Received: 5 December 2021 | Revised: 28 June 2022 | Accepted: 26 October 2022

DOI: 10.1111/jvs.13167

Journal of Vegetation Science
IAVS

RESEARCH ARTICLE

Are metapopulation species drivers of metacommunity structure in sandstone outcrop communities?

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Funding information
David Francis Barfknecht was supported by a Doctoral Fellowship from Southern Illinois University Carbondale, and David John Gibson by NSF DUE 1758497 and DUE 1941969.

Co-ordinating Editor: Hans Henrik Bruun

Abstract

Questions: The extent to which metacommunities contain species exhibiting metapopulation dynamics is poorly understood. We investigate this issue within sandstone outcrop plant communities scattered across an upland hardwood forest. We investigate the life forms of metapopulation species and relationships between taxonomic, phylogenetic, and functional diversity, composition, and environmental factors.

Location: Twenty-three sandstone outcrop communities in southern Illinois, USA.

Methods: Following vegetation surveys, species exhibiting metapopulation dynamics were identified and compared to all species based on origin, growth form, and lifecycle. Cohesion, turnover, and boundary clumping were utilized to determine metacommunity structure. Correlations evaluated associations between site-based variables, and regressions evaluated associations between diversity indices. Multivariate analyses compared sites to determine which variables contributed to compositional differences.

Results: Twenty of 130 species exhibited metapopulation dynamics and were usually annual or biennial exotics. Metacommunity elements indicated a metacommunity structure where groups of species tended to replace one another across sites, in which species exhibiting metapopulation dynamics were subordinate as opposed to dominant or transient. The largest sites were the most regularly shaped, but not the most diverse. Species richness and species exhibiting metapopulation dynamics determined phylogenetic and functional diversity, but largely non-standardized measures of diversity, indicating independence between types of diversity. Multivariate analyses showed that diversity metrics explained community composition differences, where more species-rich sites with more metapopulation species were also more phylogenetically and functionally diverse.

Conclusions: Sandstone outcrop communities exhibited diverse plant communities, where phylogenetic and functional diversity were driven by both the number of all species and the subset of metapopulation species independently. SM dynamics were usually short-lived and exotic species with their low number likely constrained via dispersal limitations. The communities exhibited a metacommunity structure indicating predictable community assemblages which tend to be replaced with others as opposed to just individual species being replaced individually, consistent with the concept of an integrated community. Functional traits indicated that these communities include species adapted to xeric, substrate-poor conditions.

KEYWORDS
correlation, functional, metacommunities, metapopulations, ordination, patch dynamics, phylogenetic, sandstone outcrops, species richness, vector analysis

1 | INTRODUCTION

As natural and anthropogenic activities continue to influence populations and communities, it remains crucial to understand the connectivity of fragmented ecosystems. Habitat fragmentation can affect ecosystem-level dynamics of spatially disjunct populations (i.e., metapopulations) and alter how spatially disjunct communities within an inhospitable matrix (i.e., metacommunities) are structured (Hanski, 1991, Hanski et al., 1996a; Hanski, 1997; Leibold et al., 2004). Regardless of whether patches are naturally or artificially created, metapopulation and metacommunity patterns arise, and can be observed in several taxonomically defined communities including plants (Alexander et al., 2012), insects (Datry et al., 2017), amphibians (Brodman, 2009), reptiles (Altermatt, 2013), fish (Falke & Fausch, 2010; Erős et al., 2017), birds (Morera Pujol, 2020), and mammals (Brown, 2018).

Plant metapopulation persistence in patchy landscapes is largely determined via efficiency of dispersal vectors of pollen, seeds, and clonal fragments, and these factors are particularly important for facultative and obligately outcrossing species (Stewart-Cox et al., 2005; Frankel & Galun, 2012; Baguette et al., 2013). However, persistence depends on suitable and distinct patches, facilitated by high diversity and connectance (Gravel et al., 2011). In addition, patch heterogeneity (i.e., the availability of several microhabitats which may be crucial for the colonization of certain species) can promote metapopulation and metacommunity persistence, where the largest patches are able to exhibit higher habitat heterogeneity and provide a greater diversity of potential niches for species to establish (Burnett et al., 1998).

Scaling upward from metapopulations to metacommunities, the interconnectivity of species assemblages can help ecologists and land managers understand the diversity driven by spatial scales (Holyoak et al., 2005). What distinguishes metacommunities from metapopulations is the ability to assess community structure via multispecies distributions, and these patterns scale from local ecosystems to biogeographical realms. Metacommunity patterns can be categorized as checkerboard, nested, Clementsian, Gleasonian, evenly spaced, and even random distributions (Leibold & Mikkelson, 2002). These patterns are based on three elements of metacommunity structure: coherence, species turnover, and boundary clumping, reflecting the extent to which species distributions, sites and community-level interactions occur. Metacommunities exhibiting significant structure, as opposed to random distributions based on random colonization, contain individual metapopulation species. Linking metapopulation and metacommunity concepts remains central in ecological research (Economo, 2011).

Furthermore, incorporating evolutionary and functional relationships between species in patchy landscapes may determine how communities are important for regional-to-local environmental filtering (Cavender-Bares et al., 2009). High phylogenetic or functional diversity compared to taxonomic diversity indicates overdispersion, indicating potential competition between separate clades, niche partitioning, limiting similarity between taxa, and character displacement, where phylogenetically and functionally diverse communities may limit closely related species' coexistence in abiotically suitable patches (Mayfield & Levine, 2010; Presley et al., 2010; Kluge & Kessler, 2011). Phylogenetically poor communities have been documented to experience invasion by species distantly related to existing natives, reflecting mechanisms related to trait assembly in communities (Gerhold et al., 2011). Phylogenetic relationships in rock outcrop communities have been shown to be determined by patch area, where phylogenetic diversity and turnover was positively correlated with patch size (Villa et al., 2018). Furthermore, taxa with certain survivorship and dispersal-related traits have higher local frequency than predicted based on regional frequency (Udd et al., 2015).

Patch characteristics (i.e., area, perimeter, area-to-perimeter ratio) exhibit different relationships with diversity. Species–area relationships predict large patches (often with greater perimeters) support more species than smaller patches (Arrhenius, 1921; Gleason, 1922; Adler et al., 2005). However, evolutionary relationships show variable responses. Patch area has been observed to show infrequent, weak effects on phylogenetic diversity and community structure (Arroyo-Rodríguez et al., 2012). While phylogenetic diversity and taxonomic diversity are usually correlated, patch size and phylogenetic diversity can have a varying association depending on environmental heterogeneity and niche availability (Arellano-Rivas et al., 2017; Matos et al., 2017). Functional diversity also has varying associations with patch characteristics. Forsyth and Gilbert (2021) observed parallel positive responses between taxonomic and functional diversity with patch area, whereas Arellano-Rivas et al. (2018) observed negative associations between functional diversity and patch shape irregularity. Understanding how different types of diversity relate to patch characteristics remains of importance for understanding metacommunity assembly.

Incorporating metapopulation, metacommunity, community composition, diversity, and patch-characteristic concepts may foster understanding underlying ecological processes driving community assembly. In addition, inferring process from diversity patterns observed in artificial or theoretical inferences can be difficult to apply to natural ecosystems, and therefore studying these relationships directly in natural ecosystems remains crucial despite rapid innovations in theoretical work (Hooper et al., 2005; Fahrig, 2019). For example, positive increases in taxonomic, phylogenetic, and functional diversity may indicate communities are unsaturated and the a priori assumption of phylogenetic inertia is maintained (more closely related species are more functionally similar; Safi et al., 2011). However, other independent and non-correlated responses may reflect patterns involving phylogenetic and functional clustering and overdispersion (Cavender-Bares et al., 2009). Metacommunities exhibiting non-random structure with shared species promote metapopulation taxa, often rapidly dispersing exotics, presuming local communities are not saturated (Marvier et al., 2004; Case, 1991).

Sandstone outcrops provide an ideal study system to investigate metapopulation and metacommunity relationships, representing discrete patches occurring within a (supposedly) inhospitable forest matrix. Since European colonization and expansion in the Midwestern United States, farming and fire suppression have facilitated degradation, fragmentation, and woody encroachment in many forest openings (Nuzzo, 1986). These naturally occurring openings surrounded by forest in southern Illinois form the basis for this study. A subset of these openings are sandstone outcrop communities, lacking closed tree canopies while dominated or characterized by species including *Schizachyrium scoparium* (Michx.) Nash., *Juniperus virginiana* L., *Quercus marilandica* Münch., *Quercus stellata* Wangenh., *Cheilanthes lanosa* (Michx.) D.C.Eaton, *Croton monanthogynus* Michx., and *Danthonia spicata* (L.) Roem & Schult. These sandstone outcrops remain distinct from the adjacent upland hardwood forest matrix, based on abiotic extremes and existing biotic communities (Heikens & Robertson, 1995).

The focus of this research was to investigate metapopulation and metacommunity structure of these sandstone outcrops in southern Illinois, incorporating relationships between taxonomic, phylogenetic, and functional diversity. We proposed that sandstone outcrop communities are characterized by phylogenetically and functionally related metapopulation species characterizing an empirical metacommunity system. We hypothesized (1) a subset of species within sandstone outcrops exhibit metapopulation dynamics, with more exotic species than expected by chance, (2) that these outcrop communities will exhibit a non-random metacommunity structure, where (3) significant correlations and regressions exist between total species richness, species exhibiting metapopulation dynamics, phylogenetic diversity, functional diversity, individual functional traits, and patch characteristics reflecting a lack of community saturation, and (4) that metapopulation species presence will explain correlations in taxonomic, phylogenetic and functional composition in this structured metacommunity.

2 | METHODS

2.1 | Study site

Sites (i.e., patches) included 23 distinct sandstone outcrops (Figure 1) in the northeastern extent of Jackson Hollow Ecological Area in Pope County, IL, varying in size and shape (Table 1). For all patches, drone imagery was used for mapping, and polygons were traced around patches to determine both area and perimeter using ArcGIS software (Version 10.6; ESRI, 2011). These sandstone outcrops lack a canopy from tall woody vegetation, unlike the adjacent hardwood forest matrix. Each opening was surveyed during June, July, August, and September 2020 to record the occurrence of non-vascular (specifically mosses) and vascular plant taxa. Nomenclature followed the United States PLANTS Database (USDA-NRCS, 2012) for non-vascular taxa and Mohlenbrock (2014) for vascular taxa. All species were included in metacommunity and multivariate analyses using occurrence data. Ubiquitous and singleton species were omitted from metapopulation analyses considering statistical significance, but included in interaction matrixes and further analyses.

2.2 | Metapopulation analyses

Using occurrence data, an Incidence Function Model (Hanski et al., 1996b) was employed for each non-excluded species. This model is based on a first-order linear Markov chain and calculates the probability of patch occurrence (incidence J_i), dependent on colonization (C_i) and extinction (E_i):

$$J_i = \frac{C_i}{C_i + E_i - C_i E_i} = \frac{1}{1 + \left(\frac{e'}{S_i^2 A_i^x}\right)}$$

where e' represents the extinction probability of a patch with unitary size, S is derived from patch isolation, A relates to patch area, and x is the decline in probability of extinction with patch size. High values of x indicate rapid decreases in extinction probability with increasing patch size (A). Hanski's Incidence Function Model is a widely used metapopulation model incorporated in empirical ecology. This function models whether species occurrence within spatially distinct habitat patches functions as a discrete-time Markov chain, where transition probabilities are dependent on patch characteristics (Hanski et al., 1996b). The model can be parameterized with single-season occurrence data from a defined patch network. The Incidence Function Models were conducted in the *vegan* package in R Software (Oksanen, 2004; Oksanen et al., 2017; Ver. 4.1.1., R Core Team, 2017). A chi-squared test of independence was employed to determine if exotic species (compared to native species), species with different growth forms (ferns, graminoids, forbs, vines, shrubs, and woody species), and species with different lifecycle durations (annual, biennial, and perennial) were more likely to exhibit metapopulations dynamics than expected by chance.

FIGURE 1 Twenty-three sandstone outcrop patches surveyed in Jackson Hollow Ecological Area in southern Illinois.

2.3 | Metacommunity analyses

To assess metacommunity structure, three values were calculated based on survey data: coherence, turnover, and boundary clumping. These three values represent elements of metacommunity structure (EMS) (Leibold & Mikkelson, 2002; Dallas, 2014). Coherence quantifies the degree to which species patterns are reducible to a single dimension, and corresponds to the negative (checkerboard patterned), insignificant (random occurrences), or positive (with some form of gradient in species occurrences across sites) association between other species (Leibold & Mikkelson, 2002). This value is the total embedded absences in a community matrix and significance is determined by comparing to simulated null matrixes. Turnover quantifies species replacements along within the species–site interaction matrix, and is recognized as a metric of beta diversity. This value is expressed as absolute species turnover, forming a traditional range-based perspective. Negative turnover indicates nested species subsets, insignificant turnover indicates a potential quasi-structure, and positive turnover indicates regular species replacements. Boundary clumping assesses how species boundary edges condense across this single dimension. Boundary clumping is expressed as Morista's Index, a widely used measure of the dispersion (Morista, 1959, 1962). This interaction matrix was generated where both sites and species were placed via reciprocal averaging. These analyses were conducted in the *metacom* (Dallas, 2014) package in R Software using 999 simulations of null models for significance testing.

TABLE 1 Measurements of total species richness (*S*), number of exotic species (ES), number of species present exhibiting metapopulation dynamics (SM), Faith's phylogenetic diversity (PD), distance-based functional diversity (FD), average leaf nitrogen content (%), specific leaf area (g/m^2), and plant height (m; avgLNC, avgSLA, and avgPH, respectively), area, perimeter, area to perimeter ratio (*A*:*P*), distance to road (DR), and mean *x* values for each site (avg*x*) for 23 sandstone outcrop communities.

Site	*S*	ES	SM	PD	FD	avgLNC	avgSLA	avgPH	Area (m^2)	Perimeter (m)	*A*:*P* (m^2:m)	DR (m)	Avg*x*
A	60	8	14	5.69	9.42	20.86	114.76	3.928	271.24	144.26	1.88	146.45	12.01
B	59	8	11	6.12	8.08	19.36	119.33	3.59	466.36	170.13	2.74	115.87	8.15
C	23	3	5	3.55	6.59	26.9	153.2	5.92	82.04	47.29	1.73	117.48	3.27
D	32	3	6	3.91	10.3	23.36	142.98	8.88	8.12	16.34	0.5	177.03	3.41
E	60	6	10	4.99	13.1	20.4	107.88	5.5	595.59	191.06	3.12	146.45	1.32
F	22	3	4	3.4	5.97	27.45	132.22	5.13	82.94	39.89	2.08	265.54	0.51
G	23	1	7	3.37	7.79	23.69	96.22	6.23	44.71	25.76	1.74	263.93	1.03
H	14	2	4	2.48	2.28	21.09	98	5.59	81.69	37.84	2.16	263.93	0.89
I	12	2	2	2.33	2.12	26.01	127	6.96	24.94	18.31	1.36	233.35	2.46
J	28	4	5	3.98	8.4	24.09	117.25	5.7	46.17	30.32	1.52	292.9	0.3
K	32	3	6	4.34	10.6	21.95	108.99	7.32	19.28	19.15	1.01	233.35	1.04
L	34	4	9	4.26	6.26	24.84	151.62	5.21	1236.17	297.3	4.16	526.25	15.84
M	33	4	8	4.23	12.8	23.56	129.11	5.28	532.57	201.16	2.65	936.64	5.46
N	26	2	7	3.78	12	22.9	122.33	5.58	102.99	47.05	2.19	1083.1	2.71
O	22	3	5	3.07	6.91	23.16	103.79	4.17	776.02	151.88	5.11	1112.1	4.18
P	30	4	7	3.59	7.61	27.9	150.54	4.52	178.77	71.86	2.49	1199	3.6
Q	48	4	8	4.81	13.7	21.08	120.61	5.51	114.72	80.91	1.42	1405	2.76
R	20	0	5	2.87	8.13	21.16	96.78	7.12	180.91	69.69	2.6	1638.3	2.67
S	22	2	5	3.43	7.95	22.06	94.95	3.63	1197.76	224.45	5.34	1813.7	4.81
T	45	5	12	5	13.7	21.05	114.67	5.49	1337.24	236.69	5.65	2311	6.06
U	41	4	6	4.69	12.9	23.1	128.25	4.62	58.73	39.26	1.5	2517	3.4
V	45	2	8	4.83	13	21.81	110.64	6.06	138.13	59.77	2.31	2632.9	4.9
W	23	4	5	3.48	7.16	18.76	116.37	4.53	339.17	75.62	4.49	2663.5	4.97

2.4 | Phylogenetic and functional trait analyses

A maximum likelihood phylogeny was constructed for all species across each surveyed sandstone outcrop opening. Both *rbcL* and *matK* nucleotide sequences were downloaded from Genbank for each species (https://www.ncbi.nlm.nih.gov/genbank/; Benson et al., 2012). In addition, the top 25 most frequent species across sites were used to generate an unweighted pair group method with arithmetic mean (UPGMA) dendrogram based on leaf nitrogen content (LNC), vegetative plant height, and specific leaf area (SLA) functional traits averaged from the TRY Database (https://www.try-db.org/TryWeb/Home.php/, Kattge et al., 2020). Each of these functional traits reflects how individual species compete for and acquire resources in their environment, specifically photosynthetically available light to create complex sugars. Taller plants are often better vertical competitors for sunlight compared to shorter plants (Caldwell, 1987) where high SLA values relate to high photosynthetic capacity per unit leaf area in a horizontal plane (Dijkstra & Lambers, 1989). Leaf nitrogen content relates to the relative photosynthetic capacity of leaves, as proteins of the Calvin cycle and thylakoids represent the majority of leaf nitrogen (Evans, 1989). Furthermore, the relative efficiency of plants using different metabolic photosynthetic pathways to create complex sugars is highly dependent on atmospheric composition as well as climatic drivers (Ward et al., 1999; Mayeux et al., 2021). While including only a subset of present taxa only allows for interpretations based on just those specific taxa, other studies have removed non-dominant taxa and often singletons from functional analyses, observing little effect on statistical bias and while retaining the ability to detect differences in functional diversity and composition between individual sites (Swenson et al., 2012; Chun & Lee, 2017; Pairo et al., 2021). The resulting phylogeny and dendrograms were used to calculate Faith's phylogenetic diversity (the phylogenetic diversity of a species set as equal to the sum of all branch lengths in the phylogeny that span the members of the set; PD), and distance-based functional diversity based on Gower's dissimilarity (FD). These analyses were conducted in the *ape* (Paradis & Schliep, 2019), *picante* (Kembel et al., 2010), and *FD* (Laliberté et al., 2014) packages in R.

2.5 | Correlation and regression analyses

Spearman's correlations were used to determine whether diversity, functional traits, and patch variables were correlated. These analyses were conducted using the base functions in R. In addition, non-linear regressions between total species richness (*S*), and species exhibiting metapopulation dynamics (SM) as predictor variables, PD, FD as well as standardized values of phylogenetic and functional mean pairwise and trait distance (MPD and MTD, respectively) as response variables were conducted (similar to Presley et al. 2018) in SigmaPlot (Version 10.0; Systat Software, Inc.Palo Alto, CA, USA).

2.6 | Multivariate analyses

Species occurrence was compiled and the resulting Bray–Curtis dissimilarity matrixes were used for constructing a taxonomic non-metric multidimensional scaling ordination (TNMDS). Vector analyses were employed to investigate community compositional differences based on total species richness per site (*S*), number of exotic species (ES), and SM based on Hanski's Incidence Function Model, PD, FD, averaged values for LNC, specific leaf area, and plant height per site based on the 25 most frequent species across all sites (avgLNC, avgSLA, and avgPH, respectively), patch area, perimeter, area-to-perimeter ratio (*A*:*P*), distance to nearest road (i.e., Trigg Tower Road; DR), and the mean of *x* values of SM taxa for each site (avg*x*). High avg*x* values at a site indicate high extinction probability for species exhibiting metapopulation dynamics as patch area decreases. Vector direction within each ordination denotes the greatest rate of change of the factor across the ordination, while the length of the vector relates to the strength of the relationship.

3 | RESULTS

3.1 | Study sites

Across all 23 sandstone outcrops surveyed, 130 non-vascular and vascular plant species were observed (Appendix S1). The most frequently observed species were *Juniperus virginiana*, *Ulmus rubra* Muhl., and *Thuidium* Bruch & Schimp. sp. (present at 23, 21, and 21 sites, respectively). The most-species-rich sites (A and E) occurred directly next to a road. Averaged trait values among the top 25 most frequent species were 22.89% ± 0.51 LNC, 119.89 mm^2/mg ± 3.67 SLA, and 5.49 m ± 0.26 PH (Appendix S2).

3.2 | Metapopulation analyses

Twenty (15%) of 130 observed species exhibited metapopulation dynamics based on the Incidence Function Model (Table 2). These non-woody species included a fern, five graminoid (one Cyperaceae and four Poaceae species), four composite (Asteraceae), six forb, two vine, and two shrub species. Five exotic species exhibited significant metapopulation dynamics. Exotic species exhibiting metapopulation dynamics occurred more often relative to native species than expected by chance ($x_1^2 = 5.00$; $p = 0.03$), as did annuals and biennials compared with perennial species ($x_2^2 = 7.90$; $p = 0.02$), but not different growth forms ($x_5^2 = 6.45$; $p = 0.26$). Sites with high numbers of SM taxa were often directly east of Trigg Tower Road (i.e., site A; 14 species) and the largest sites based on area (i.e., site T; 12 species). Overall, there were no significant differences in avg*x* values based on growth forms ($F_{4,19} = 0.39$; $p = 0.81$). and between annuals, biennials, and perennials ($F_{2,19} = 1.54$; $p = 0.24$). In addition, values of *x* for SM dynamics (mean avg*x* = 4.16 ± 0.76) did not differ significantly between native and exotic species ($t_{18} = 0.42$; $p = 0.68$), growth form ($F_{2,18} = 0.50$; $p = 0.62$), or between annuals, perennials, and biennials ($F_{2,18} = 1.54$; $p = 0.24$). Most SM were neither ubiquitous nor singletons across all sites (6.95 ± 0.88 sites present out of 23 sites per individual SM taxon). The most frequent SM taxa were *Sedum pulchellum* Michx., *Parthenocissus quinquefolia* (L.) Planch., *Bidens bipinnata* L., and *Ambrosia artemisiifolia* L. (present in 16, 14, 12, and 11 of 23 sites, respectively).

3.3 | Metacommunity analyses

Coherence, species turnover, and boundary clumping all were positive and significant, indicating a non-random metacommunity pattern. Coherence indicated that the metacommunity structure of these sandstone outcrops was neither checkerboard nor random ($z = 1.73$ $p < 0.01$). Turnover, specifically absolute species turnover, further classified the metacommunity structure not consisting of several nested metacommunities ($z = 2.11$; $p = 0.04$). Significantly positive boundary clumping based on Morista's Index ($z = 15.44$; $p < 0.01$), excluded potential even-spaced gradient and Gleasonian structures. The species–site interaction matrix showed that several species were frequent across many sandstone outcrops, and several groups of species co-occurred with regular replacement (Figure 2). These observations reveal a metacommunity pattern where species assemblages tend to be replaced across sites as opposed to individual species simply being individually replaced.

3.4 | Correlation and regression analyses

Area, perimeter, area-to-perimeter ratio (*A*:*P*), distance to nearest road (DR), and avg*x* were all significantly positively correlated (Table 3). However, all of these variables were significantly negatively correlated with average specific leaf area (avgSLA) and plant height (avgPH). Similar to landscape variables, diversity variables excluding ES and FD were significantly positively correlated, while avgLNC was negatively correlated with average leaf nitrogen content (avgLNC). Non-linear regression analyses showed that PD and FD were dependent on total species richness (*S*) and SM (Figure 3). Regarding standardized values, only mean pairwise distances were significantly dependent on *S* (total species richness; MPD: $r^2 = 0.28$, $p = 0.04$; MTD: $r^2 = 0.04$, $p = 0.84$). Neither mean pairwise nor trait differences were significantly dependent on SM (*S*: $r^2 = 0.15$, $p = 0.19$; SM: $r^2 = 0.02$, $p = 0.78$).

TABLE 2 Species with significant metapopulation dynamics based on Hanski's Incidence Function Model.

Species	Code	Family	Growth form	Annual, perennial, or biennial	Primary mode of pollination	Frequency (total sites present)	Intercept *z* score	Intercept *p* value	Log (area) *z* score	Log (area) *p* value	*x* value
Ambrosia artemsiifolia	AMAR	Asteraceae	Forb	Annual	Wind	11	−10.45	<0.01	2.2	0.03	6.22
Bidens bipinnata	BIBI	Asteraceae	Forb	Annual	Bees	12	−9.96	<0.01	2.33	0.02	8.24
Carex glaucodea	CAGL	Cyperaceae	Graminoid	Perennial	Wind	4	−6.53	<0.01	1.93	0.05	9.39
*Cerastium fontanum**	CEFO	Caryophyllaceae	Forb	Perennial	Insect or self	4	−5.98	<0.01	2.02	0.04	17.25
Chasmanthium latifolium	CHLA	Poaceae	Graminoid	Perennial	Wind	9	−10.08	<0.01	2.05	0.05	4.75
Croton monanthogynus	CRMO	Euphorbiaceae	Forb	Annual	Bees or flies	7	−9.73	<0.01	2.43	0.04	3.06
Danthonia spicata	DASP	Poaceae	Graminoid	Perennial	Wind	7	−2.37	0.02	2.32	0.04	0.14
Impatiens capensis	IMCA	Balsaminaceae	Forb	Annual	Bees	2	−3.24	<0.01	2.52	0.03	85.21
Lactuca hirsuta	LAHI	Asteraceae	Forb	Biennial	Bees	7	−4.08	<0.01	2.02	0.04	0.12
*Lespedeza cuneata**	LECU	Fabaceae	Shrub	Perennial	Bees	6	−8.12	<0.01	2.04	0.04	7.58
*Microstegium vimineum**	MIVI	Poaceae	Graminoid	Annual	Wind	9	−10.48	<0.01	2.25	0.03	1.55
Parthenocissus quinquefolia	PAQU	Vitaceae	Vine	Perennial	Bees	14	−10.87	<0.01	1.99	0.04	4.69
Pilea pumila	PIPU	Urticaceae	Forb	Annual	Wind or self	3	−4.7	<0.01	1.98	0.05	30.45
Poa sylvestris	POSY	Poaceae	Graminoid	Perennial	Wind	5	−7.94	<0.01	2.03	0.04	5.54
Polystichum acrostichoides	POAC	Dryopteridaceae	Fern	Perennial	N/A	4	−3.24	<0.01	−1.94	0.05	0.12
*Rosa multiflora**	ROMU	Rosaceae	Shrub	Perennial	Bees	5	−8.1	<0.01	1.93	0.05	4.77
Sedum pulchellum	SEPU	Crassulaceae	Forb	Annual	Bees	16	−9.42	<0.01	2.75	0.04	1.03
Smilax bona-nox	SMBO	Smilacaceae	Vine	Perennial	Flies	9	−5.77	<0.01	−2.82	0.03	0.23
Solidago canadensis	SOCA	Asteraceae	Forb	Perennial	Bees or self	3	−3.27	<0.01	−2.62	0.03	0.13
*Verbascum thapsus**	VETH	Scrophulariaceae	Forb	Biennial	Bees	2	−8.14	<0.01	1.96	0.05	0.62

Note: Species with asterisks (*) are exotic invasive species. Codes are presented in Figure 4.

Abbreviation: N/A, not applicable.

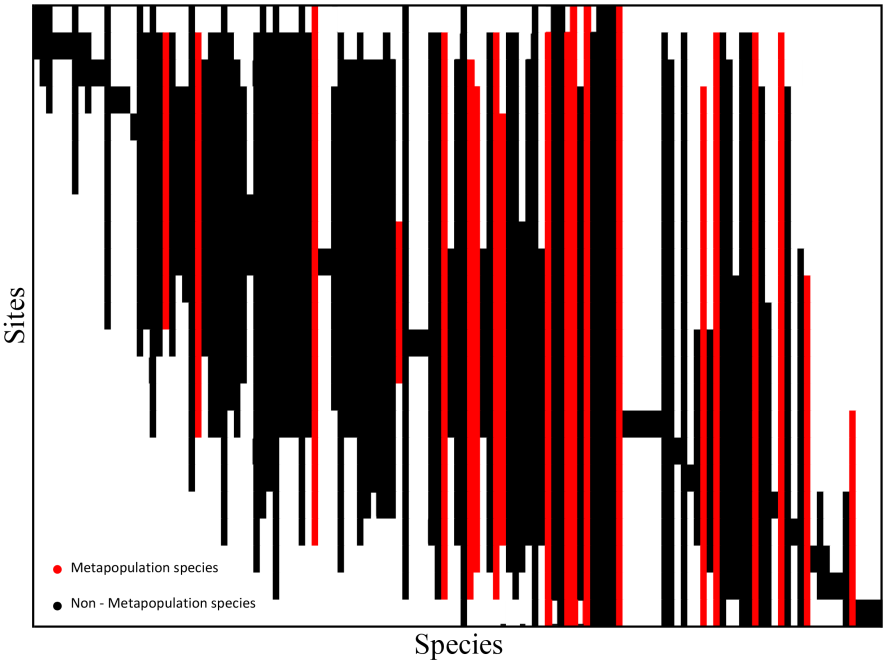

FIGURE 2 Interaction matrix for the species occurring at sandstone outcrop openings surveyed. Black areas indicate where species are present and species are ordered based on the central distribution of each species' occurrence. Sites and species are placed in order based on reciprocal averaging. Red columns correspond to species that exhibit significant metapopulation dynamics (based on Hanski et al., 1996a, 1996b incidence function model; see Table 2).

3.5 | Multivariate analyses

The two-dimensional TNMDS ordination was based upon all observed taxa, but only the SM were displayed graphically along with sites (Figure 4). Many exotic SM taxa occurred along the periphery of the TNMDS ordination, while the native and frequent taxa *Sedum pulchellum* and *Pathenocissus quiquefolia* were centrally located. Geographically closer sites were often closer in the ordination (e.g., sites A and B and sites U, V, and W) indicating compositional similarity, while geographically distant sites (e.g., C and D) were positioned further apart from each other with higher community dissimilarity compared with closer sites. Significant vectors included total species richness (*S*), exotic species richness (ES), SM, PD, FD, avgSLA, and avg*x* (Appendix S3). Vectors PD and *S* explained the greatest proportions of variance within the ordination. Metapopulation species *Impatiens capensis* Meerb., *Pilea pumila* (L.) Gray, and *Microstegium vimineum* (Trin.) A.Camus were associated with high levels of diversity, and sites with *Chasmanthium latifolium* (Michx.) H.O.Yates, *Danthonia spicata, and Smilax bona-nox* L. were associated with low levels of diversity. Vector avg*x* had a slightly differing trajectory compared to other significant vectors, with sites D and L and *Impatiens capensis* and *Pilea pumila* associated with high values and sites G, I, and R as well as *Chasmanthium latifolium* associated with low values.

4 | DISCUSSION

4.1 | Surveys and outcrop characteristics

Despite harsh conditions such as low moisture and shallow soil with exposed substrate, these sandstone outcrops support a diverse array of plant taxa, supporting a broad assemblage of plants in a phylogenetic (non-vascular, monocotyledon, and eudicotyledon representatives) and functional group context (moss, fern, graminoid, ford, vine, shrub, and woody species). The largest outcrops did not necessarily exhibit the highest levels of diversity, reflecting the opportunity for colonization from the regional species pool. However, diversity variables were all positively associated, indicating a high conservation value of these sandstone outcrops, but the value of individual species was largely dependent upon their naturalistic or otherwise intrinsic value to ecologists, land managers, and others who visit these outcrops (Lean & Maclaurin, 2016). Furthermore, PD and FD of these communities were largely driven by the total number of species present as well as the number of SM dynamics, and these variables were all positively related. These relationships between species richness and MPD and MNTD indicate that neither phylogenetic or functional clustering nor overdispersion occurs across this network of communities (Kluge & Kessler, 2011). In addition, a positive relationship between phylogenetic and functional diversity indicates phylogenetic inertia and conservatism, and as expected, that closely related species were also often more functionally similar compared to distantly related species (Tilman et al., 1997; Lawton et al., 1998). The relationships between SM dynamics and PD and FD indexes identify the number of these species as drivers of both phylogenetic and functional metacommunity structure.

Concerning leaf functional traits, several correlations illuminate complex interactions between diversity and patch characteristics. Negative LNC and diversity relationships may indicate that the most diverse communities select for species, including metapopulation species, which can tolerate nutrient-poor environments (Yulin et al., 2005). This selection may result from lack of available substrate (i.e., extensive areas of shallow to no soil), leading to increased competition for both space and nutrients.

TABLE 3 Measurements of Spearman's rank correlation matrix ($df = 22$) for total species richness (S), number of exotic species (ES), number of species present exhibiting metapopulation dynamics (SM), Faith's phylogenetic diversity (PD), distance-based functional diversity (FD), average leaf nitrogen content (%), specific leaf area (g/m^2), and plant height (m; avgLNC, avgSLA, and avgPH, respectively), patch area, perimeter, area to perimeter ratio ($A{:}P$), distance to road (m; DR), and average x values per site (avgx) for 23 sandstone outcrops.

	S	ES	SM	PD	FD	avgLNC	avgSLA	avgPH	Area	Perimeter	A:P	DR
S												
ES	0.69*											
SM	0.97*	0.65*										
PD	0.99*	0.64*	0.97*									
FD	0.83*	0.25	0.85*	0.83*								
avgLNC	−0.88*	−0.20	−0.91*	−0.89*	−0.93*							
avgSLA	−0.06	0.40	−0.16	−0.07	−0.3	0.29						
avgPH	−0.26	−0.53*	−0.32	−0.27	−0.2	0.29	0.79*					
Area	0.22	0.45*	0.28	0.22	0.15	−0.25	−0.84*	−0.97*				
Perimeter	0.28	0.54*	0.34	0.27	0.21	−0.29	−0.78*	−0.99*	0.96*			
A:P	0.21	0.23	0.27	0.22	0.14	−0.22	−0.85*	−0.95*	0.99*	0.94*		
DR	0.06	−0.29	0.15	0.06	0.26	−0.24	−0.99*	−0.83*	0.87*	0.82*	0.88*	
avgx	0.35	0.53*	0.41	0.36	0.21	−0.31	−0.70*	−0.97*	0.92*	0.96*	0.92*	0.76*

Note: Numbers are correlation coefficients (r values), while asterisks (*) correspond to significant correlations ($p < 0.05$).

The physiological link between LNC and photosynthetic capability is well studied, and given a finite supply of biologically available nitrogen, individual species must exist within a continuous spectrum of capturing more light with larger leaf areas with low photosynthetic ability or less light with smaller leaf areas with high photosynthetic ability (Hikosaka, 2004). The trade-offs between the extremes of this spectrum are based on photosynthetic nitrogen use efficiency, where species with higher efficiency exhibit higher growth rates and tend to occur in more disturbed or high-productivity habitats compared to species with lower efficiency. This spectrum of how plants utilize limiting resources (light, water, moisture and both nitrogen- and phosphorus-rich nutrients) in the environment and its overall relationship to life-history strategy trade-offs has been observed at a global scale, and has supplied a useful framework to examine species strategies as shaped by evolutionary history (i.e., the plant economics spectrum, *sensu* Reich, 2014). Without a significant relationship between SLA and LNC, it appears that the most frequent species in sandstone outcrop communities sit at several locations along this spectrum.

Positive SLA and plant height relationships suggest that tall species with large leaves are frequent across these sites. Given that these two functional traits are negatively related to patch characteristics, tall, large-leaved species are associated with the small, irregularly shaped sites. This association indicates a potential for woody encroachment, a phenomenon common in global drylands and often associated with changes in land-use or disturbance regimes which give woody plants a competitive advantage over herbaceous vegetation (Maestre et al., 2021). Larger and more regularly shaped sites further away from the road tended to support plants with low SLA and plant height as well having a higher probability of metapopulation species going locally extinct with decreases in area compared to small sites close to the road. Patch quality (in this case, based on total area and regularity) may have a significant effect on local extinctions and future colonization events (Franzén & Nilsson, 2010). Specific leaf area explained multivariate relationships in taxonomic and phylogenetic composition, and specific leaf area and functional traits explained variation in phylogenetic (avgLNC and avgSLA) and functional composition (avgPH, see Appendixes S2, S3). Overall, distance-based functional diversity calculated from all three functional traits was an important and variable driver of biodiversity among the sandstone outcrops.

A majority of species in the regional species pool that occur in the adjacent forest matrix do not establish within these sandstone outcrops. This restriction may be due to the physiological barrier of low water availability, selecting for drought-tolerant taxa. For example, *Juniperus virginiana* and *Ulmus rubra* were frequent in these sandstone outcrops and are common in other xeric forest openings in the region (Heikens & Robertson, 1995; Delong & Gibson, 2012). Nevertheless, few xeric-tolerant tree species occur within these communities. Moreover, these tree species are often smaller and shorter in stature compared to those which occur in the adjacent forest matrix.

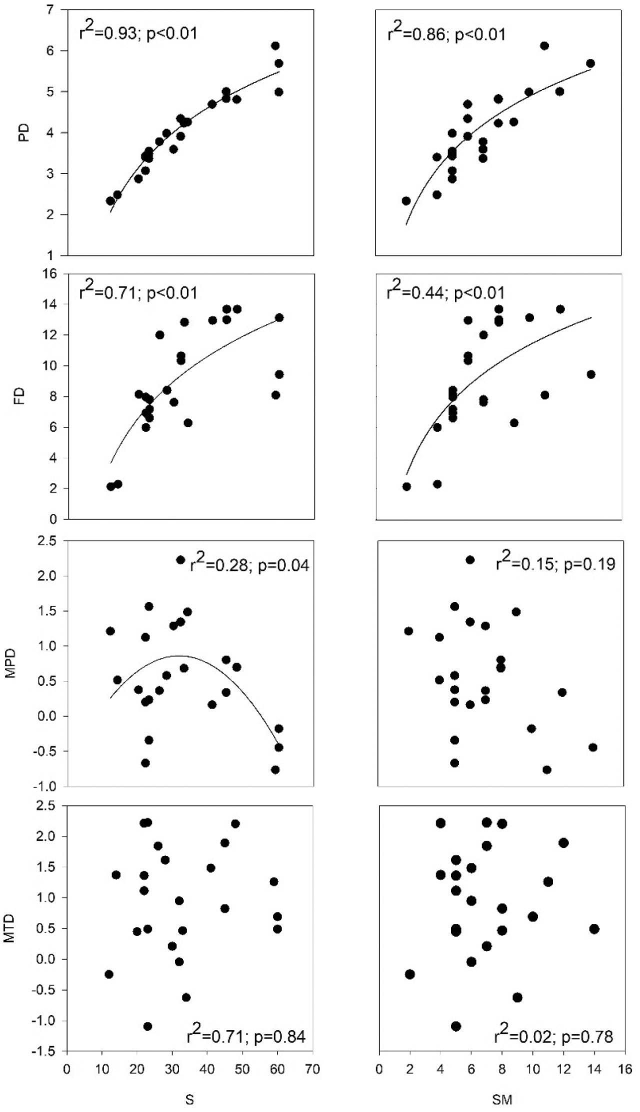

FIGURE 3 Non-linear regressions between total species richness (*S*) and the number of species exhibiting metapopulation dynamics (SM) with phylogenetic and functional diversity (PD and FD; regressions fitted with a logarithmic term) as well as mean pairwise distance and mean trait distances (MPD and MTD; regressions fitted with a second-order polynomial term).

4.2 | Species exhibiting metapopulation dynamics

A small portion (15%) of metapopulation species was observed, and this small number is likely due to the sessile nature and limited dispersal ability of most plants (Tilman, 1994; Eriksson, 1996; Hanski et al., 1996b; Brederveld et al., 2011). These sandstone outcrops are scattered across an upland forest matrix, which provides a barrier to dispersal (Sáyago et al., 2018). The relatively taller forest vegetation surrounding the sandstone outcrops can block pollen and seed transfer between outcrops without efficient pollinators and dispersers. In addition, sites which had the most metapopulation species were more diverse (based on correlations and multivariate analyses) but were not larger, more regularly shaped, or closer to the road than less diverse outcrops. Species richness not exhibiting a relationship with patch area contradicts the long-standing species–area hypothesis (Arrhenius, 1921; Gleason, 1922). In addition, previous studies have found differing effects of roads on both species' dispersal as well as gene flow (Taylor et al., 2012; Suárez-Esteban et al., 2013, 2014; Lemke et al., 2019). We found that the area-dependent metapopulation extinction probability (avg*x* values) was highest in large, regularly shaped sites, highlighting how area availability in patches may be crucial for metapopulation persistence.

Metapopulation species tended to occur within a limited number of plant families (Asteraceae and Poaceae) and were often exotic species, indicating that certain evolutionary clades were more likely to exhibit metapopulation dynamics and exotic species may disperse more between patches compared to native species. Several other studies have used Hanski's Incidence Function Model and observed composite species (Asteraceae) as metapopulations. Dornier et al. (2011) observed metapopulation dynamics of an annual composite species finding that closely placed metapopulations exhibited low extinction probabilities and beneficial rescue effects compared to more isolated populations. Some composites and grasses identified as metapopulations in this study were wind-pollinated, with reproduction independent of living pollinator density and efficiency. This observation shows that despite the adjacent forest matrix acting as a barrier to other species within these sandstone outcrops, wind pollination and dispersal may aid metapopulation species dispersal across all sites. Furthermore, species unable to colonize individual patches are likely limited more by the harsh abiotic conditions and dispersal barriers rather than competition (Theoharides & Dukes, 2007; Robledo-Arnuncio, 2011). In addition, over half of the SM dynamics were primarily bee-pollinated. Campbell and Husband (2007) observed that when pollinators and potential mates are scarce or isolated, small populations of certain composites experience increased floral visitation rates while experiencing genetic drift and allozyme polymorphism. Regardless, in this study system, a lack of insect pollinators does not appear as a threat to metapopulation persistence. Regarding exotic species, a review by Vilà and Ibáñez (2011) observed that as exotic invasives continue to increase in abundance across the global landscape, they accumulate at patch edges compared to the interior of suitable patches. Furthermore, studies such as Quintana-Ascencio and Menges (1996) observed shrubs to have higher *x* values compared to perennial herbs, whereas this study did not observe any differences in any growth types and between annuals, biennials, and perennials.

Highly species-rich communities also having the most SM dynamics indicates that co-occurring species in diverse patches are not competitively excluding immigrating species establishment. However, low-diversity patches rarely experience immigration of species due to dispersal limitation or local competition. In addition, positively related PD and FD across sites indicates an overall lack of both phylogenetic and functional overdispersion or clustering across individual sites. A positive non-linear regression between PD and FD diversity with species richness supports this idea and

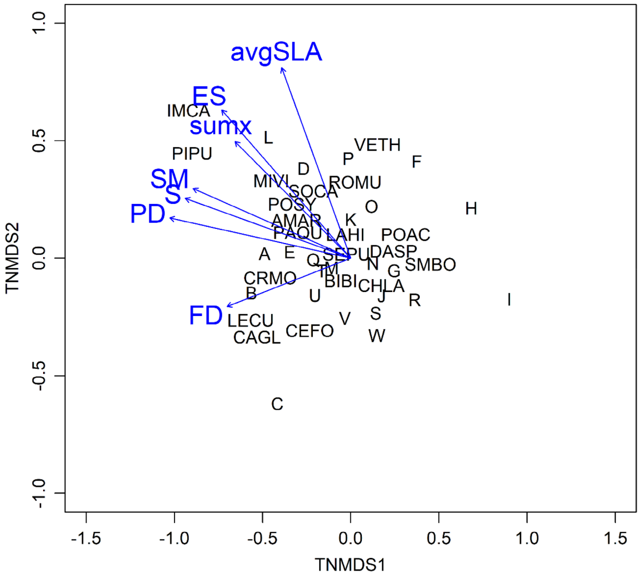

FIGURE 4 Taxonomic non-metric multidimensional scaling ordination (TNMDS) (stress = 0.18) displaying sites (A–W) and species exhibiting metapopulation dynamics (Hanski et al., 1996a, 1996b incidence unction model). Significant vectors are plotted (see Appendix S3). Species codes available in Table 2.

indicates a random selection of species based on evolutionary and functional relationships. However, these relationships may indicate that species experience low competition based on evolutionary and functional relationships as species diversity increases, indicating the new taxa (potentially incoming exotic invasives) may still be able to colonize these patches based on the presence of empty niches and discrete colonization opportunities. (Mayfield & Levine, 2010; Kluge & Kessler, 2011; Enders et al., 2019). These trends in diversity are supported in both correlations and regression (as diversity indices exhibited a positive correlation) and in multivariate analyses (where diversity indices shared similar ordination trajectories). However, relationships between standardized measures of PD and FD were not observed, indicating that while communities are unsaturated, the a priori assumption of phylogenetic inertia may not pertain to this study system (Safi et al., 2011). However, regular and frequent disturbances contribute to the open canopy of communities and make unused resources available (Heino et al., 2003; Tilman, 2004). The unsaturated nature of these sandstone outcrops seems to be based on dispersal limitations and chronic harsh abiotic conditions (low availability of water and substrates rather than acute disturbance events) as opposed to intense interspecific competition based on evolutionary or functional relationships.

Although metapopulation theory typically attempts to assess dynamics at a regional scale, it is frequently employed to investigate patch dynamics with localized populations within distinct patches (Freckleton & Watkinson, 2002). However, some species observed in this study which exhibited metapopulation dynamics were occasionally observed (often at lower abundances) in the adjacent forest matrix. This phenomenon highlights the assumption that suitable patches exist among an uninhabitable matrix is not necessarily true in nature and that truly discrete suitable matrixes are challenging or impossible to define a priori in certain systems (Freckleton & Watkinson, 2002). Given that several species (both those with or without metapopulation dynamics) within this system can be found in both the outcrops and adjacent forest matrix, these species would be considered either spatially extended populations, or extended local populations (Freckleton & Watkinson, 2002, 2003). However, non-metapopulation species exclusive to these sandstone outcrops can be considered remnant populations, which experience infrequent colonization and migration (due to taller forest vegetation) and rare extinction due to high stress tolerance and low competition for physical space.

4.3 | Metacommunity structure

The metacommunity structure that we observed in these sandstone outcrops is characterized by species groups with similar responses to environmental filters and reciprocal ecological relationships, resulting in coordinated range limits and compositional similarity across the landscape (Heino et al., 2015). This type of empirical metacommunity structure, along with other non-random metacommunity structures, assumes that species distributions are driven by biotic interactions or abiotic responses to the environment. These metacommunity patterns are characterized by species occurrences appearing as discrete communities which replace one another as a group (Leibold & Mikkelson, 2002). The sandstone outcrop communities in this study therefore are characterized by predictable species and composition which shared distinct occurrences across suitable patches. Lewinsohn et al. (2006) describe this type of metacommunity structure as a result of compartmentalized assemblages with "recognizable subsets" of interacting species which are more linked within than across subsets. These assemblages can occur due to interdependent species interactions along an environmental gradient (Callaway, 1997), consistent with the integrated community concept (Lortie et al., 2004), or because the presence of species pair-wise combinations is not independent (Gilpin & Diamond, 1982). Aggregated community assemblages of this type can arise from positive interactions among co-occurring species, especially in stressful habitats or shared microhabitat preferences (Bertness & Callaway 1994, Callaway, 1997, Duarte et al., 2021). This concept, known as the stress gradient hypothesis, has been tested and supported in other research, particularly in arid plant communities (Armas et al., 2011). In addition, Duarte et al. (2021) also observed that distantly related taxa which coexist are more likely to exhibit high levels of nursing species as well as facilitation, highlighting the importance of including ecophylogenetic analyses when monitoring stressful environments. Moreover, these metacommunities are resilient to diversity losses and invasions and occur across broad taxonomic and geographical distinctions (Keith et al., 2010; Presley & Willig, 2010; Bried et al., 2015; Jiménez et al., 2020).

In conclusion, metapopulations were observed in these sandstone outcrop communities, which were proportionately more likely to be short-lived (annual or biennial) exotic species, while the most frequent (non-metapopulation) species were trees. Sandstone outcrop communities exhibited a metacommunity structure, characterized by predictable species assemblages which are interchanged as a unitary occurrence across the landscape, which promote the existence of metapopulations. Taxonomic, phylogenetic, and functional diversity (but not individual functional traits) were intercorrelated across patches, where phylogenetically similar species were also functionally similar. Phylogenetic and functional diversity were driven individually by both the total number of species as well as the number of metapopulation species. In addition, while larger, more regularly shaped patches did not necessarily maintain higher levels of diversity, they did support metapopulations prone to extinction due to patch area loss. Finally, the number of metapopulation species present explained significant differences in the composition of sandstone outcrop metacommunities, where sites with higher levels of taxonomic, phylogenetic, and functional diversity also had more metapopulation species.

AUTHOR CONTRIBUTIONS

David Francis Barfknecht collected field data and conducted analyses. David Francis Barfknecht and David John Gibson collaborated on the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

We thank Tad Dallas, Bryan Foster, Samuel Ramirez, Kevin Rohling, Nick Seaton, and Saroj Thapa, for their efforts with data collection, assistance with drone imagery, and advice regarding both analyses and graphical considerations.

DATA AVAILABILITY STATEMENT

All datasets and supplemental ate available on Dryad: https://datadryad.org/stash/dataset/doi:10.5061/dryad.g79cnp5r5.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1 Incidence (x for presence) of plant species in 23 sandstone outcrop communities in Jackson Hollow Ecological Area, southern Illinois, USA.

Appendix S2 Functional traits of the 25 most frequent species observed within 23 sandstone outcrop communities including leaf nitrogen content (%; LNC), specific leaf area (g/m^2; SLA), plant height (m; PH), and growth form (GF).

Appendix S3 Non-metric multidimensional scaling (NMDS) axis scores and vector analysis (r^2 and p value) corresponding to taxonomic NMDS (TNMDS) (Fig. 4).

How to cite this article: Barfknecht, D.F. & Gibson, D.J. (2023) Are metapopulation species drivers of metacommunity structure in sandstone outcrop communities? *Journal of Vegetation Science*, 34, e13167. Available from: https://doi.org/10.1111/jvs.13167