

Species characteristics affect local extinctions

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PREMISE OF THE STUDY: Human activities threaten thousands of species with extinction. However, it remains difficult to predict extinction risk for many vulnerable species. Species traits, species characteristics such as rarity or habitat use, and phylogenetic patterns are associated with responses to anthropogenic environmental change and may help predict likelihood of extinction.

METHODS: We used historical botanical data from Kalamazoo County, Michigan, USA, to examine whether species traits (growth form, life history, nitrogen-fixation, photosynthetic pathway), species characteristics (community association, species origin, range edge, habitat specialization, rarity), or phylogenetic relatedness explain local species loss at the county level.

KEY RESULTS: Across Kalamazoo County, prairie species, species at the edge of their native range, regionally rare species, and habitat specialists were most likely to become locally extinct. Prairie species experienced the highest local extinction rates of any habitat type, and among prairie species, regionally rare and specialist species were most vulnerable to loss. We found no evidence for a phylogenetic pattern in plant extinctions.

CONCLUSIONS: Our study illustrates the value of historical datasets for understanding and potentially predicting biodiversity loss. Not surprisingly, rare, specialist species occupying threatened habitats are most at risk of local extinction. As a result, identifying mechanisms to conserve or restore rare or declining species and preventing further habitat destruction may be the most effective strategies for reducing future extinction.

KEY WORDS extinction; habitat loss; habitat specialist; herbarium; historical data; prairie; random phylogenetic pattern; range edge; rarity; species traits.

Species extinction rates are predicted to rise by an order of magnitude over the next few hundred years (Mace et al., 2005; Pimm et al., 2014; Mankga and Yessoufou, 2017). However, there is large variability in predictions of extinction risk. For example, anywhere from 0.17% to 42.5% of plant species could go extinct within a century (Pereira et al., 2010). Two factors could improve our ability to predict extinction risk and which taxa are most vulnerable to extinction: trait-based approaches (Sodhi et al., 2008; Saar et al., 2012; Luiz et al., 2016) and phylogenetic analyses (are some clades more susceptible to extinction than others?) (Fitzpatrick et al., 2008; Davies et al., 2011; Parhar and Mooers, 2011; Yessoufou et al., 2012; Davies and Yessoufou, 2013). Studies of historical and recent data on plant distributions and abundance can test the effectiveness of both traits and phylogeny for predicting extinction (Primack et al., 2004; Fitzpatrick et al., 2008; Willis et al., 2008; Nualart et al., 2017; Meineke et al., 2018; Lang et al., 2019).

Species traits and characteristics have emerged as a valuable framework for predicting responses to global changes (McGill et al., 2006; Lavorel et al., 2007; Mouillet et al., 2013). For example, short plants with large leaf areas are associated with negative responses to climate warming (Venn et al., 2011), and species characteristics that reflect aspects of rarity and habitat affinity influence how species respond to habitat conversion and disturbance (Farnsworth and Ogurcak, 2008; Sodhi et al., 2008; Leão et al., 2014; Palma et al., 2016). Such species traits and characteristics also likely influence extinction risk, as species with biological and ecological characteristics that are ill-suited to survival in altered habitats will likely be at high risk of extinction (Brook et al., 2008; Leão et al., 2014; Palma et al., 2016). In butterflies, for example, species with narrow niche breadth, restricted resource use, poor dispersal ability, and low reproductive rates are at high risk of extinction (Kotiahho et al., 2005; Öckinger et al., 2010), while in mammals, characteristics such as geographic range and life history strategy have been associated

with extinction risk (Davidson et al., 2017). In plants, native species (Suding et al., 2005; Weigmann and Waller, 2006; Rogers et al., 2008), forbs (Leach and Givnish, 1996; Soons and Heil, 2002; Smart et al., 2005; Weigmann and Waller, 2006), perennials (Grashof-Bokdam, 1997; Verheyen et al., 2003; Suding et al., 2005), habitat specialists (Rich and Woodruff, 1996; Fischer and Stöcklin, 1997; Preston, 2000; Preston et al., 2002; Davies et al., 2004; Kolb and Diekmann, 2004), and species experiencing high rates of habitat loss (Duncan and Young, 2000; Lienert et al., 2002; Aedo et al., 2015; Auffrett et al., 2018), among others, experience high rates of local extinction. Identifying traits associated with species that have been lost from a given geographic area or habitat may help elucidate the characteristics that help or harm species in the face of global change and may aid in the development of strategies to manage and conserve species with similar characteristics (Cardillo et al., 2006; Farnsworth and Ogurcak, 2008; Razgour et al., 2013; Romeiras et al., 2014; Bai et al., 2018).

Phylogenetic signatures in extinction events can also provide insights into patterns of species loss (Jones et al., 2005; Purvis, 2008). A strong phylogenetic signal implies that certain families are more susceptible to loss than others (Purvis et al., 2000a; Mankga and Yessoufou, 2017). Phylogenetic patterns in extinction risk have been detected in birds (Bennett and Owens, 1997; Russell et al., 1998; Purvis et al., 2000b; von Euler, 2001; Fritz and Purvis, 2010), mammals (McKinney, 1997; Harcourt, 1998; Russell et al., 1998; Purvis et al., 2000b; Johnson, 2002), amphibians (Stuart et al., 2004; Bielby et al., 2006), insects (Kotiaho et al., 2005), marine taxa (McKinney, 1997; Roy et al., 2009), and plants (Schwartz and Simberloff, 2001; Sjöström and Gross, 2006; Davies et al., 2011; Yessoufou et al., 2012; Leão et al., 2014). In cases where there is a phylogenetic signal in extinction risk, species traits likely influence extinction (McKinney, 1997; Fisher and Owens, 2004; Willis et al., 2008; Fritz and Purvis, 2010; Saar et al., 2012; Loza et al., 2017), and phylogeny can help predict extinction risk even when the relevant traits are unknown (Fritz and Purvis, 2010; Davies et al., 2011; Yessoufou et al., 2012). Alternatively, a random phylogenetic pattern of extinction implies that extinction events are not determined by traits conserved among related species. Instead, extinction may be influenced by an unmeasured, not phylogenetically conserved trait or by an external mechanism that does not strongly select against particular traits, such as habitat loss (Fritz and Purvis, 2010; Daru et al., 2013; Yessoufou and Davies, 2016). Although uncommon (McKinney, 1997; Yessoufou and Davies, 2016), random phylogenetic patterns of extinction have been observed in mammals (Arregoitia et al., 2013) and plants (Fréville et al., 2007; Fitzpatrick et al., 2008; Lapiedra et al., 2015; Yessoufou et al., 2017). However, compared to the research done in well-studied vertebrates, there are fewer studies of the phylogenetic structure of plant distributions and extinction (Loza et al., 2017; Mankga and Yessoufou, 2017).

Incorporating historical data on species losses could be a valuable resource for detecting trait and phylogenetic patterns in recent species extinctions (Primack et al., 2004; Grass et al., 2014; Nualart et al., 2017; Meineke et al., 2018; Lang et al., 2019). Mass species extinctions spanning hundreds of millions of years have commonly been examined using the paleontological record, in which fossils provide the approximate date of last occurrence before an extinction event (Jablonski, 1994). However, understanding contemporary extinction events may require examining more contemporary, local species records, because

of two discrepancies between the paleontological record and more recent extinctions. First, comparing causes of extinction over geological time scales versus more recent time is difficult (Jablonski, 1994; Barnosky et al., 2011; Pimm et al., 2014; De Vos et al., 2015; Plotnick et al., 2016). For example, in amphibians, habitat-based extinction risk was reversed in contemporary taxa compared to fossil taxa: fossil amphibian taxa declined in stagnant waters while contemporary amphibian taxa declined in flowing waters (Tietje and Rodel, 2017). Second, the paleontological record is often used to examine species extinction on a global scale rather than for studies of local species losses because widely distributed and common species are more likely to appear in the fossil record (Liow et al., 2008; Plotnick et al., 2016) and because the fossil record is often too incomplete to be analyzed at the species level or on local scales (Pereira et al., 2012; Plotnick et al., 2016). Herbarium and museum records provide a more recent record of such local, species-specific extinction events (Lang et al., 2019), span centuries, include a large sample of species (Primack et al., 2004; Meineke et al., 2018), and likely reflect localized changes to the environment that have recently driven species to local extinction (defined here as disappearance at a small spatial scale, such as within a given county) (Pelini et al., 2011; Pimm et al., 2014). As a result, herbarium records have been used to identify characteristics associated with extirpations ranging from local to continental scales (Duncan and Young, 2000; Bertin, 2002; Blomqvist et al., 2003; DeCandido et al., 2004; Primack et al., 2004; Smart et al., 2005; Williams et al., 2005; Miller-Rushing et al., 2006; Willis et al., 2008; Knapp et al., 2010; Pyke and Ehrlich, 2010; Willis et al., 2010; Duncan et al., 2011; Gregor et al., 2012; Wolkovich et al., 2013; Grass et al., 2014; Palma et al., 2016; Dolan et al., 2017; Nualart et al., 2017; Willis et al., 2017).

Here, we use historical data from Kalamazoo County, Michigan, USA, to examine patterns of local extinction events. The flora of Kalamazoo County was surveyed extensively from the 1890s to 1947 and again from 1994 to 2003. Over this period, it has experienced both urbanization and intensified agricultural land use, reflecting similar changes across historically grassland-dominated sites in central North America. Using these two datasets, which record species presence and absence in the county, we address two questions: (1) Is local extinction influenced by species traits and characteristics? and (2) Is there a phylogenetic pattern to local extinction?

MATERIALS AND METHODS

Study system

Kalamazoo County covers ~1492 km² in southwestern Michigan, USA. Rivers, streams, and lakes cover ~3.2% of the area. The surrounding land consists of forests, wetlands, prairie remnants, and land developed for urban and agricultural use (McKenna, 2004).

Kalamazoo County boasts a diverse and well-documented flora, with more species reported (1651; McKenna, 2004) than in most other county-level floras in North America (Jarnevich et al., 2006). The county was first surveyed from the 1890s to 1940s (Hanes and Hanes, 1947) and was resurveyed in the 1990s (primarily during 1994–2003; McKenna, 2004). These historical records describe the

various community types and presence/absence of native and introduced vascular plants in Kalamazoo County. The 1136 species included in our study were recorded in both the Hanes and Hanes (1947) and McKenna (2004) records.

Historical dataset

During the original surveys, C. and F. Hanes surveyed sites across Kalamazoo County, took detailed field notes, collected plant samples, and eventually compiled their data into a checklist of species in the county's first published flora (hereafter "original surveys"). In the 1990s (1994–2003), D. McKenna expanded the species checklist by surveying the same sites across Kalamazoo County, examining more than 5000 herbarium specimens, referencing the Hanes field notes and vegetation maps completed by the General Land Office in the mid-1800s (Comer et al., 1995, 1997), and communicating with local botanists (McKenna, 2004) (hereafter "1990s surveys"). We note that different survey methods and sampling intensities across these two periods may affect the data available. Given the extensive sampling across at least a decade during both surveys, we believe that the county-level botanical record is of high quality (Jarnevich et al., 2006; Fréville et al., 2007; Niissalo et al., 2017). In addition, McKenna (2004) found 133 new species, including some native species likely missed during the original surveys.

Using these two records, we designated species as locally extinct (designated as "0") or non-extinct in Kalamazoo County (designated as "1") (McKenna, 2004). Locally extinct species were recorded in the county during the original surveys but were no longer found in the county during the 1990s surveys. For species listed as locally extinct, we cross-referenced with herbarium records to check whether the species had been found in Kalamazoo since the 1990s (<http://michiganflora.net/specimen-search.aspx>).

Species in Kalamazoo County occur in several unique, discrete plant communities (defined here as in McKenna, [2004]: an "assemblage of species in a given habitat type with characteristic growth form, structure, seasonality, dynamics and composition"). Each species included in McKenna (2004) included a notation for the plant community (or communities) in which the plant was historically reported or found during the 1990s surveys. Specific community types were also more broadly categorized as prairie, wetland, or forest (categories described in McKenna, [2004]; Appendix S1). Kalamazoo County has been exposed to varying degrees of human alteration (post-settlement; i.e., excluding alterations made by Native Americans), such as road development, urbanization, and intensive agricultural use. When a plant was associated with an anthropogenic feature of the landscape, McKenna (2004) denoted its habitat as "old field," "roadside," "railroad right-of-way," or "garden"; we grouped these species into a "man-made habitat" category.

We determined the geographic rarity of each species by calculating the proportion of Michigan counties in which a species is found (USDA PLANTS Database: <https://plants.usda.gov/java/>). For scale, Michigan covers 250,490 km², and most counties in lower Michigan each cover 905–2486 km² (www.indexmundi.com). We use this regional rarity metric as a proxy for local rarity because our knowledge of historical population sizes in Kalamazoo County is minimal or lacking for most species, and a standardized scale is needed for comparing between species (Hartley and Kunin, 2003).

We classified each species by a number of categorical characteristics and traits.

1. *Community association*: Defined as the community type (forest, prairie, wetland, or man-made habitat) that a species is most commonly found in, determined from McKenna (2004) (Appendix S1). For species that had gone extinct, community association was based on where it was historically reported (McKenna, 2004). We hypothesize that habitats that have experienced high rates of degradation and loss (e.g., prairies) will experience high rates of species loss (Duncan and Young, 2000; Lienert et al., 2002; Walker and Preston, 2006; Aedo et al., 2015; Auffret et al., 2018).
2. *Species origin*: Classified as native or nonnative in Michigan, determined from the USDA PLANTS Database. We hypothesize that native species are more likely to be lost than nonnative species, as native species are more often lost than nonnative species in several other habitat types (Suding et al., 2005; Weigmann and Waller, 2006; Farnsworth and Ogurcak, 2008) and invasive species may thrive in the face of human disturbance and anthropogenic environmental change (Dukes and Mooney, 1999).
3. *Range edge*: Classified as "edge" or "central" species, determined from the USDA PLANTS Database. A species was considered at the edge of its range if Michigan is at the border of its native range. We hypothesize that edge species will be more vulnerable to species loss, due to evidence of increased local extinction rates at the edge of species' ranges (Lienert et al., 2002; Doherty et al., 2003; Farnsworth and Ogurcak, 2008; Boakes et al., 2017).
4. *Habitat specialization*: Defined as the number of unique habitat types in which a species was found in Kalamazoo County, as determined by McKenna (2004). This serves as an indicator of whether a species is a specialist that persists in only a few community types, or a generalist that persists in several different community types. We hypothesize that habitat specialists are more likely to succumb to local extinction, as has been reported in other studies of forests and grasslands (Pimm, 1991; Fischer and Stöcklin, 1997; Preston, 2000; Davies et al., 2004; Kolb and Diekmann, 2004; Kotiaho et al., 2005).
5. *Life history*: Classified as annual, annual/biennial, annual/perennial, biennial, or perennial, determined from the USDA PLANTS Database. We hypothesize that perennial species will be more susceptible to local extinction, because annuals are often better colonizers of urbanized environments (Palma et al., 2016) and have been shown to persist longer in small patches of habitat (Collins et al., 2009).
6. *Growth form*: Classified as forbs, ferns, vines, woody (trees, shrubs), or graminoid (grasses, sedges, rushes), as determined from the USDA PLANTS Database. We hypothesize that forb species are more vulnerable to loss, as forbs are lost more often than other growth forms in other forest and grassland systems (Leach and Givnish, 1996; Smart et al., 2005; Sjöström and Gross, 2006; Weigmann and Waller, 2006).
7. *Nitrogen-fixation*: Classified as an "N-fixer" (a species that can fix nitrogen) or not, determined using state wildflower websites. We hypothesize that N-fixers are more likely to disappear because in grasslands, soil nitrogen levels increase through deposition and fertilization (Sala et al., 2000) and N-addition

experiments commonly reduce the abundance of species with N-fixing symbionts (Leach and Givnish, 1996; Suding et al., 2005).

8. *Photosynthetic pathway* (“C3/4”): Classified as C3 or C4, determined using state wildflower websites. We hypothesize that C3 species are more likely to become locally extinct, as previously found in Minnesota grasslands (Suding et al., 2005).

Data analysis

We present two sets of data analyses. First, we examine extinction in all the habitat types across Kalamazoo County (“Kalamazoo County”). Then, because prairies represent the most vulnerable habitat type in the area (Chapman and Brewer, 2008) and experience the highest proportion of extinction events, we present analyses wherein only prairie species extinctions are considered (“Prairie species”). We performed all analyses in R (R Core Team, 2015).

Kalamazoo County—We tested for correlations between all traits and characteristics using chi-square tests of independence, which determine whether two categorical variables are correlated. We considered characteristics correlated if $P \leq 0.05$.

We used a generalized linear model with a binomial distribution to examine the effect of each species characteristic on the status (locally extinct/non-extinct) of prairie species in Kalamazoo County. We included status as the response variable, and species origin, range edge, habitat specialization, life history, growth form, N-fixation, and photosynthetic pathway as categorical predictor variables. Rarity was included as a continuous covariate to control for the likelihood that rare species should be lost more often than common ones. We hypothesized that rare native species, rare habitat specialists, rare N-fixers, and rare species at the edge of their native range might respond differently than rare invasive species, rare generalists, rare non-N-fixers, and rare central species, so interactions between rarity and those characteristics were included.

Because the majority of the traits and characteristics considered were correlated (Appendix S2), we used backwards elimination to simplify the regression. In backwards elimination, the predictor with the highest P value greater than alpha ($\alpha = 0.05$) is removed. The model is refit, and this procedure repeats until no collinear predictors are included and all P values are less than α . We provide Akaike Information Criterion values for the models and P values of removed variables in Appendix S3. The final model included community association, rarity, N-fixation, growth form, range edge, habitat specialization, and the interactions of community association \times rarity and N-fixation \times rarity as predictor variables. Post hoc tests were used to evaluate differences between treatment levels when the effect of a species trait or characteristic was significant ($P \leq 0.05$).

We also performed a multiple correspondence analysis (MCA), an explanatory/descriptive analysis technique that reduces large sets of associated categorical variables into smaller sets of components that summarize the information in the data without any underlying assumptions about the data's distribution (Abdi and Valentin, 2007). This analysis, although it does not allow for use of continuous data, allows us to consider all categorical characteristics rather than removing correlated variables. Results from the two analyses were similar, but because of the benefits and

shortcomings of both of these methods we present the backwards elimination results in the main text and the MCA in Appendices S4 and S5.

Prairie species—Because prairies represent the most threatened habitat type in Kalamazoo County and because prairie species (i.e., species commonly found in, but not necessarily exclusive to, prairie habitats) experience more extinction events than species found in other community types (see below), we used a generalized linear model with a binomial distribution to examine the effect of each species characteristic on the status (locally extinct/non-extinct) of prairie species in Kalamazoo County. As described above, we included status as the response variable, and species origin, range edge, habitat specialization, life history, growth form, N-fixation, and photosynthetic pathway as categorical predictor variables, rarity as a continuous covariate, and the interactions between rarity \times species origin, rarity \times habitat specialization, rarity \times N-fixation, and rarity \times range edge. We again used backwards elimination to simplify the regression and provide Akaike Information Criterion values for the models and P values of removed variables in Appendix S6. The final model included rarity, habitat specialization, growth form, N-fixation, and the interaction of rarity \times N-fixation as predictor variables. Post hoc tests were used to evaluate differences between treatment levels when the effect of a species trait or characteristic was significant ($P \leq 0.05$).

To control for phylogenetic nonindependence, we obtained a phylogenetic tree for the prairie species of Kalamazoo County from Phylomatic (<http://phylodiversity.net/phyloomatic>), using the Zanne et al. (2014) tree (Fig. 1; Webb and Donohue, 2005; Webb et al., 2008). We only provide a phylogenetic analysis of prairie species, because of incomplete phylogenetic data for species from the other habitat types. We first tested whether each binary species characteristic was phylogenetically conserved the “phylo.d” function in the R package “caper” version 1.0.1 (Fritz and Purvis, 2010). “Phylo.d” calculates the D statistic, a test statistic that compares the observed phylogenetic signal in a binary trait with the signal under a continuous Brownian motion model of trait evolution and applies a threshold: if species have a continuous trait value above the threshold, they are assigned a score of 0 and those whose trait value is below the threshold are assigned a score of 1 (Fritz and Purvis, 2010). $D = 1$ indicates a random signal while $D = 0$ indicates conservatism. Pr(Brownian) provides the probability that the binary trait state results from a Brownian (nonrandom) phylogenetic structure. For nonbinary traits and characteristics, we tested for phylogenetic conservatism using the “phylosignal” function in the package “picante” in R version 1.3-0 (Kembel et al., 2010), following Fitzpatrick et al. (2008) and Saar et al. (2012). “Phylosignal” measures Blomberg's K , a test statistic that also compares the observed phylogenetic signal in a trait with the signal under a Brownian motion model of trait evolution (Blomberg et al., 2003). $K = 0$ indicates random or convergent evolution; $K = 1$ indicates trait conservatism; $K > 1$ indicates species being more similar than expected. Groups with a PIC.variance of $P \leq 0.05$ show phylogenetic signal (Blomberg et al., 2003).

To control for phylogenetic correlations, we performed phylogenetic logistic regression (Paradis and Claude, 2002; Ives and Garland, 2010; Daru et al., 2013). We again performed backwards elimination, in a manner similar to Purvis et al. (2000a).

RESULTS

Kalamazoo County

A total of 43 species (3.79% of the flora) are documented to have disappeared from Kalamazoo County from the early to late 20th century (McKenna, 2004).

Species characteristics were associated with extinction across the county. Prairie species experience high rates of loss, as do habitat specialists, species at the edge of their native range (Table 1; Fig. 2A–C), and regionally rare species (Table 1; Fig. 3A). Forbs and vines tend to experience high rates of loss (Table 1; Fig. 2D). Prairie species become locally extinct even when relatively common (Table 1; Fig. 4), and the local extinction of N-fixing species depends on rarity (Table 1). For both N-fixers and non-N-fixers, rare species tend to go extinct more often; this is especially true for N-fixers. However, this rarity \times N-fixation interaction should be interpreted cautiously because only two N-fixing species went extinct in Kalamazoo County during 1890–2003, and growth form and N-fixation are highly correlated (Appendix S2).

Prairie species

Prairie species experience more extinction events than species found in forests, wetlands, and man-made community types (Table 1; Fig. 2A). Of the 164 prairie species found in Kalamazoo County, 23 (14.02%) became locally extinct between the 1890s and 1990s. In comparison, 0.03% of species found in man-made habitats, 0.02% of wetland species, and 0.01% of forest species disappeared in the same time frame (Fig. 2A).

Regionally rare species and habitat specialists (species found in one or two habitat types) are more likely to become locally extinct than more common and generalist prairie species (Table 1; Figs. 3B and 5A). Growth form also significantly affected extinction, with forbs and vines tending to have higher extinction rates than graminoids and woody species (Table 1; Fig. 5B). Rare non-N-fixing species are more at risk of extinction (Table 1), but N-fixation is again

TABLE 1. Results from three separate analyses testing effects of species characteristics and traits on the status (locally extinct/non-extinct) of species in Kalamazoo County, Michigan, USA. The analyses include (1) all species (backwards elimination on a generalized linear model (GLM), binomial distribution), (2) prairie species (backwards elimination on a GLM, binomial distribution), and (3) prairie species (phylogenetic logistic regression (phyloglm), binomial distribution). *** $P \leq 0.0001$; ** $P \leq 0.01$; * $P \leq 0.05$; $P \leq 0.1$.

Source	df	All species (GLM) χ^2	Prairie species (GLM) χ^2	Prairie species (phyloglm) Z-value
Community association	3	12.20**	–	–
Rarity	1	11.25***	6.04*	–2.63**
Habitat specialization	3	25.10***	18.87***	–3.12**
N-fixation	1	3.63	2.46	–
Growth form	4	14.34**	13.96**	–
Range edge	1	3.97*	–	–
Rarity \times community association	1	14.41**	–	–
Rarity \times N-fixation	3	5.82*	4.98*	–

highly correlated with growth form (Appendix S2), so this finding should be interpreted cautiously.

When accounting for phylogeny, only rarity and habitat specialization influence prairie species' extinction. Extinction status is randomly distributed across the phylogeny (status $D = 0.827$; Fig. 1; Appendix S7). Life history, growth form, N-fixation, and photosynthetic pathway are phylogenetically conserved, but range edge, native origin, habitat specialization, and rarity are not (Appendix S7).

DISCUSSION

Community association, habitat specialization, and regional rarity influence local plant extinctions in Kalamazoo County, Michigan. Across the county, prairie species, forbs and vines, species at the edge of their native range, and rare species experience high rates of loss. Among prairie species (the habitat type experiencing half of the observed extinctions), rare species and habitat specialists become extinct most often when controlling for evolutionary relationships. Despite the fact that most species traits are phylogenetically conserved, we detect no phylogenetic signal in extinction. By using historical botanical records, this work documents regional extinction events and identifies species traits and characteristics associated with extinctions in grassland habitats. Furthermore, it demonstrates how herbaria, which are still underutilized in studies of biodiversity loss and habitat conversion (Meineke et al., 2018), can help identify at-risk species and guide conservation of rare species.

Habitat loss as a driver of extinction

Compared to species from forest, wetland, and man-made habitats, prairie species were the most likely to become extinct between 1890 and 1990 in Kalamazoo County. Once among the most abundant plant communities in Kalamazoo County (consisting of more than 149,302 acres in the 1820s; McKenna, 2004), prairie and savanna habitat is now one of the most threatened in southwestern Michigan, since nearly all of Michigan's prairies were destroyed or altered by agriculture or development by 1980 (Chapman, 1984). Habitat succession due to lack of fire has also contributed to loss of prairie habitat (Chapman, 1984). Today, prairie remnants constitute <0.1% of Michigan's historical acreage (Chapman and Brewer, 2008), and prairies and savannas are essentially extinct in Kalamazoo County (McKenna, 2004). For reference, terrestrial forest and wetlands covered 154,445 and 131,600 acres prior to European settlement, respectively, and Kalamazoo has lost ~50% of its forests and ~35% of its wetlands (www.landscape.org/michigan/overview). Habitat loss and destruction represent the leading cause of biodiversity loss (Vitousek et al., 1997; Wilcove et al., 1998; Mace et al., 2005; Newbold et al., 2016); they contribute to loss of suitable area, fragment the landscape, and degrade habitat quality (Fahrig, 1997), all of which may affect species survivorship, establishment, and spread (Pimm, 1991; Tilman et al., 1994; Thompson et al., 1998; Leckie et al., 2000; Baskin and Baskin, 2001; Bellemare et al., 2002; Henle et al., 2004; Honnay et al., 2005; Halley et al., 2016; Nualart et al., 2017; Ceia-Hasse et al., 2018). Therefore, similar to studies wherein species experiencing high rates of habitat loss disappeared from New Zealand (Duncan and Young, 2000), Spain (Aedo et al., 2015), Switzerland (Lienert et al., 2002), England (Walker and

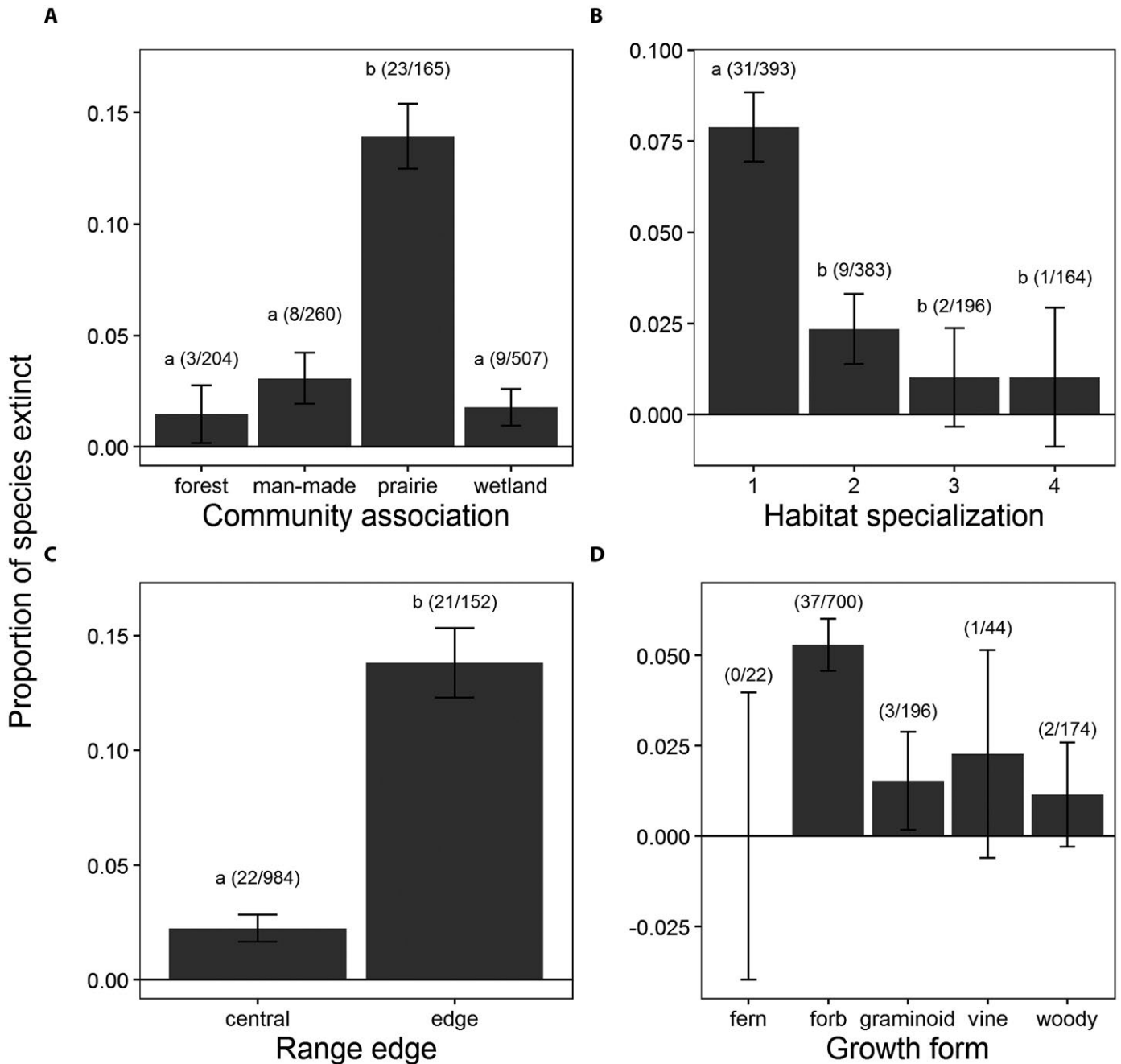


FIGURE 2. Proportion of species (least square means \pm SE from the backwards elimination-generalized linear model for Kalamazoo County, Michigan, USA) that went locally extinct in Kalamazoo County during 1890–1990 by each species characteristic: (A) community association, (B) habitat specialization (number of habitat types occupied), (C) range edge (position of Michigan relative to the edge of a species’ native range), and (D) growth form. Letters represent significant pairwise differences at the $\alpha = 0.05$ level. Values in parentheses represent the number of extinct species over the total number of species in that group.

Preston, 2006), and European grasslands (Auffret et al., 2018), the loss of 14% of the county’s prairie species is likely due to the disproportionate amount of prairie habitat lost in the 19th and 20th centuries. This loss of natural grasslands and their biodiversity reflects the ongoing conversion of historically prairie-dominated landscapes across the midwestern United States, and the effects of past and continuing habitat loss and changes in land use will likely

cause further contemporary declines of vulnerable species (Watson et al., 2016; Auffret et al., 2018).

Species characteristics and extinction risk

Habitat specialists were more likely to disappear from Kalamazoo County, consistent with the hypothesis that specialization

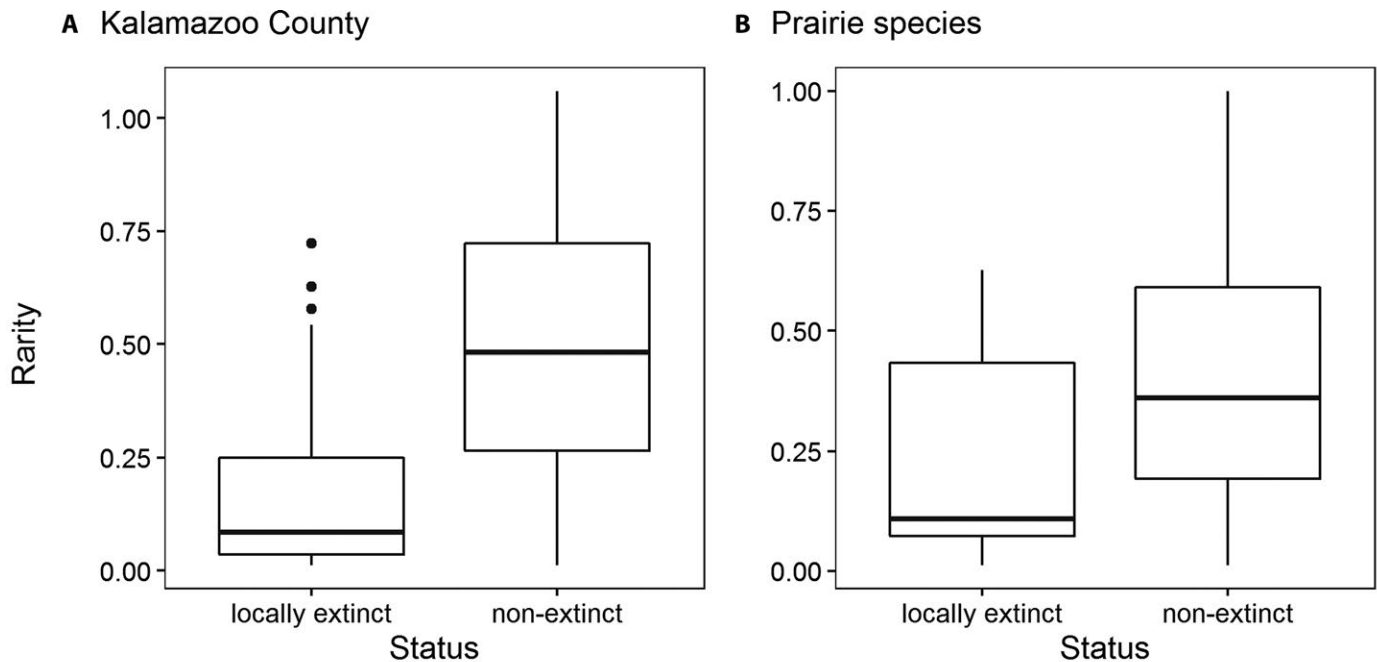


FIGURE 3. Effect of rarity (proportion of Michigan counties a species is found in) on the status (locally extinct/non-extinct) of (A) all species in Kalamazoo County, Michigan, USA, and (B) prairie species in Kalamazoo County.

correlates with extinction risk (Jablonski, 1994; Erwin and Anstey, 1995; McKinney, 1997; Purvis et al., 2000b) and supporting results from previous work on plant extinctions (Rich and Woodruff, 1996; Fisher and Stöcklin, 1997; Preston, 2000; Preston et al., 2002; Davies et al., 2004; Kolb and Diekmann, 2004; Walker and Preston, 2006). The highest predicted extinction rate for generalist species is 7%, while 43% of specialists are predicted to go extinct, as determined from an analysis of extinction risk for endemic plant and vertebrate species based on habitat specificity (Malcolm et al., 2006; Pereira et al., 2010). Species with smaller range sizes have

also been shown to be at higher risk, which may be correlated with habitat specificity (Bennett and Owens, 1997; Russell et al., 1998; Purvis et al., 2000a; Lienert et al., 2002; Cardillo, 2003; Fisher and Owens, 2004; Cooper et al., 2008). This decline in habitat specialists could be due to habitat rarity, given that prairie, while once abundant in Kalamazoo County, had a limited range across Michigan (Chapman and Brewer, 2008). Alternatively, specialist declines could be due to habitat loss: as prairie habitat remnants disappear or are altered by agriculture and invasion, prairie specialists that are unable to disperse to and survive in other habitat types slowly disappear (Diamond, 1984; Lawton and May, 1995; Owens and Bennett, 2000; Purvis et al., 2000c; Kotze and O'Hara, 2003; Kotiaho et al., 2005; Auffret et al., 2018).

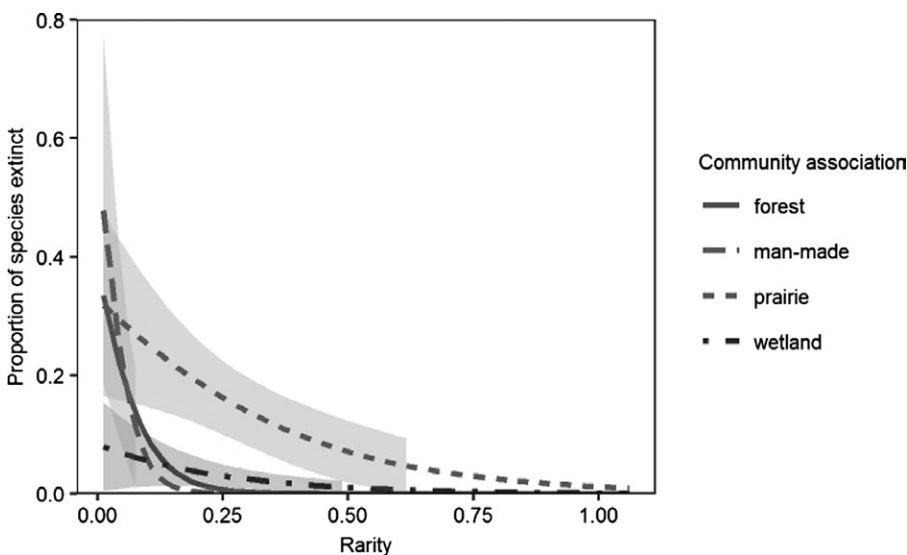


FIGURE 4. Effect of rarity (proportion of Michigan counties a species is found in) and community association on the proportion of species that went locally extinct in Kalamazoo County, Michigan, USA, during 1890–1990. Shaded areas represent 95% confidence intervals.

The random-loss hypothesis predicts that rare species account for most species declines, partially due to random loss of individuals as density declines (Goldberg and Miller, 1990; Oksanen, 1996; Stevens and Carson, 2002). Although we estimated rarity based on geographic spread rather than population density, as the cited studies do, our results support the idea that rare species are often lost regardless of their characteristics, both at the county level and within prairie species. This is consistent with other studies in New Zealand (Duncan and Young, 2000), rural and semi-urban grasslands in Australia (Williams et al., 2005), Minnesota grasslands (Suding et al., 2005), and the Balearic Islands (Lapiedra et al., 2015). However, some rare species may have been more likely to appear extinct due to observation error.

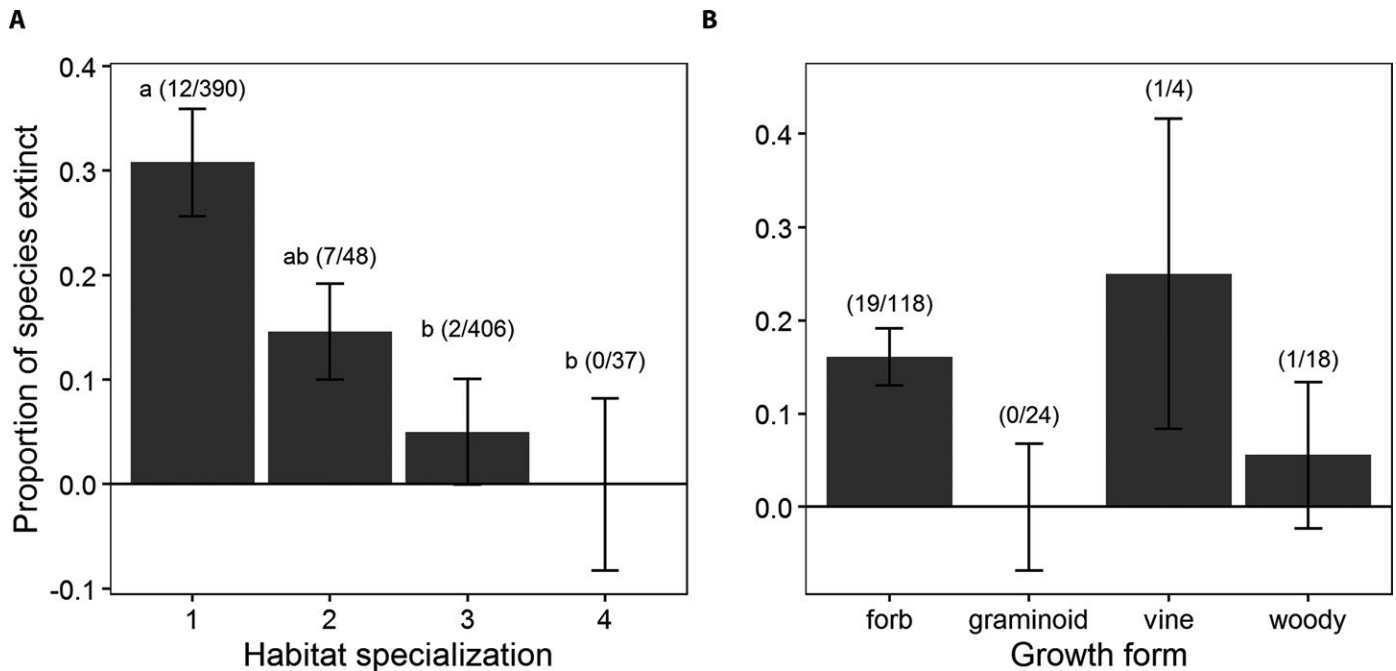


FIGURE 5. Proportion of prairie species (least square means \pm SE from the backwards elimination-generalized linear model for prairie species) that went locally extinct in Kalamazoo County, Michigan, USA, during 1890–1990 by (A) habitat specialization (number of habitat types occupied) and (B) growth form. Letters represent differences at the $\alpha = 0.05$ level. Values in parentheses represent the number of extinct species over the total number of species in that group.

Finally, species at the edge of their native range may be at higher risk of extinction, as found in Switzerland (Lienert et al., 2002) and New England (Farnsworth and Ogurcak, 2008). This may be because southwestern Michigan is at the edge of a floristic zone: it is both the northeastern-most edge of tallgrass prairie habitat and a climatic transition zone between northern oak–hickory forests and southern hardwood forests (McCann, 1979).

Species traits and extinction risk

Growth form also may influence extinction. Forbs and vines tend toward higher rates of loss than woody or graminoid species for both the county and prairie species. Forbs and low-growth forms also are more prone to loss in Wisconsin forests and grasslands, Britain, and Australia (Leach and Givnish, 1996; Blomqvist et al., 2003; Smart et al., 2005; Williams et al., 2005; Sjöström and Gross, 2006; Weigmann and Waller, 2006; Fréville et al., 2007; Saar et al., 2012), and vines had a higher probability of extinction over a 122-yr period in New York (Robinson et al., 1994) and in Brazilian rain forests (Leão et al., 2014). Meanwhile, graminoid and woody species tend to persist and/or increase in abundance (Robinson et al., 1994; Turner et al., 1996; Williams et al., 2005). In our study, the relationship between growth form and extinction disappeared when phylogenetic relationships were controlled for, likely due to the high phylogenetic conservatism of growth form. Although some of the above-cited studies considered phylogenetic patterns of extinction, many do not account for phylogenetic conservatism in their analyses, so the tendency for growth form to influence extinction should be investigated further (Leão et al., 2014). We also found that rare non-N-fixing species are at risk, but N-fixation and growth form are highly correlated traits and this association may reflect loss of forbs.

An avenue for future research in this system is to examine how the species traits associated with local extinctions compare to those of species introduced during the same time frame. Here, we do not examine species introductions because of the potential bias of missed species during the original surveys. However, the 1990s surveys report that >400 species are nonnative, and 133 species found in the 1990s may represent new invasions given that they were not reported in 1947, although they may have been missed during the original survey (McKenna, 2004). Comparing the functional traits of invasive versus extinct species would inform whether invasive species are replacing extinct species or filling a vacant niche in the invaded habitat, as functional diversity is predicted to either remain the same (Tecco et al., 2009) or decline with the extinction of local plant species and addition of invasive species (Carvalho and Castro, 2017).

Phylogenetic patterns of extinction

Phylogenetic patterns did not explain extinction of prairie species in Kalamazoo County. Fréville et al. (2007) and Fitzpatrick et al. (2008) detected no phylogenetic pattern to extinction in 93 species over 60 yrs and 100 species over 80 yrs, respectively; we similarly detect no phylogenetic pattern in 164 prairie species over ~100 yrs. It is possible that our failure to detect a phylogenetic signal in extinction risk resulted from small sample size and short time frame (most studies detecting phylogenetic signal exceed 500 species). However, extinction may show less phylogenetic signal if species are highly susceptible to a general driver of risk such as habitat loss (Fritz and Purvis, 2010; Daru et al., 2013) rather than to specific anthropogenic changes that might select against particular traits (e.g., nitrogen addition selecting against N-fixers; Suding et al., 2005),

although phylogenetic signals in extinction risk have been detected when habitat loss is suspected to be a primary driver of extinction in some cases (e.g., Schachat et al., 2016; Mankga and Yessoufou, 2017). Alternatively, the traits important to extinction in this area may not be phylogenetically conserved and may not be measured in this study. We find that several non-conserved traits related to species distribution, including rarity and habitat specialization, predict extinction in our dataset, which may explain the random phylogenetic pattern to extinction in Kalamazoo County.

CONCLUSIONS

Our results illustrate how historical collections can be used more extensively to examine patterns of regional and local species losses and to help identify species characteristics and traits associated with susceptibility to loss.

Given the susceptibility of prairie species to extinction and the likely importance of land-use change as an extinction driver in this region, restoration may be one mechanism to prevent further extinctions or even to reintroduce many of the extinct taxa in this region. Indeed, locally extinct species have been planted into restored prairies in Kalamazoo County. In a study of 29 prairies across southwest Michigan, eight extinct species were included in restoration seed mixes, and three of the eight (*Silphium laciniatum*, *S. terebinthinaceum*, and *Echinacea purpurea*) were able to establish in a substantial proportion of sites (7 of 13, 4 of 10, and 22 of 23, respectively; Grman et al., 2015). It remains to be seen whether the recent increase in prairie restoration will slow or reverse the declines of these taxa.

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AUTHOR CONTRIBUTIONS

M.A.Z. compiled the historical datasets and did all statistical and phylogenetic analyses. D.D.McK. collected the 1990s survey data and provided background on the historical datasets. J.A.L. helped formulate the questions and aided with analyses. M.A.Z. wrote the manuscript. All authors contributed to revisions.

DATA ACCESSIBILITY

All species, characteristic, and phylogenetic data for Kalamazoo County generated for this study are available as .csv files from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.231m570> (Zettlemoyer et al., 2019). Herbarium records accessed are available at Michigan Flora (<https://michiganflora.net>), species data were collected from USDA PLANTS (<https://plants.sc.egov.usda.gov/java/>), and the McKenna (2004) historical

records can be accessed at <https://quod.lib.umich.edu/cgi/p/pod/dod-idx/flora-and-vegetation-of-kalamazoo-county-michigan.pdf?c=mbot;idno=0497763.0043.301;format=pdf>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Plant community types.

APPENDIX S2. Chi-square tests of independence.

APPENDIX S3. Backwards elimination for Kalamazoo dataset.

APPENDIX S4. Multiple correspondence analysis dimensions.

APPENDIX S5. Multiple correspondence analysis results.

APPENDIX S6. Backwards elimination for prairie species dataset.

APPENDIX S7. Phylogenetic signal of species traits and characteristics.

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