



Relationships of community diversity with distributions of rare species, non-native plants, and compositional stability in a temperate forest–open habitat landscape

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Abstract

Three hypotheses regarding relationships between community diversity and occurrences of rare and non-native species and community stability include: (1) diverse communities contain the greatest numbers of rare species, (2) hotspots of native species richness and abundance also support many non-native species, and (3) community diversity promotes stability. We explored these hypotheses by sampling plant communities during two years (2018, 2021) in 151, 0.05-ha plots across a landscape of temperate forests and open habitats (e.g., prairies) in Ohio, USA. Occurrence of rare plant species corresponded with the most species-rich and diverse (Shannon diversity index) communities in one or both study years. Species richness of native and non-native plants was positively associated both years but cover was not. Stability of species composition between 2018 and 2021 was unrelated to 2018 species richness and was negatively related to community diversity and evenness. The most diverse sites were not the most compositionally stable. Although statistically significant relationships occurred between community diversity measures and rare and non-native species distributions and community compositional stability, the relationships were often weak or mainly only evident at the extremes. Moreover, variance partitioning indicated that occurrences of rare and non-native species and community compositional stability were more closely associated with location effects within the landscape and community type than they were to community diversity. Nevertheless, when especially high or low, community diversity measures may facilitate predicting levels of other community components of conservation priority, such as rare species occurrences.

Keywords Context dependency · Forested wetland · Native and non-native species relationship · Oak savanna · Species richness

Introduction

A variety of research approaches have developed an array of ideas and hypotheses regarding relationships among ecological community diversity, invasibility by non-native species,

and stability (Reiners et al., 2015). Three of the hypotheses of keen interest in fundamental and applied community ecology include whether: (1) sites high in diversity of common species also contain numerous rare species, (2) distributions of native and non-native species richness and abundance co-vary spatially, and (3) community diversity promotes community stability.

Regarding whether diversity hotspots and rare species are co-located, diverse communities and rare species could coincide if they respond similarly to edaphic or disturbance factors (Irl et al., 2015). For example, sites with edaphic conditions favorable for a diverse array of plant species, including rare species, could produce positive relationships between species diversity and rare species (Stohlgren et al., 2005). In contrast, if rare species inhabit unique sites unfavorable for most species (e.g., soil with extreme properties), a negative relationship between species diversity and rare species

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may be anticipated (Tetetla-Rangel et al., 2017). High species diversity per se could foster rare species colonization by creating a diversity of biotic structure and activity, such as attracting pollinators benefiting common and rare plants alike (Lennon et al., 2011). Contrastingly, high species diversity could reduce favorability for rare plant occurrence via high levels of competition, depleting soil resources, or attracting biotic damaging agents such as herbivores (Levine et al., 2004). If community diversity and rare species occurrences are correlated, applications for ecological conservation include using diversity as a surrogate for forecasting likely locations of rare species and conserving diverse communities could in turn conserve rare species (Crisfield et al., 2020).

Considering distributional correspondence between native and non-native plant species richness, sampling studies have reported variable relationships (e.g., negative if competition predominates and positive if facilitation predominates) at fine scales (e.g., $< 10 \text{ m}^2$) and commonly positive relationships at broader scales such as $\geq 100\text{--}1000 \text{ m}^2$ (Fridley et al., 2007; Gill et al., 2021; Peng et al., 2019). Positive native and non-native species relationships at broad scales could result from both species groups responding similarly to favorable habitat factors, a sampling effect whereby sites with many native species have a greater probability of containing a native that facilitates invasions, greater heterogeneity or availability of regeneration niches in larger areas, or net outcomes of competition and facilitation among patches favoring invasion (García-Baquero Moneo et al., 2022; Levine & D'Antonio, 1999; Palmer & Maurer, 1997; Tomasetto et al., 2019). However, native and non-native species relationships at broad scales have often been weak (e.g., Abella & Tendick, 2013; Schetter et al., 2013; Stohlgren et al., 2005) and not always positive (e.g., Symonds & Pither, 2012; Vilà et al., 2007). These weak or negative relationships could result from landscape features such as diverse native sites corresponding with environments not conducive to invasion or having high biotic resistance, diverse native sites being far from non-native propagule sources or constraining dispersal, or invasional meltdown whereby invading species facilitate further invasion and reduce resident native species diversity (Fridley et al., 2007; Simberloff & Von Holle, 1999). These observations suggest that identifying the direction and strength of native and non-native species relationships may aid evaluating context dependency of the patterns and inform habitat management applications including prioritizing site locations for non-native species surveys and treatments.

Studies of relationships between the diversity and species compositional stability of communities have reported a range of positive, negative, and no relationship findings (e.g., Bruelheide & Luginbühl, 2009; MacDonald et al.,

2015; Wang et al., 2010). Diversity and compositional stability could be positively related through processes such as the insurance effect, whereby greater diversity increases the chance some species will persist or that species abundance changes will average out, resulting in minimal change compared with species-poor communities subject to large change if a few species shift in abundance (Allison, 2004; McCann, 2000; Tilman et al., 2006). Alternatively, compositional stability could relate more strongly to species functional diversity (e.g., annual or perennial growth forms) or presence of dominant species stabilizing a community, resulting in no or weak community diversity–stability relationships (Hillebrand et al., 2008; Sasaki & Lauenroth, 2011; Valencia et al., 2020). Understanding diversity–stability relationships could have several applications for managing ecological communities. Applications include identifying expected ranges of variability of compositional change among communities varying in diversity or supporting management activities that increase species diversity, if diversity–stability relationships are positive and increasing community stability is a management goal.

Assessing the degree of generality or context dependency of these relationships between community diversity measures and occurrences of rare and non-native species and degree of community stability is a major goal in community ecology (Catford et al., 2022). Knowledge of how consistently community concepts portray observed variation within and among landscapes can aid in identifying the types of communities or landscapes in which different concepts can be expected to reliably forecast spatial and temporal variation and be applied to habitat conservation and management at appropriate temporal and spatial scales (Beck, 1997; Bestelmeyer et al., 2003; Eviner & Hawkes, 2008; Wainwright et al., 2018). By investigating spatial distributional patterns of three plant community features (occurrences of rare and non-native species and community compositional stability) in 151 study sites across a landscape containing a diversity of forested and open habitats in eastern North America, we pursued a primary goal of exploring three hypotheses regarding relationships between community diversity and community components. These null hypotheses included: (1) community diversity measures (species richness, evenness, and Shannon diversity) are unrelated to rare species occurrences, (2) native and non-native species richness and cover are unrelated, and (3) community diversity is unrelated to species compositional stability. Our secondary goal was exploring the combined importance of community diversity and context-dependent variables (location effects within the landscape, community type, and year) with occurrences of rare and non-native species and community compositional stability.

Methods

Study area

We performed the study within a network of 17 preserves managed by Metroparks Toledo as public conservation and recreational lands in and surrounding the city of Toledo, Lucas and Fulton counties, northwestern Ohio, USA (Fig. 1). The preserves range in size from 11 to 1737 ha and total 4737 ha. Climate is temperate, including daily average low/high temperatures of $-9/0$ °C in January and $16/29$ °C in July and 85 cm/year of precipitation (SD = 5; 1955–2021 records, Toledo Airport weather station, Midwestern Regional Climate Center, Champaign, IL). In the U.S. Environmental Protection Agency ecoregional

classification system, the preserves were in the Erie Lake Plains level 3 ecoregion and Oak Openings and Maumee Lake Plains level 4 (finest scale division) ecoregions (Omernik & Griffith, 2014). The Oak Openings ecoregion is a low-relief (generally < 10 m), sandy landscape on former glacial lake plain that currently contains a mixture of deciduous upland and wetland forests, plantations of conifer trees, and open habitats (e.g., prairies; Schetter et al., 2013). The Maumee Lake Plains, bisected by the Maumee River, is a low-lying region predominately containing wetland and sub-mesic deciduous forests with some open meadows and shoreline marshes along Lake Erie. Land use surrounding the preserves is primarily agricultural, suburban with low-density housing and woodlots, and urban with a higher density of houses and buildings (Martin & Root, 2020).

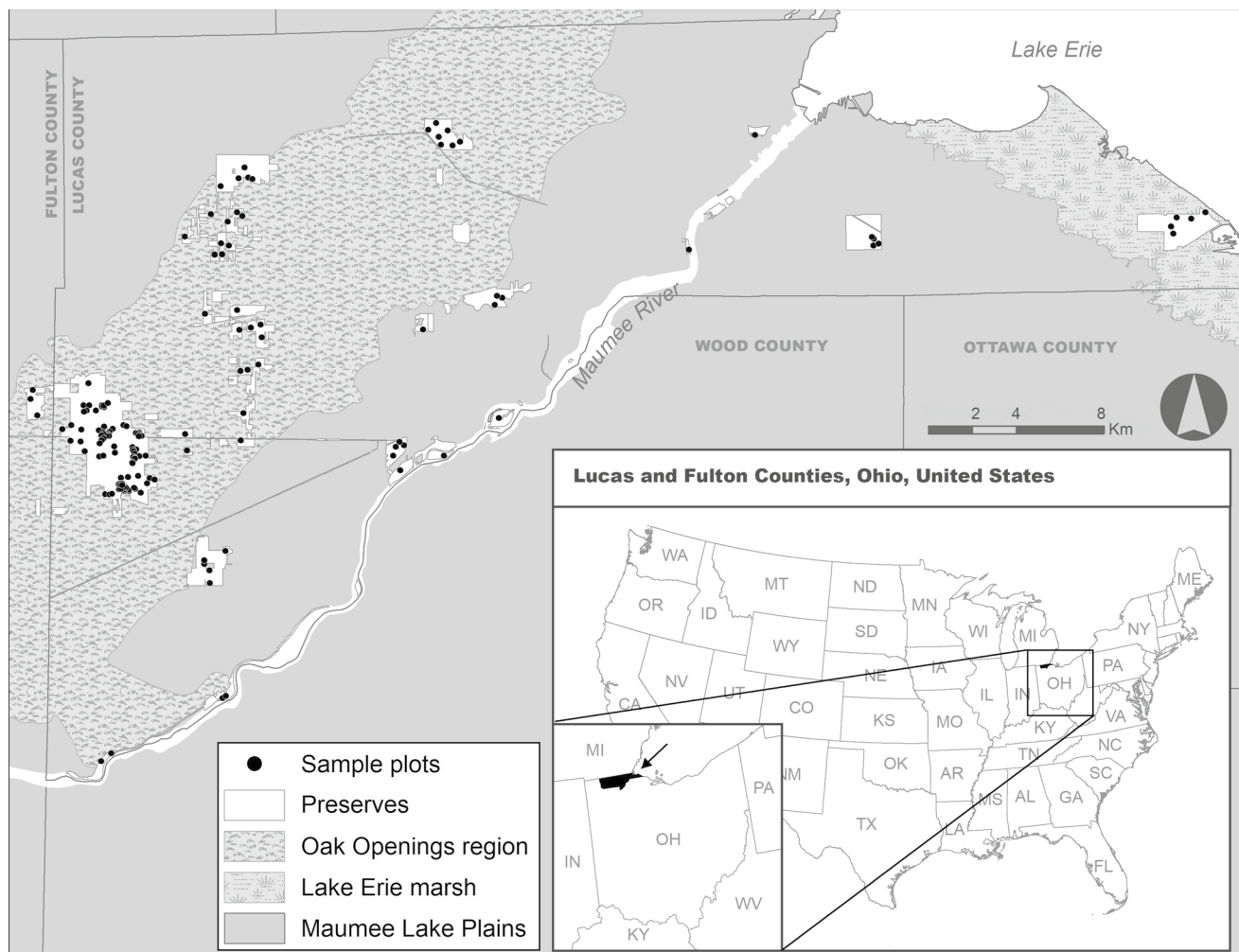


Fig. 1 Location of 151 plots in which plant communities were inventoried in 2018 and 2021 in a temperate forest–open habitat landscape in northwestern Ohio, USA

Data collection

Based on aerial imagery and a published plant community classification for the study region (Schetter & Root, 2011), we stratified preserves according to plant community types (forested wetland, oak forest, oak woodland, oak savanna, conifer plantation, prairie/meadow, and shoreline marsh; Table 1, Fig. 2). We then used random geographic coordinates to locate plots within polygons of community types, with no more than one plot per geographically distinct polygon (i.e., surrounded by polygons of other community types). Sample plots per preserve were allocated

approximately proportional to preserve size, with an average of 1 plot/30 ha. We sampled 151 plots, approximately equally distributed among community types, except for the relatively infrequent oak woodland and shoreline marsh communities (Table 1). Plots spanned a geographic extent of 57 km, and between-plot distance averaged 12 km.

During the summer growing season (June through mid-September), we sampled plots in 2018 and again in 2021. June through August precipitation during sampling was 93% (2018) and 121% (2021) of the 1955–2021 average of 26 cm (SD = 3). In each 0.05-ha (20 m × 25 m) plot, we inventoried the vascular plant community by visually categorizing the

Table 1 Summary of plant communities sampled within a temperate forest–open habitat landscape in northwestern Ohio, USA

Community type	No. plots	Environment	Example trees	Example herbs or shrubs
Forested wetland	38	Rivers, depressions	<i>Acer saccharinum</i> , <i>Carya</i> spp., <i>Populus deltoides</i>	<i>Boehmeria cylindrica</i> , <i>Lindera benzoin</i>
Oak forest	27	Unmanaged uplands	<i>Quercus velutina</i> , <i>Quercus alba</i> , <i>Acer rubrum</i>	<i>Carex pensylvanica</i> , <i>Desmodium nudiflorum</i>
Oak woodland	5	Managed uplands	<i>Q. velutina</i> , <i>Q. alba</i> , <i>Prunus serotina</i>	<i>Pteridium aquilinum</i> , <i>Vaccinium pallidum</i>
Oak savanna	24	Managed, open	<i>Q. velutina</i> , <i>Q. alba</i> , <i>Sassafras albidum</i>	<i>Rubus flagellaris</i> , <i>Lupinus perennis</i>
Conifer plantation	29	Planted 1950s–60s	<i>Pinus resinosa</i> , <i>Pinus strobus</i> , <i>Pinus sylvestris</i>	<i>Erechtites hieraciifolius</i> , <i>Polygonum virginianum</i>
Prairie/meadow	23	Dry–wet, open	–	<i>Dichanthelium clandestinum</i> , <i>Solidago rugosa</i>
Shoreline marsh	5	Lake Erie shoreline	–	<i>Polygonum pensylvanicum</i> , <i>Typha angustifolia</i>

Conifer plantations were either unmanaged or managed via tree thinning within the last 5–20 years

Fig. 2 Examples of plant community types in a temperate forest–open habitat landscape (northwestern Ohio, USA) in which hypotheses regarding relationships of community diversity measures with distributions of rare plant species, non-native plants, and community stability were investigated. Plots in community types clockwise starting from the upper left include: forested wetland, oak forest, meadow, and oak savanna. Photos by S.R. Abella, August 2017



aerial cover of each species rooted in each plot as 0.1, 0.25, 0.5, and 1%; 1% intervals to 10% cover, and 5% intervals to 100% cover. The maximum cover a species could attain on a plot was 100%. Cover summed for all species on a plot could exceed 100% if foliage of multiple species overlapped. If they were less than 1 cm in trunk diameter at a height of 1.4 m, we included individuals of tree species in cover categorizations. Nomenclature and classification of species as native or non-native to the USA follow Natural Resources Conservation Service (2022). We classified rare species as those state-listed as rare in Ohio (Ohio Department of Natural Resources, 2020). The community dataset with species classifications is in Online Resource 1.

Data analysis

For each plot and sampling year, we calculated species richness/0.05 ha (in total and sub-divided as native or non-native and rare species), cover of native and non-native species, the Shannon diversity index, and community evenness (Shannon diversity / $\ln(\text{species richness})$) in PC-ORD 7.07 (McCune & Mefford, 1999). We based Shannon diversity on relative cover (cover of species_{*i*} / \sum cover of all species on a plot). Also using relative cover, we calculated Sørensen % similarity of species composition for 2018 compared with 2021 (hereafter 2018:2021) for each plot to portray compositional stability.

To assess each of the three hypotheses, we performed three complementary analyses. First, we calculated bivariate correlations between variables for each hypothesis (H1: total species richness, evenness, and Shannon diversity with rare species richness in 2018 and 2021; H2: native with non-native species richness and cover in 2018 and 2021; and H3: total species richness, evenness, and Shannon diversity in 2018 with 2018:2021 Sørensen similarity). To accommodate nonlinear relationships, we used Spearman's rank coefficients for these analyses (De Winter et al., 2016).

The bivariate analyses revealed that relationships between variables were often most apparent at the low and high extremes of variables, so, secondly, we compared means of response variables each year across quartiles of predictor variables (Spiegelman & Gates, 2005). Variables included rare species richness as the response variable and total species richness, evenness, and Shannon diversity as predictor variables for H1; non-native species richness and cover as response variables and native species richness and cover as predictor variables for H2; and 2018:2021 Sørensen similarity as the response variable and total species richness, evenness, and Shannon diversity as predictor variables for H3. To compare means of response variables across quartiles of predictor variables, we used permutational analysis of variance (PERMANOVA; Anderson, 2001) in PAST 4.09 (Hammer, 2022). When PERMANOVA was significant at

$P < 0.05$, we separated means using sequential Bonferroni comparisons.

Third, to integrate multiple predictor variables and assess context dependency of relationships between response and predictor variables across years, community types, and spatial locations, we used variance partitioning (Selya et al., 2012). We partitioned variance by fitting generalized linear mixed models in SAS 9.4 (PROC GLIMMIX; SAS Institute, 2009). For each hypothesis to model response variables (H1: rare species richness; H2: non-native species richness and cover; and H3: 2018:2021 Sørensen similarity, as an arcsine-transformed proportion), we first fit full models including all quantitative predictor variables (H1: total species richness, evenness, and Shannon diversity; H2: native species richness and cover; and H3: total species richness, evenness, and Shannon diversity). Models for H1 and H2 also included plot as a random variable (repeated-measures subject) and year (2018, 2021) and community type (seven types, Table 1) as categorical predictor variables. The model for H3 included plot as a random variable and community type as a predictor variable, but did not include year because 2018:2021 Sørensen similarity incorporated both years. The quantitative predictor variables for H3 used 2018 values to model subsequent species compositional stability. Models included normal distributions and identity link functions, except for rare species richness (H1), which required a negative binomial and log link function (Irwin et al., 2013). We used *F*-statistics and *P* values from the full models to identify predictor variables significant at $P < 0.05$ to include in variance partitioning. If multiple quantitative or categorical predictor variables were significant at $P < 0.05$, we included the one quantitative and the one categorical variable accounting for the most variance. We partitioned variance hierarchically by sequentially fitting models containing only the plot random variable then plot as a random variable with increasing numbers of predictor variables, starting with quantitative (if significant from full models) then categorical variables (Selya et al., 2012).

Results

Hypothesis 1: rare species

Of the total 762 vascular plant species on plots, 54 were state-listed, rare species (Online Resource 1). There were 41 rare species on plots in 2018 and 47 rare species in 2021. The most frequently occurring rare species were wild lupine (*Lupinus perennis*; 9% of plots in 2018 and 2021), Canada frostweed (*Helianthemum canadense*; 7% and 11%), Great Lakes goldenrod (*Euthamia gymnospermoides*; 7% and 9%), wild indigo (*Baptisia tinctoria*; 7%

and 6%), Eaton's rosette grass (*Dichanthelium spretum*; 5% and 6%), and racemed milkwort (*Polygala polygama*; 2% and 8%).

Species richness (per 0.05 ha) of rare plants was weakly but significantly positively ($P < 0.05$) correlated with total species richness in both 2018 and 2021 and with the Shannon diversity index in 2021 (Fig. 3). Rare species richness was not correlated with community evenness in either year. In PERMANOVA, mean rare species richness was significantly lower in plots in the lower quartiles of total species richness (Table 2). Variance partitioning revealed that plot as a random variable accounted for the largest portion (42%) of variability in rare species richness, with remaining variability accounted for by total species richness (24%) and community type (34%; Fig. 4).

Hypothesis 2: non-native species

There were 126 non-native species, comprising 16% of species (106 of 649 total species) in 2018 and 15% (97 of 647 species) in 2021. Predominant non-native species were similar between years. The five most frequent non-native species were the same in 2018 and 2021, except that autumn olive (*Elaeagnus umbellata*) was in the top five in 2018 but seventh in 2021 after being replaced in the top five by bluegrass (*Poa compressa*). The most frequent non-native species were multiflora rose (*Rosa multiflora*; 33% of plots in 2018, 31% in 2021), Amur honeysuckle (*Lonicera maackii*; 26%, 27%), glossy buckthorn (*Frangula alnus*; 26%, 31%), autumn olive (25%, 17%), garlic mustard (*Alliaria petiolata*; 23%, 21%), and bluegrass (17%, 22%). All of these are perennials except for the biennial garlic mustard.

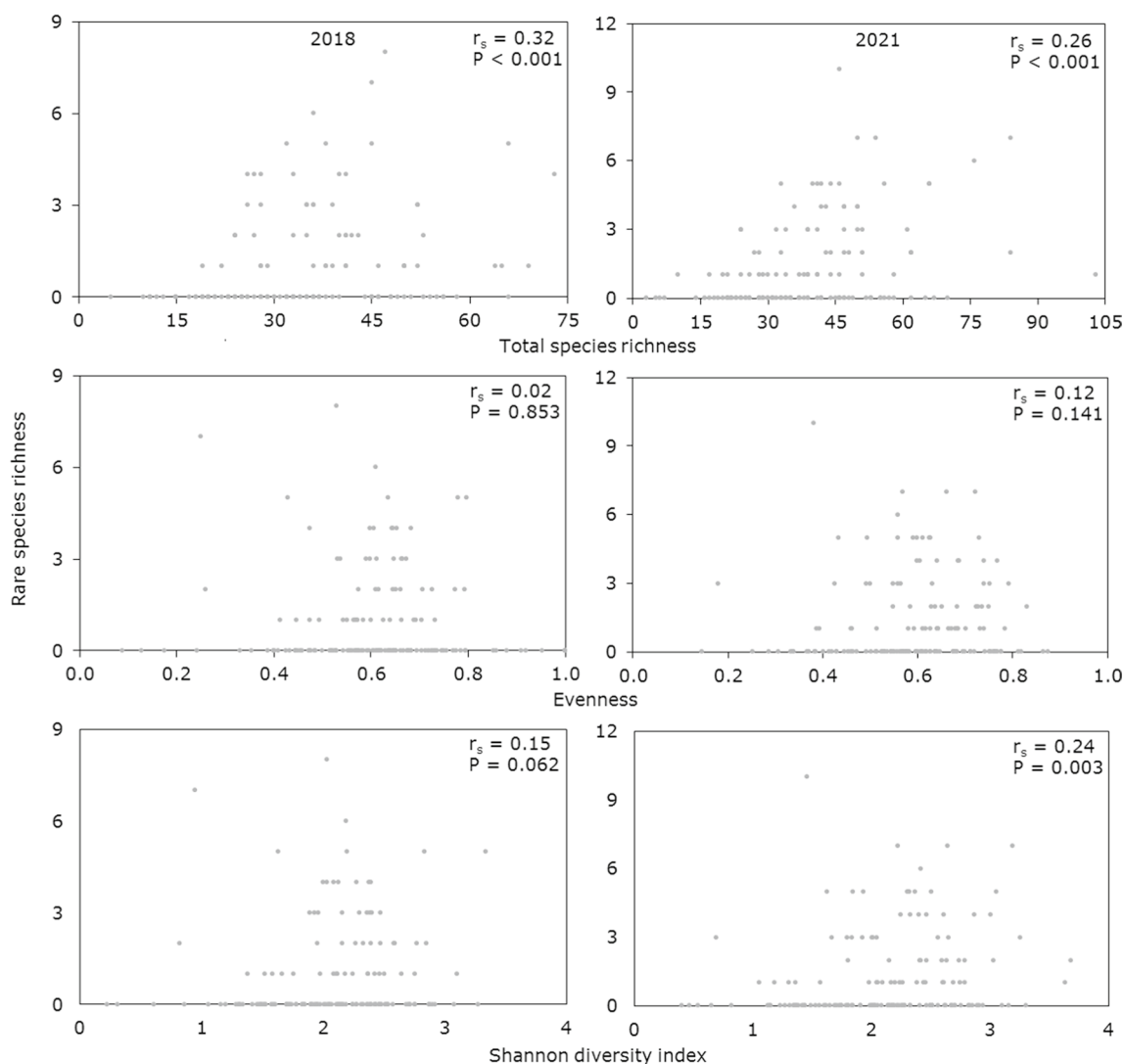


Fig. 3 Scatterplots and Spearman's correlations of plant community diversity measures with the species richness (0.05 ha) of rare plants (Hypothesis 1) in a temperate forest–open habitat landscape in northwestern Ohio, USA

Table 2 Permutational analysis of variance comparing response variables across quartiles of predictor variables for three hypotheses examined in a temperate forest–open habitat landscape in northwestern Ohio, USA

Predictor variables	Response variables	Predictor variable quartile (low–high as 1–4)			
		1	2	3	4
Hypothesis 1		Response variable mean (SEM)			
2018 total species richness	2018 rare species richness	0.2 (0.1) a	0.9 (0.2) b	1.4 (0.3) b	1.2 (0.3) b
2021 total species richness	2021 rare species richness	0.4 (0.1) a	0.6 (0.2) a	1.9 (0.4) b	2.1 (0.4) b
2021 Shannon diversity index	2021 rare species richness	0.7 (0.3) a	1.0 (0.2) ab	1.8 (0.3) b	1.5 (0.4) ab
Hypothesis 2					
2018 native species richness	2018 non-native species richness	3.6 (0.5) a	3.0 (0.4) a	5.0 (0.8) ab	6.5 (0.8) b
2021 native species richness	2021 non-native species richness	3.0 (0.5) a	4.8 (0.6) ab	4.8 (0.6) ab	6.5 (0.7) b
Hypothesis 3					
2018 total species richness	2018:2021 Sørensen similarity	48 (4) ab	59 (3) b	51 (3) ab	44 (3) a
2018 evenness	2018:2021 Sørensen similarity	56 (4) b	53 (3) b	51 (3) ab	41 (3) a

Response variables that differed across predictor variable quartiles at $P < 0.05$ are included in the table

Species richness is per 0.05 ha. Means within a row without shared letters differ at $P < 0.05$. Pseudo- F -statistics and P values for all response variables, including those not differing significantly, are in Online Resource 2

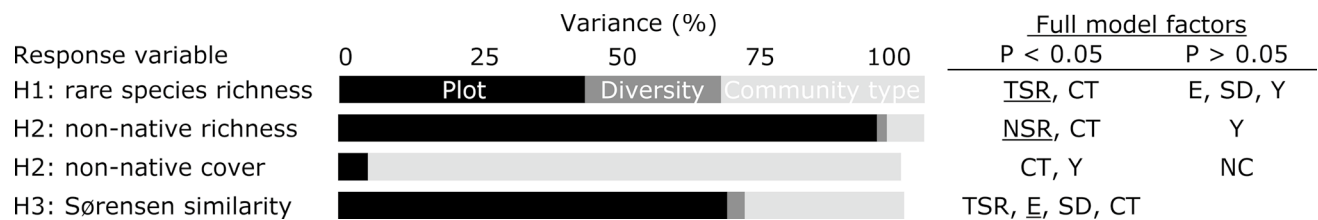


Fig. 4 Partitioning variance in plant community response variables attributable to predictor variables for three hypotheses (H1–3) in a temperate forest–open habitat landscape in northwestern Ohio, USA. Variance components include plot ($n = 151$) as a random variable, a quantitative community diversity measure, and community type (seven community types) and year (2018, 2021) as categorical variables. The diversity measure included as the final variance component

for a response variable is the underlined variable in the full model factors. Abbreviations of factors listed in full models: *CT* community type, *E* evenness, *NC* native cover, *NSR* native species richness, *SD* Shannon diversity index, *TSR* total species richness, and *Y* year. If variance attributable to predictor variables does not total 100%, the remaining variance is residual variance. F -statistics and P values for full models are in Online Resource 3

Non-native species richness was weakly but significantly positively correlated with native species richness in both years (Fig. 5). Non-native cover, however, was not correlated with native cover. Mean non-native species richness was significantly higher in only the highest quartile of native species richness in PERMANOVA (Table 2). Non-native cover did not differ significantly across any quartile of native cover. Variance partitioning for non-native richness indicated that the random variable plot accounted for the most variability (91%), with small portions accounted for by native species richness (1%) and community type (8%; Fig. 4). In contrast, community type accounted for most (91%) of the variability in non-native cover.

Hypothesis 3: community compositional stability

Stability of 2018:2021 species composition ranged widely among plots, from 0% Sørensen similarity indicating complete

species turnover, to 94% similarity indicating nearly complete stability. About half of plots (52%) exhibited $\geq 50\%$ 2018:2021 compositional stability.

Stability was not significantly correlated with 2018 species richness and was weakly negatively correlated with 2018 community evenness and diversity (Fig. 6). The least compositionally stable communities were concentrated in the upper quartile of species richness and evenness based on PERMANOVA (Table 2). Plot as a random variable accounted for the largest portion (66%) of variance in 2018:2021 similarity (Fig. 4). Remaining variance was attributable to community evenness (2%), community type (29%), and residual (3%).

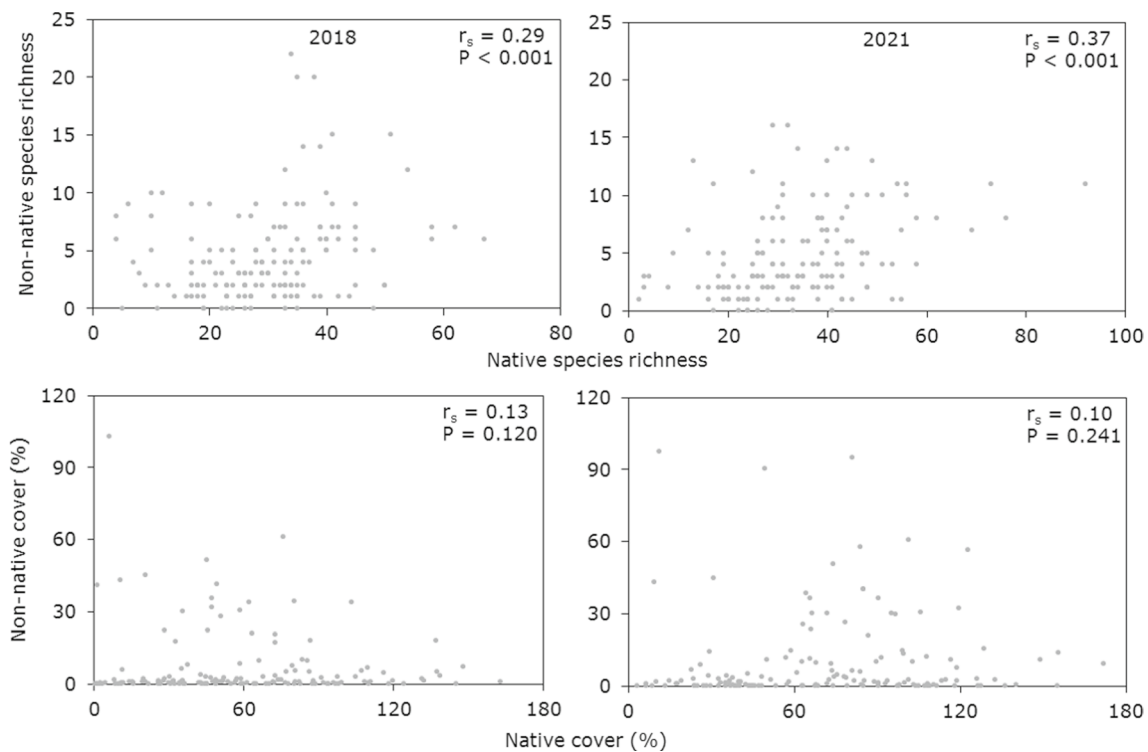


Fig. 5 Scatterplots and Spearman's correlations of native and non-native species relationships (Hypothesis 2) in a temperate forest–open habitat landscape in northwestern Ohio, USA. Species richness is per 0.05-ha plot

Discussion

Hypothesis 1: community diversity–rare species relationships

In general, the least diverse plots contained few rare species, while plots with intermediate and upper quartiles of total species richness and diversity contained the most rare species. A potential mechanism whereby distributions of rare and common species could be related is by responding similarly to habitat conditions (Lennon et al., 2011). In our study, high total and rare species richness usually coincided in open habitats containing few or no trees. With the exception of one oak woodland plot, 19 of the top 20 plots with the most rare species (3–10 species/0.05 ha) either year were in open communities (oak savannas, prairies/meadows, and more open, managed conifer plantations), compared with the more densely treed oak woodlands, oak forests, and forested wetlands usually containing few rare species. The open or partly shaded habitats (in the cases of oak savannas and managed conifer plantations) may be most conducive for the most species by being relatively free of deep shade as an ecological filter by trees to optimize species coexistence, as Leach and Givnish (1999) hypothesized for oak savannas.

Not all open habitats concurrently supported high total and rare species richness, however. The main open habitats

that did not contain many rare species included shoreline marshes (around Lake Erie) and meadows. The species-poor (12–20 total species/0.05 ha in 2018 and 3–28 species/0.05 ha in 2021) shoreline marshes were frequently disturbed through re-occurring flooding and contained much open water. Our finding of low species richness is consistent with experimental results in Lake Erie marshes where plant colonization was limited by both deep and fluctuating water and by shallow water with high turbidity from dynamic sediments (Barry et al., 2004). In meadows, our plots had either low total species richness or highly variable richness between years potentially associated with degree of woody plant encroachment or aggressive herbaceous plants such as *Solidago* spp. (Siefert, 2012). Since meadows plots had near or over 100% plant cover, it is possible competitive exclusion in part depressed species richness, perhaps coupled with surrounding forests serving as barriers to dispersal of light-demanding species (Sperry et al., 2019).

Plots with relatively high total species richness but few rare species primarily occurred in treed ecosystems (oak forests, forested wetlands, and unmanaged conifer plantations). This could relate to the fact that most of the state-listed rare plants in our study region are open habitat specialists because of the general uniqueness of open habitat compared with forests in the state and the disproportionate losses of open habitat (Schetter & Root, 2011). Many of the habitat

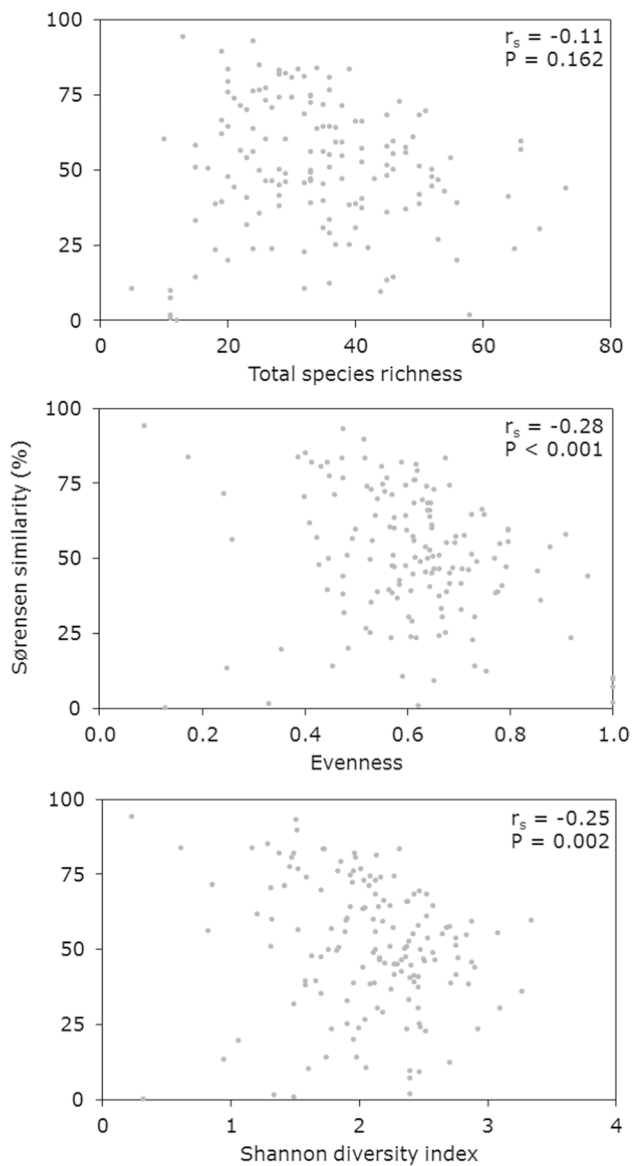


Fig. 6 Scatterplots and Spearman's correlations of 2018 community diversity measures with community compositional stability expressed as 2018:2021 Sørensen similarity (Hypothesis 3) in a temperate forest–open habitat landscape in northwestern Ohio, USA. Species richness is per 0.05-ha plot

losses stem from urban–suburban and agricultural development and lack of frequent fires that historically maintained open savanna–prairie habitats in the Oak Openings portion of the study area (Schetter et al., 2013).

Hypothesis 2: native and non-native species relationships

We found weak support for the idea that hotspots of native and non-native species richness coincide on the landscape, as the correlations between native and non-native species

richness were significant but weak ($r_s \leq 0.37$). While strong general patterns in native and non-native distributional relationships were not evident, context-dependent patterns appeared at the extremes or within community types. In comparing the Spearman correlation and PERMANOVA results dividing native species richness into quartiles, a pattern emerged whereby plots with many native species did not necessarily contain the most non-native species, but instead had the fewest instances where non-natives were absent or sparse. In fact, plots with the maximum numbers of non-native species we recorded were concentrated in mid-levels of native richness of approximately 30–50 species/0.05 ha. Hotspots of native species in our study were characterized more by a consistent presence of non-native species rather than by maximum numbers of non-native species. There also was a pattern in upper levels of non-native species richness, where 100% (2018) and 95% (2021) of the most heavily invaded plots (≥ 10 non-native species/0.05 ha) were in open habitats or conifer plantations. In 2021, for example, the 22 plots containing ≥ 10 non-native species consisted of half conifer plantations, a third meadows/prairies, and the remainder oak savanna or shoreline marsh and only one forested plot (a forested wetland).

Even weaker native and non-native species relationships for cover compared with for species richness are consistent with a prior study we conducted in a semi-arid, forested-meadow landscape in western North America (Abella et al., 2012). It is possible that competitive interactions between native and non-native species, potentially contingent on identity of dominant species (Avolio et al., 2019), are more important for relationships for cover than for species richness, weakening any native and non-native cover correspondence. High cover of either a native or non-native species or group of species could limit cover of the other group, especially if the high cover is supplied by highly competitive species. For example, the non-native glossy buckthorn, a tall shrub known to be a strong competitor with native species (Kalkman et al., 2019), often comprised much of the cover in forested wetland plots that had low native cover in our present study. Likewise, the competitive, native perennial forb wrinkleleaf goldenrod (*Solidago rugosa*), which in open habitats can form dense stands difficult to invade (Abrahamson & Gadgil, 1973), supplied much of the cover on some of our prairie/meadow plots containing low non-native cover. If instead much of a plot's cover is supplied by dominant but less competitive species, or by a collection of species with moderate or low competitive abilities, then plots spanning a range of plant covers may exhibit little relationship between native and non-native cover as native or non-native species could be more interchangeable in their competitive abilities. The potentially fluctuating importance of competitive interactions, contingent on whether species identities matter, could limit any type of consistent relationship between

native and non-native cover across the landscape. For species richness, in contrast, the relative strength of competitive interactions could be less important, such as when even small patches of habitat free from a dominant competitor could enable establishment or persistence of less competitive species (Palmer & Maurer, 1997). This would promote species coexistence and positive relationships between native and non-native species richness. Regardless of the mechanisms, the lack of a pattern between native and non-native plant cover suggests that native cover cannot be used to reliably predict non-native cover across the landscape.

Hypothesis 3: diversity-stability relationships

There could be several reasons why the most diverse sites were not the most compositionally stable. Many correlational studies and experiments reporting positive relationships between diversity and stability focused on stability of ecosystem functions such as productivity (Ives & Carpenter, 2007; Xu et al., 2021). Although some studies found positive relationships between diversity and species compositional stability (e.g., MacDonald et al., 2015; Yang et al., 2012), many found that diversity is unrelated or negatively related to compositional stability, similar to our results (e.g., Bruelheide & Luginbühl, 2009; Foster et al., 2002; Sankaran & McNaughton, 1999; Sasaki & Lauenroth, 2011; Wang et al., 2010). Although species can differ in contributions to ecosystem productivity, species can theoretically be interchangeable for productivity. Species are not interchangeable for stability of species composition, which could render compositional stability less sensitive to diversity than are functional measures (Abella et al., 2018). If some species are lost, others could compensate by increasing productivity to maintain stability, but for composition, species replacement automatically fosters instability.

Another factor that could affect compositional stability is longevity of a community's species or dynamics of dominant species (Valencia et al., 2020). Communities with abundant short-lived plants, which could have high temporal turnover, could be hypothesized to be least compositionally stable (Snell Taylor et al., 2018). In our dataset, cover of annual–biennial plants was weakly negatively correlated with community compositional stability ($r_s = -0.31$, $P < 0.001$). Communities with major dominant species could be anticipated to be stable or unstable, contingent on the degree of stability of the dominant disproportionately influencing community compositional stability (Valencia et al., 2020). The cover of a plot's dominant species (i.e., the species with the greatest cover) was uncorrelated with community compositional stability in our study ($r_s = 0.07$, $P = 0.376$).

Another reason for the lack of positive association between diversity and compositional stability in our study

could be that the most diverse sites were inherently unstable because of natural disturbances or other factors. Diverse oak savannas could be an example of a community with naturally temporally unstable species composition. Oak savannas in Midwestern North America, such as those in our study area, depend on re-occurring fires or other disturbances to limit development of dense sapling layers of tree species (Taft, 2020). Savanna species richness temporarily increases after disturbance arrests sapling encroachment, then declines as time since fire increases (Abella et al., 2020). High community diversity has minimal effect on sapling encroachment because much of the savanna plant diversity is in the groundlayer, dominated by forbs, graminoids, and small shrubs, often quickly overtopped within four years by tree species resprouting from root systems after fire-induced top killing (Taft, 2020). These observations suggest that at peak diversity after fire, savanna sites would subsequently be compositionally unstable as attrition of groundlayer species commences with resumption of sapling encroachment, limiting positive relationships between diversity and compositional stability.

Variance partitioning

The variance partitioning results offered insight into why correlations were generally weak between community diversity measures and rare species occurrence, non-native plant distributions, and community compositional stability. Much variance in these community features was attributable to either plot as a random variable, community type, or both, with comparatively low variance attributable to the community diversity measures. Plot as a random variable in our repeated-measures analysis reflects variability in temporal change among plots and spatial location effects within the landscape (sensu Urban et al., 2002). Location effects could result from many factors, including on-site edaphic conditions, disturbance history, and influences of the surrounding landscape, such as seed dispersal and inputs (Holmes & Matlack, 2019; Sperry et al., 2019). While identifying the relative importance of these factors was beyond the scope of our study, our results suggest that these types of factors could be more closely associated with spatial distributions of rare and non-native species and community compositional stability than is community diversity. Although with more limited sampling than the present study, two prior studies in our study region support this view. At 39 sites in the Oak Openings region, Schetter et al. (2013) found minimal relationship between native and non-native plant species richness, which typically instead each varied independently with landscape factors such as distance to roads and proximity to anthropogenic disturbances. In a study of land-use legacy effects at 22 oak forest sites, only sites that had been cleared for cultivation 80+ years earlier contemporarily

contained state-listed rare plant species (Abella & Schetter, 2021). As average plant species richness was identical (34 species/0.05 ha) between previously cleared and uncleared sites, rare species occurrence was more associated with environmental differences than with community richness. A major environmental difference was that cleared sites still remained more open (compared with uncleared sites with greater tree canopy cover) 80 years after clearing, enabling persistence of the light-demanding rare species otherwise absent from oak forests developing closed canopies when free from disturbances (Abella & Schetter, 2021). Further research that more fully partitions the location effect into its components (e.g., soil properties, disturbance history, and landscape variables such as human population density) incorporates variability within and among community types, or that experimentally manipulates community diversity across landscape and community type gradients could offer additional insight into spatial and temporal patterns of rare and non-native plant abundance and community stability which were generally only weakly explained by community diversity in our study.

Applications for conserving ecological communities

In returning to the idea of context dependency and degree of generality in ecological concepts and hypotheses (Beck, 1997; Catford et al., 2022; Eviner & Hawkes, 2008), our results of lack of generally strong relationships between community diversity and rare species, non-native species, and compositional stability raise a question as to in what circumstances community diversity measures could contribute to predicting these community properties across the landscape. Our results suggest that diversity measures had the most potential for predicting the other community properties at the lower or upper extremes of community diversity measures. Rare species were least likely to occur in the least diverse sites, suggesting that these habitats should not be prioritized for rare species surveys when inventory resources are limited for maximizing detection of rare species. This conclusion differs from landscapes where low-diversity sites support many rare species, often in unique edaphic conditions (Tetetla-Rangel et al., 2017). Sites at the upper extreme of native species richness also contained the most non-native species in our study, suggesting that detecting non-native invaders is likely to be maximized on such sites within the landscape. Diversity did not beget species compositional stability, as the most diverse sites had similar or lower compositional stability compared with lower-diversity sites. Illustrative of this, diverse oak savannas had low compositional stability, as fewer than four years without fires or other disturbances to arrest tree encroachment can trigger major species compositional change via replacement of herbaceous with taller woody species (Taft, 2020).

Diversity thus appears to offer minimal barrier to compositional change induced by a process such as woody plant encroachment. If disturbances (such as prescribed fires) are frequent, however, the combination of high species diversity and high turnover in temporal species compositional change through repeated fluctuations could be viewed as a positive when a conservation goal includes maximizing diversity in its multiple forms including community turnover through time. Although diversity correlating positively with stability is typically viewed favorably for conserving ecosystem functions such as productivity, negative relationships between diversity and stability of species composition could be favorable for other applications in conserving ecological communities.

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Author contributions All authors contributed to the study conception and design; KSM, TLW, and SRA collected the data; SRA analyzed the data and wrote the manuscript; all authors edited and approved the manuscript drafts.

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Data availability The plant community dataset analyzed in the paper is available in Online Resource 1, which includes a listing of species recorded on plots during the study.

Declarations

Conflict of interest The authors declare no known conflicts of interest.

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ONLINE RESOURCE 2 Statistics for permutational analysis of variance comparing response variables across quartiles of explanatory variables for three hypotheses (H1-3) examined in a temperate forest-open habitat landscape in northwestern Ohio, USA. Statistics correspond with Table 2 of the paper

Explanatory variables	Response variables	Pseudo- $F_{3,147}$	P
H1: Rare species			
2018 total species richness	2018 rare species richness	5.0	0.003
2018 evenness	2018 rare species richness	2.0	0.122
2018 Shannon diversity index	2018 rare species richness	2.0	0.116
2021 total species richness	2021 rare species richness	8.9	<0.001
2021 evenness	2021 rare species richness	0.3	0.803
2021 Shannon diversity index	2021 rare species richness	3.0	0.033
H2: Non-native species			
2018 native species richness	2018 non-native species richness	6.3	<0.001
2021 native species richness	2021 non-native species richness	5.9	<0.001
2018 native species cover	2018 non-native species cover	0.6	0.649
2021 native species cover	2021 non-native species cover	1.2	0.313
H3: Stability			
2018 total species richness	2018:2021 Sørensen similarity	3.2	0.024
2018 evenness	2018:2021 Sørensen similarity	3.4	0.019
2018 Shannon diversity index	2018:2021 Sørensen similarity	2.1	0.101

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ONLINE RESOURCE 3 Statistics for generalized linear mixed models for three hypotheses (H1-3) examined in a temperate forest-open habitat landscape in northwestern Ohio, USA. Statistics correspond with Fig. 4 of the paper

Response variables	Predictor variables		
	Community type	Year	Continuous variables
	<i>F</i> -statistic (P value)		
H1: Rare species richness	15.0 (<0.001)	2.8 (0.010)	E, 1.3 (0.249); SD, 1.0 (0.316); TSR, 4.9 (0.029)
H2: Non-native species richness	7.0 (<0.001)	1.7 (0.193)	NSR, 85.5 (<0.001)
H2: Non-native species cover	9.0 (<0.001)	6.4 (0.013)	NC, 0.3 (0.574)
H3: Sørensen similarity	9.8 (<0.001)	—	E, 25.4 (<0.001); SD, 17.2 (<0.001); TSR, 16.0 (<0.001)

Abbreviations for continuous variables: E, evenness; NC, native cover; NSR, native species richness; SD, Shannon diversity index; and TSR, total species richness. Degrees of freedom were as follows: H1: 1, 147 for all variables except for 6, 147 for community type; H2: 1, 149 for all variables except for 6, 149 for community type; and H3: 1, 141 for all variables except for 6, 141 for community type. Year is not a predictor variable for H3 because the Sørensen similarity index already incorporates the 2018 to 2021 comparison