding how ecological communities respond to landscape structure is essential for managing ecosystems and maintaining biodiversity in an era of rapid global change, but important questions about community responses to landscape structure remain incompletely answered.

Empirical studies have found inconsistent results about the effects of landscape spatial structure on plant communities, making it difficult to establish general patterns to apply to conservation management (Ewers and Didham 2006, Fahrig 2013). In some systems, increasing patch size and connectivity (which are generally correlated) have been shown to positively influence species richness (Harrison 1997, Damschen et al. 2006, Morgan and Farmilo 2012), but negative responses have also been reported (Abadie et al. 2011). In other cases, landscape spatial structure has been found to have no detectable impacts on plant communities and diversity has instead been explained primarily by other factors, such as local environmental variables (Dupré and Ehrlén 2002, Guirado et al. 2007, Herrera and Laterra 2011). Although some work suggests that the effects of spatial structure are system-specific (Petit et al. 2004), this raises the question of whether variation among results from different systems could be explained at least in part through a more holistic modeling process that considers environmental covariates and plant life histories.

Because ecological communities are the products of multiple factors including local environment, distur-

Manuscript received 9 February 2015; revised 19 May 2015; accepted 21 May 2015. Corresponding Editor: G. A. Fox.

[4] E-mail: kawriver@gmail.com

bance, and land-use history, landscape structure may not have a significant influence on community patterns until other drivers are accounted for (Weiher et al. 2004, Mortelliti et al. 2010). For example, fire history can have effects on grassland plant communities (Peterson and Reich 2008) that should be considered in studies of the effects of spatial structure. Notably, landscape experiments that manipulate patch connectivity while holding other variables constant have provided strong evidence that landscape structure can have significant effects on diversity (Gonzalez et al. 1998, Damschen et al. 2006). In addition, landscape spatial structure is often correlated with environmental gradients in natural settings, underscoring the importance of analyzing its influence in a context in which individual factors can be teased apart (Ibáñez et al. 2014). Surprisingly, a holistic approach to studying effects of landscape structure in which other diversity drivers are accounted for remains relatively rare despite the recent popularity of studies of habitat fragmentation (Ewers and Didham 2006, Harrison et al. 2006, Mortelliti et al. 2010).

Because different species often vary in sensitivity to spatial structure, analyses of total species richness alone may not accurately capture community responses to spatial structure (Ewers and Didham 2006, Koper et al. 2010, Lindborg et al. 2012). For example, habitat generalists that can grow in the matrix surrounding focal habitat patches would not be expected to be influenced by patch size or isolation. Thus, unique plant guilds, such as species that are particularly sensitive to disturbance and land-use history, may respond differently to landscape structure than the community as a whole does (Abadie et al. 2011, Ramalho et al. 2014). An approach that considers such guilds may detect significant compositional shifts caused by landscape structure even when total species richness does not change (Matthews et al. 2014). Understanding which species respond to landscape structure could help explain inconsistent results of previous studies (Banks-Leite et al. 2012).

Sampling design may also influence whether effects of landscape structure on communities are detected in observational studies. Examining patterns of species density (the number of species that occur in samples of a fixed area) is one useful alternative to analyzing patch-level richness because fewer potentially confounding mechanisms are expected to influence species density than patch-level richness (reviewed by Giladi et al. 2014). For example, the random sampling hypothesis suggests that more species will be found with greater sampling effort, which is needed to sample larger patches; this mechanism would not impact measurements of species density. Recent review papers suggest that studying patterns of species density may hold promise for untangling the long-standing ecological puzzle of community responses to landscape spatial structure (Fahrig 2013, Giladi et al. 2014). We analyze species density, termed "richness" here, for consistency with the literature.

We investigate the relative importance of landscape spatial structure for total plant species richness and the richness of a guild of specialist plant species in a naturally patchy system. We tested a two-stage hypothesis. First, we hypothesized that plant species richness would be higher in larger, more connected patches after accounting for local environmental variation and disturbance history. Second, we hypothesized that landscape spatial structure would have a greater effect on the richness of specialist species than on generalist richness, because the unique life history traits of specialists may make them more vulnerable to local extinctions and less able to recolonize and because they are less likely to occur in the matrix habitat surrounding glades.

METHODS

Study system

We studied the relative influence of landscape and local factors on plant communities in dolomite glades across the Ozark highlands of Missouri, USA. Glades are dry grasslands characterized by shallow soil with frequent dolomite (carbonate sedimentary bedrock) outcrops. Glades occur at mid- to upper-slope positions on south- and west-facing hills, where intense solar radiation reduces woody plant establishment, throughout the Ozark highlands of Missouri. Glades are relatively insular in that they are generally surrounded by closed-canopy woodlands. Largely because their shallow, rocky soils are poorly suited to agriculture and other anthropogenic uses, glades represent a relatively intact system compared to most grasslands in the central United States.

Glades are a fire-adapted ecosystem that, like other upland habitats in the Ozarks, burned as often as every three years prior to the widespread fire suppression that began in the 20th century (Guyette and McGinnes 1982). Although fire effects on plant communities have been little studied in glades, evidence from other Midwest grasslands indicates that fire can increase plant diversity by reducing competition and increasing plant establishment through litter removal (Cavender-Bares and Reich 2012). Fire also plays a role in maintaining grassland habitat structure by limiting the establishment of woody vegetation (Peterson and Reich 2008). Many glades are currently managed with prescribed fire.

The glade flora consists of numerous grassland generalist species, many of which are species of Great Plains prairie affinity, that may also occur in other Ozark habitats, such as prairies, savannas, pastures, and roadsides, but are generally uncommon in the dense woodland matrix that typically surrounds glades. Glades also contain many habitat specialist species that are almost completely restricted to glade habitats, including several regional endemics and other species of conservation concern (Yatskievych 1999, 2006, 2013). Glade specialists tend to have patchy, sporadic distributions within the glade landscape (Miller-Struttmann 2013). These species also tend to be long-lived perennials that disperse poorly or infrequently and are sensitive to land-use legacies, such as the effects of the intensive open-range livestock grazing that occurred across the Ozarks in the early 1900s (Nelson 2005).

Glades have been described from natural history and conservation perspectives by several authors (Steyermark 1940, Erickson et al. 1942, Kucera and Martin 1957, Nelson and Ladd 1983, Baskin and Baskin 2000, Ware 2002), but there has been little previous quantitative analysis of the drivers of local plant diversity in glades.

Sampling and site selection

To characterize glade plant communities, we sampled 56 glade study sites across Missouri's Ozark region. We consulted with land managers to identify glades that had been managed with prescribed fire. We then selected glades for study if they met the following criteria. (1) They met Nelson's (2005) definition of a dolomite glade: upland grassland communities punctuated by periodic bedrock outcrops, with shallow soil (<50 cm) and low (<10%) woody vegetation cover. (2) They were sites that local experts and managers thought were either historically ungrazed or only mildly grazed by domestic livestock to avoid possible disturbance legacy effects on plant communities. And, (3) because our goal was to investigate the relative importance of processes in fire-maintained intact glade plant communities, sites had to be maintained with frequent (~3–6 yr) low-intensity prescribed fires, matching the historical disturbance regime (Nelson and Ladd 1983).

Plant community sampling procedure

We sampled plant communities using a modified (narrower) version of Whittaker's (1960) vegetation plot design to enable fitting plots into small glades. At each study site, we established one 2 × 50 m (100 m^2) study plot. We used the total number of species that occurred in this plot as our measure of species richness (i.e., density). To measure site environmental characteristics, we established five 0.5 × 0.5 m (0.25 m^2) quadrats evenly spaced throughout the larger plot, in which we recorded total herb cover as well as cover of rock, bare soil, shrubs, and plant litter.

Sampling was timed to visit sites at peak bloom; each study site was visited during both the early (May–early July) and late (late July–September) blooming season of either 2012 or 2013 to maximize species detection. Species from both visits were combined to produce a single master species occurrence list for each site, from which we generated our species richness variables. Study plots were randomly located within glades but had to be more than 5 m from glade edges and more than 50 m from roads to avoid habitat edges and ruderal disturbance.

Plants were identified according to the Flora of Missouri (Yatskievych 1999, 2006, 2013). Plants that could not be identified to species were analyzed at the generic level (<3% of all species).

We defined specialist glade species as species with a coefficient of conservatism of 7 or greater, and generalists as species with a coefficient of conservatism below 7. The coefficient of conservatism is an index that ranges from 0 to 10, representing the fidelity of a species to undisturbed, late successional remnant habitats; values are generally assigned at the state level by local experts (Swink and Willhelm 1994). We used coefficient of conservatism values for Missouri as determined by Ladd (1992).

Environmental variables

Soil resource availability.—We collected soil from a depth of 15 cm in five locations evenly spaced along the 50 m central transect and bulked the samples for each plot. Soil was analyzed at Brookside Labs (New Knoxville, Ohio, USA) for organic matter and texture (sand, silt, and clay content). We used clay and organic matter content as indicators of soil resource availability, since they were strong bivariate predictors of species richness, and they are indicators of soil moisture-holding capacity, which is often a predictor of plant diversity (Kammer et al. 2013).

Fire history.—Fire regimes are characterized by the frequency, intensity, and timing of fires. We focused on frequency because of its known importance for grassland diversity (Cavender-Bares and Reich 2012) and because records of fire frequency were consistently available across our sites. Using these records, we calculated two fire history variables: fire frequency (total fires in the previous 12 years) and time since the most recent fire.

Landscape structure

Numerous landscape metrics related to patch area, patch configuration, and patch geometry have been used by ecologists to quantify landscape spatial structure; different metrics may be more biologically relevant for different systems and groups of organisms (Kupfer 2012). Habitat area and configuration can have independent effects on communities, but because they are generally correlated in natural settings, only experimental approaches that manipulate landscape structure can effectively tease apart unique effects of area and connectivity on natural communities (Haddad et al. 2015). In this study, we hypothesized that the amount of glade habitat and its proximity to our study sites would influence functional connectivity experienced by grassland plants and did not attempt to separate the effects of area and connectivity, which are strongly related in our system. We defined landscape spatial structure as the distance- and area-weighted amount of glade habitat within a biologically relevant distance of study sites.

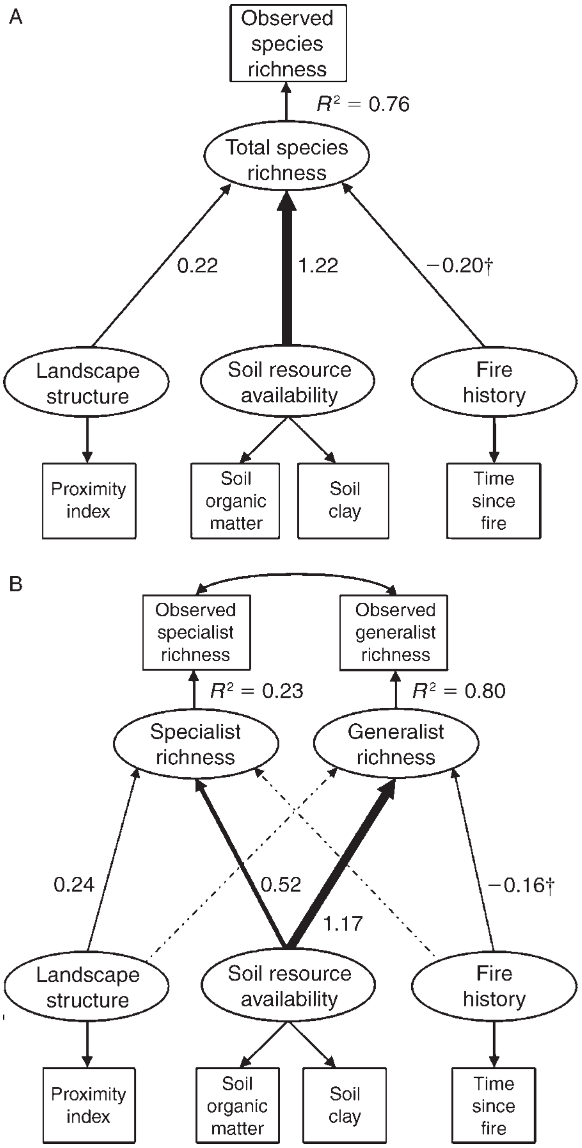

FIG. 1. A diagram of structural equation model for (A) total species richness and (B) richness of generalist and specialist species. Rectangles represent observed variables and ovals represent latent variables. Solid, straight lines represent significant relationships ($P < 0.05$) and are labeled with standardized path coefficients. The double-headed arrow between observed specialist and generalist richness in panel (B) represents a covariance between the prediction errors for those variables. The paths indicated with a dagger (†) represent a trend ($0.05 < P < 0.1$), and the dashed line represents a hypothesized relationship that was nonsignificant ($P > 0.1$).

To quantify glade spatial structure, we used a GIS layer of glade maps for Missouri (Nelson 2014). We exported glade rasters from ArcGIS (ESRI 2011) and used Fragstats (McGarigal et al. 2012) to calculate the mean proximity index, an area- and distance-weighted measure of habitat connectivity, for our study sites. Proximity index increases as habitat area increases and distance between patches decreases in a landscape (Gustafson and Parker 1992). For example, a landscape containing few small, isolated habitat patches would receive a low proximity index value, and a landscape consisting of several larger patches that are close together would receive a high value. One pitfall of proximity index is that it can be influenced by choice of buffer distance, but this is only a major shortcoming when biologically irrelevant buffer distances are chosen (McGarigal et al. 2012). Although some researchers have quantified isolation using simpler landscape metrics such as nearest-neighbor distance, such metrics may not relate well to ecological processes (Kupfer 2012).

To consider multiple scales of landscape influence that could be important for glade plant communities, we calculated proximity index at multiple radii around study sites (500 m, 1 km, 5 km, and 10 km), following methods similar to Lindborg and Eriksson (2004). The proximity index values we calculated were strongly correlated regardless of which buffer distance was used ($R^2 > 0.99$ for all pairwise combinations of buffer distances). In subsequent analyses, we used the 1 km buffer, which other studies have found to be the most important spatial scale for grassland plant communities (Lindborg and Eriksson 2004). Dispersal distances for most grassland plants are less than 1 km (Kinlan and Gaines 2003), suggesting it is a biologically appropriate distance at which to consider landscape influences. Study plots were separated by at least (and generally much more than) 500 m, leading to occasional partial overlap of the 1 km landscape buffers. Although overlap of analyzed landscape buffers is considered suboptimal because portions of the same landscape are analyzed twice for different sites, small amounts of overlap have negligible effects (Eigenbrod et al. 2011).

Analysis

We used structural equation modeling (SEM) to investigate the influences of local and regional factors on glade plant communities. SEM is an analytical approach designed for evaluating hypotheses about complex networks of cause–effect relationships in natural systems. SEM allows for specifying hypotheses involving both observed and also unobserved variables, whose values are estimated indirectly based on measured indicator variables (Grace 2006).

To test the relative importance of landscape spatial structure for the entire plant community and for species groups with varying life history characteristics, we first created a structural equation meta-model (Appendix A: Fig. A1), representing hypothesized general relationships. We then developed two parameterized SEMs for (1) total species richness and (2) generalist and specialist richness. Both models included six observed exogenous variables (soil clay, soil organic matter, proximity index, time since fire, and fire frequency) and three exogenous latent variables (soil resource availability, fire history, landscape structure). The first model contained one

FIG. 2. Photograph of a dolomite outcrop in Rocky Top Glade at Lake of the Ozarks State Park in Camden County, Missouri, USA. Photo credit: J. E. D. Miller.

latent, single-indicator endogenous variable, total species richness, with paths from all exogenous latent variables to the endogenous variable. The second model was similar except with two endogenous, single-indicator variables: generalist species richness and specialist species richness.

We then developed specific SEMs by removing nonsignificant variables and paths (Fig. 1; Grace 2006). Since fire frequency had no significant effect on either total species richness or specialist richness, we removed that predicator variable from both models and used only time since fire to represent fire history. We also ran versions of the first model that included additional exogenous environmental predictors: rock cover, herb cover, bare soil cover, the coefficient of variation (CV) of rock cover, the CV of bare soil cover, topographic slope, year of sampling, and quadratic terms for time since fire and proximity index. We compared these models using Akaike's information criterion corrected for sample sizes (AIC_c) in the lavaan.modavg.R package (Byrnes 2012), which indicated that none of these variables improved the model (Appendix C: Table C1). SEMs were analyzed using the lavaan package (Rosseel 2012) in R, version 2.15.2 (R Development Core Team 2012). We also used supplemental linear models to test for interactions between predictor variables. We found that none of these were significant (Appendix D: Table D1), so we do not discuss these models further.

Proximity index and time since fire were log 10 transformed, fire frequency was natural log transformed, and soil clay % was square-root transformed to meet assumptions of homogenous variances and normal distributions. Variable screening was performed in R, version 2.15.2 (R Development Core Team 2012). We tested residuals from both SEMS for spatial autocorrelation by calculating Moran's index in the Ape package in R (Paradis et al. 2004).

RESULTS

We found a total of 204 plant species, of which 55 were glade specialists, across the 56 study sites we analyzed here. Forbs made up the majority of the herbaceous glade flora: 80% of the specialist species and 79% of the generalist species. Species richness at our 100-m^2 study sites ranged from 14 to 62, with a median of 36.5 total species and 11 habitat specialists per site. Although a few ubiquitous glade species were present at nearly every site, species turnover between sites was high overall, with the average site containing only 18% of total species. Ninety-two species, or nearly half of the total species we encountered, occurred at three or fewer sites. Generalist richness and specialist species richness were correlated ($r^2 = 0.32$, $P < 0.01$).

Our final model explained 76% of the variation in total species richness with soil, glade spatial structure, and time since fire (Fig. 1A). Although there was no significant bivariate relationship between glade spatial structure and total species richness (Appendix B: Table B1), landscape structure had a significant effect once soil and fire were accounted for in the SEM, as we hypothesized. Overall, local site variables were more important for total species richness than landscape spatial structure. Our latent variable for soil resource availability, indicated by clay and organic matter content, was the strongest predictor of species richness; species richness was positively related to soil clay and organic matter content. Fire frequency was not a significant predictor of species richness, but time since fire did have a positive trend ($P = 0.08$) in relation to total species richness, with richness declining as time since fire increased.

Our final model for richness of individual guilds explained 23% of the variation in specialist species richness with soil and landscape structure and 80% of generalist species richness with soil and time since fire (Fig. 1B). As we hypothesized, landscape structure had a stronger effect on specialists than on generalists, for which it was not significant. Landscape structure had a significant bivariate relationship with specialist species richness, but this relationship became stronger in the SEM once soil variation was controlled. Soil resource availability had a significant effect on specialist richness, but had a stronger influence on generalist species richness (Fig. 1B). Fire history was not a significant predictor for specialist richness but did have a marginally significant effect on generalists. Decomposing total species richness into unique species guilds showed that some apparent drivers of total richness are in fact only acting on specific guilds: spatial structure for specialists and fire for generalists, in this case.

Residuals from both SEMs were not spatially autocorrelated (Moran's Index [MI] = -0.02, $P = 0.91$ for total richness; MI = -0.05, $P = 0.64$ for specialist richness; MI = 0.01, $P = 0.74$ for generalist richness).

DISCUSSION

Our results highlight the importance of conducting plant diversity studies in a framework that considers the simultaneous effects of multiple drivers and the role of environmental covariates (or patch quality) in particular. Although there was no significant bivariate relationship between landscape spatial structure and total species richness, their relationship became significant once we accounted for other environmental factors, as we hypothesized. Soil resource availability was by far the strongest driver of species richness, and controlling for soil characteristics was essential for seeing the more subtle influences of landscape structure and fire. These results provide some of the first empirical support for recent calls for more researchers to consider patch quality in studies of the effects of landscape fragmentation (Ibáñez et al. 2014, Pflueger and Balkenhol 2014).

We found that landscape structure affected specialist species richness, but not generalist richness. This is consistent with previous research that has found that larger-scale processes (e.g., landscape spatial structure) may play a greater role for specialist species, while local processes (e.g., environment) may have higher relative importance for generalist species (Harrison 1999, Pueyo et al. 2008). One plausible explanation for the greater sensitivity of specialists to landscape structure is that local extinctions could be more likely and recolonizations less likely for specialists than for other species—at any given level of patch size and connectivity—due to the unique life history characteristics of these species. Glade specialists are generally considered to be poor dispersers that are sensitive to anthropogenic disturbance, making them likely candidates for extirpation in smaller, more isolated glades.

Alternatively, the influence of landscape structure on specialist species could be caused by environmentally mediated mechanisms, such as edge and core area effects, since the larger glades at the higher end of the connectivity spectrum offer more core area of open, xeric glade environment away from the cooler woodland edge. Similar edge effects have been documented in another specialist-rich edaphic ecosystem, serpentine outcrops in California (Harrison 1997). However, previous research indicates that glade specialists are not necessarily better adapted to environmental stress than other glade species, suggesting that they might not benefit disproportionately from large areas of harsh, open glade away from the relatively mesic edge habitat (Miller-Struttman 2011). Larger regional species pools of glade specialists in regions with higher glade cover could also cause greater local specialist richness. Such top-down effects have previously been observed in serpentine communities (Harrison et al. 2006).

Greater habitat heterogeneity within larger habitat patches is another mechanism that has been shown to facilitate species coexistence (Öster et al. 2007, Wulf and Kolk 2014). However, the measures of heterogeneity that we examined were not significantly correlated with either landscape spatial structure or species richness response variables (Appendices B and C: Tables B1 and C1). We note that glades across the gradient of spatial structure are characterized by high heterogeneity in soil depth because of the underlying shelf-like dolomite formations (Ware 2002), and environmental heterogeneity is not necessarily greater in larger glades.

Landscape spatial structure can also affect plant communities via altered species interactions, although we did not test this possibility explicitly. Theory predicts that competitive pressure may be lower in isolated patches because fewer competitors may be able to disperse there (Caswell and Cohen 1993). That explanation, however, seems unlikely to be applicable to glades, since the dominant competitors are warm-season grasses which are ubiquitous in glades. Variations in herbivory and granivory associated with glade spatial structure, however, could influence plant community assembly, as research in other patchy systems has documented (Santos and Telleria 1994, Asquith et al. 2015). In addition, decreased pollinator visitation in fragmented landscapes has been shown to negatively affect plant reproduction (Aguilar et al. 2006). In glades, specialist plants often have floral adaptations that increase their attractiveness to pollinators, suggesting that pollination success may be more of a limiting factor for specialists than it is for glade generalists (Miller-Struttmann 2013). Thus, decreased pollinator diversity and abundance in isolated glades could be one explanation for the sensitivity of specialists to glade spatial structure.

Our model explained 80% of the variation in generalist species richness, but only 23% of the variation in specialist richness, suggesting that additional, unmeasured factors influence the distributions of specialists. Poor dispersal abilities of specialists may stochastically limit their distributions, even in well-connected patches with favorable abiotic conditions. Land-use legacies, such as the intensive open-range grazing that occurred commonly in the Ozarks in the early 1900s, may also affect contemporary distributions of glade specialist plants (Miller-Struttmann 2013). Although we attempted to avoid sampling historically disturbed sites, it is likely that there is some spectrum of historic disturbance within our data set. Grazing disturbance has been shown to cause persistent legacy effects on plant communities many decades after domestic livestock have been removed from a landscape (Fraterrigo et al. 2006, Fortuny et al. 2014). It is also possible that soil texture, which has a strong effect on specialist species richness in our data set, could mediate effects of historic grazing disturbance, since a given level of grazing intensity may cause more severe perturbation on malleable sandy soils than clay soils (Root et al. 2011).

Our results may not be fully representative of the longer term impacts of isolation on glade specialist species. Glade communities are often viewed as relics of the warmer, drier climate of past millennia in the Ozarks, and extinction debt from the gradual increase in glade isolation may not be fully paid. In other words, the full effects of landscape spatial structure may not become apparent until after a significant time delay, as work in several other systems has documented (Lindborg and Eriksson 2004, Vellend et al. 2006, Ramalho et al. 2014).

Conservation implications

Our results suggest that maintaining populations of specialist species in smaller, more isolated glades may be challenging over the long term. Maintaining existing glade connectivity (i.e., preventing further glade habitat loss) and increasing landscape connectivity through the restoration of degraded glades should be conservation priorities. Prescribed fire appears to be one important management tool for maintaining an open and connected glade landscape (Templeton et al. 2001). More experimental studies of how various fire and mechanical thinning regimes affect glade plant diversity and woody vegetation would help land managers make informed decisions for glade conservation.

Total species richness was most strongly affected by soil characteristics, and conservation efforts that are aimed at maintaining high total plant diversity could benefit from prioritizing glades with higher soil resource availability (i.e., higher clay and organic matter content) for restoration and management, since these appear to be hotspots for both total glade plant diversity and specialist diversity. These glades may be at particularly high risk from woody encroachment, a major threat to glade plant diversity, since woody vegetation appears to establish more prolifically in richer soils. However, we found that species composition shifts with species richness along the soil resource gradient in glades, and some specialist species occur most commonly in areas of low-resource soils (J. E. D. Miller, *unpublished data*), highlighting the importance of conserving glades across the spectrum of soil environments. Finally, our results indicate that local soil characteristics could be used by land managers to set diversity targets for restoration projects, since soil appears to limit species richness in glades. In other words, successful restorations can be expected to vary in species richness correspondent to the local environment.

Acknowledgments

We are grateful to everyone who provided assistance with various aspects of this project, including site selection, the assembly of fire records, and hospitality during field trips, all of whom are too numerous to list here. In addition, we wish to thank our many excellent field assistants, as well as Bull Shoals Field Station, the Missouri Botanical Garden, Paul Nelson (for providing glade maps), and Justin Thomas (for providing plant identification assistance). Amy Alstad, Shannon Grover, Phil Hahn, Monica Turner, and two anonymous reviewers provided helpful comments that improved the manuscript. Support for J. B. Grace was provided by the USGS Ecosystems and Climate & Land Use Programs. This material is based upon work supported by National Science Foundation (NSF) DEB-0947432 and the NSF Graduate Research Fellowship under Grant No. 2012149884. Any opinion, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature Cited

Abadie, J.-C., N. Machon, A. Muratet, and E. Porcher. 2011. Landscape disturbance causes small-scale functional homogenization, but limited taxonomic homogenization, in plant communities. Journal of Ecology 99:1134–1142.

Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecology Letters 9:968–980.

Asquith, N. M., S. J. Wright, and M. J. Clauss. 2015. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology 78: 941–946.

Banks-Leite, C., R. M. Ewers, and J. P. Metzger. 2012. Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. Ecology 93: 2560–2569.

Baskin, J. M., and C. C. Baskin. 2000. Vegetation of limestone and dolomite glades in the Ozarks and Midwest regions of the United States. Annals of the Missouri Botanical Garden 87:286–294.

Byrnes, J. 2012. lavaan.modavg.R package. http://jarrettbyrnes.info/ubc_sem/lavaan_materials/lavaan.modavg.R

Caswell, H., and J. E. Cohen. 1993. Local and regional regulation of species-area relations: a patch-occupancy model. Pages 99–107 *in* R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.

Cavender-Bares, J., and P. Reich. 2012. Shocks to the system: community assembly of the oak savanna in a 40-year fire frequency experiment. Ecology 93:52–69.

Damschen, E. I., N. M. Haddad, J. L. Orrock, J. J. Tewksbury, and D. J. Levey. 2006. Corridors increase plant species richness at large scales. Science 313:1284–1286.

Dupré, C., and J. Ehrlén. 2002. Habitat configuration, species traits and plant distributions. Journal of Ecology 90:796–805.

Eigenbrod, F., S. J. Hecnar, and L. Fahrig. 2011. Sub-optimal study design has major impacts on landscape-scale inference. Biological Conservation 144:298–305.

Erickson, R., L. Brenner, and J. Wraight. 1942. Dolomitic glades of East-Central Missouri. Annals of the Missouri Botanical Garden 29:89–101.

ESRI [Environmental Systems Research Institute]. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands, California, USA.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews of the Cambridge Philosophical Society 81:117–142.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40: 1649–1663.

Fortuny, X., C. Carcaillet, and S. Chauchard. 2014. Land use legacies and site variables control the understorey plant communities in Mediterranean broadleaved forests. Agriculture, Ecosystems and Environment 189:53–59.

Fraterrigo, J. M., M. G. Turner, and S. M. Pearson. 2006. Interactions between past land use, life-history traits and understory spatial heterogeneity. Landscape Ecology 21:777–790.

Giladi, I., F. May, M. Ristow, F. Jeltsch, and Y. Ziv. 2014. Scale-dependent species-area and species-isolation relationships: a review and a test study from a fragmented semi-arid agro-ecosystem. Journal of Biogeography 41:1055–1069.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamic, abundance, and distribution in a microecosystem. Science 281: 2045–2048.

Grace, J. B. 2006. Structural equation modeling and natural systems. University Press, Cambridge, UK.

Guirado, M., J. Pino, and F. Rodà. 2007. Comparing the role of site disturbance and landscape properties on understory species richness in fragmented periurban Mediterranean forests. Landscape Ecology 22:117–129.

Gustafson, E. J., and G. R. Parker. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecology 7:101–110.

Guyette, R., and E. A. McGinnes. 1982. Fire history of an Ozark glade in Missouri. Transactions of the Missouri Academy of Sciences 16:85–93.

Haddad, N. M., et al. 2015. Habitat fragmentation and its lasting impact on Earth ecosystems. Science Advances 1:1–9.

Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. Ecology 78:1898–1906.

Harrison, S. 1999. Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. Ecology 80:70–80.

Harrison, S., H. D. Safford, J. B. Grace, J. H. Viers, and K. F. Davies. 2006. Regional and local species richness in an insular environment: serpentine plants in California. Ecological Monographs 76:41–56.

Herrera, L. P., and P. Laterra. 2011. Relative influence of size, connectivity and disturbance history on plant species richness and assemblages in fragmented grasslands. Applied Vegetation Science 14:181–188.

Ibáñez, I., D. S. W. Katz, D. Peltier, S. M. Wolf, and B. T. Connor Barrie. 2014. Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess–multiresponse dynamics. Journal of Ecology 102:882–895.

Kammer, P. M., C. Schöb, G. Eberhard, R. Gallina, R. Meyer, and C. Tschanz. 2013. The relationship between soil water storage capacity and plant species diversity in high alpine vegetation. Plant Ecology and Diversity 6:1–10.

Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020.

Koper, N., K. E. Mozel, and D. C. Henderson. 2010. Recent declines in northern tall-grass prairies and effects of patch structure on community persistence. Biological Conservation 143:220–229.

Kucera, C. L., and S. C. Martin. 1957. Vegetation and soil relationships in the glade region of the southwestern Missouri Ozarks. Ecology 38:285–291.

Kupfer, J. A. 2012. Landscape ecology and biogeography: rethinking landscape metrics in a post-FRAGSTATS landscape. Progress in Physical Geography 36:400–420.

Ladd, D. 1992. Coefficients of conservatism for the Missouri vascular flora. Nature Conservancy, St. Louis, Missouri, USA.

Laurance, W. 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biological Conservation 141:1731–1744.

Lindborg, R., and O. Eriksson. 2004. Historical landscape connectivity affects present plant species diversity. Ecology 85:1840–1845.

Lindborg, R., A. Helm, R. Bommarco, R. K. Heikkinen, I. Kühn, J. Pykälä, and M. Pärtel. 2012. Effect of habitat area and isolation on plant trait distribution in European forests and grasslands. Ecography 35:356–363.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Matthews, T. J., H. E. Cottee-Jones, and R. J. Whittaker. 2014. Habitat fragmentation and the species-area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. Diversity and Distributions 20: 1136–1146.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, Massachusetts, USA. http://www.umass.edu/landeco/research/fragstats/documents/fragstats.help.4.2.pdf

Miller-Struttman, N. 2011. Causes of rarity in glade-endemic plants: implications for responses to climate change. Washington University.

Miller-Struttmann, N. E. 2013. Rarity and reproductive biology: habitat specialists reveal a complex relationship. Botany 359:349–359.

Morgan, J. W., and B. J. Farmilo. 2012. Community (re)organization in an experimentally fragmented forest landscape: insights from occupancy-scale patterns of common plant species. Journal of Vegetation Science 23:962–969.

Mortelliti, A., G. Amori, and L. Boitani. 2010. The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. Oecologia 163: 535–47.

Nelson, P. 2005. Terrestrial natural communities of Missouri. Missouri Department of Natural Resources, Jefferson City, Missouri, USA.

Nelson, P. 2014. Missouri 2014 natural glades. Missouri Department of Natural Resources, Jefferson City, Missouri, USA.

Nelson, P., and D. Ladd. 1983. Preliminary report on the identification, distribution and classification of Missouri glades. Proceedings of the Seventh North American Prairie Conference. Southwest Missouri State University, Springfield, Missouri, USA.

Öster, M., S. A. O. Cousins, and O. Eriksson. 2007. Size and heterogeneity rather than landscape context determine plant species richness in semi-natural grasslands. Journal of Vegetation Science 18:859–868.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Peterson, D. W., and P. B. Reich. 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. Plant Ecology 194:5–16.

Petit, S., L. Griffiths, S. S. Smart, G. M. Smith, R. C. Stuart, and S. M. Wright. 2004. Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. Landscape Ecology 19:463–472.

Pflueger, F. J., and N. Balkenhol. 2014. A plea for simultaneously considering matrix quality and local environmental conditions when analysing landscape impacts on effective dispersal. Molecular Ecology 49:2146–2156.

Pueyo, Y., C. L. Alados, O. Barrantes, B. Komac, and M. Rietkerk. 2008. Differences in gypsum plant communities associated with habitat fragmentation and livestock grazing. Ecological Applications 18:954–64.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Ramalho, C. E., E. Laliberte, P. Poot, and R. J. Hobbs. 2014. Complex effects of fragmentation on remnant woodland plant communities of a rapidly urbanizing biodiversity hotspot. Ecology 95:2466–2478.

Root, H. T., J. E. D. Miller, and B. McCune. 2011. Biotic soil crust lichen diversity and conservation in shrub-steppe habitats of Oregon and Washington. Bryologist 114:796–812.

Rosseel, Y. 2012. lavaan: an R package for structural equation modeling. Journal of Statistical Software 48:1–36.

Santos, T., and J. L. Telleria. 1994. Influence of forest fragmentation on seed dispersal of *Juniperus thurifera*. Biological Conservation 70:129–134.

Steyermark, J. 1940. Studies of the vegetation of Missouri. I: Natural Plant Associations and succession in the Ozarks of Missouri. Field Museum of Natural History Botanical Series 4. Field Museum Press, Chicago, Illinois, USA.

Swink, F., and G. Willhelm. 1994. Plants of the Chicago region. Fourth edition. Indiana Academy of Science, Indianapolis, Indiana, USA.

Templeton, A. R., R. J. Robertson, J. Brisson, and J. Strasburg. 2001. Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. Proceedings of the National Academy of Sciences USA 98: 5426–5432.

Vellend, M., K. Verheyen, H. Jacquemyn, A. Kolb, H. Van Calster, G. Peterken, and M. Hermy. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87:542–548.

Ware, S. 2002. Rock outcrop plant communities (glades) in the Ozarks: a synthesis. Southwestern Naturalist 47:585–597.

Weiher, E., S. Forbes, T. Schauwecker, and J. B. Grace. 2004. Multivariate control of plant species richness and community biomass in blackland prairie. Oikos 106:151–157.

Whittaker, R. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279–338.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607–615.

Wulf, M., and J. Kolk. 2014. Plant species richness of very small forests related to patch configuration, quality, heterogeneity and history. Journal of Vegetation Science 25:1267–1277.

Yatskievych, G. 1999. Steyermark's flora of Missouri. Second edition. Volume 1. Missouri Department of Conservation and Missouri Botanical Garden, Jefferson City and St. Louis, Missouri, USA.

Yatskievych, G. 2006. Steyermark's flora of Missouri. Second edition. Volume 2. Missouri Botanical Garden Press, St. Louis, Missouri, USA.

Yatskievych, G. 2013. Steyerkmark's flora of Missouri. Second edition. Volume 3. Missouri Botanical Garden Press, St. Louis, Missouri, USA.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–F are available online: http://dx.doi.org/10.1890/15-0245.1.sm