Title: Herbarium specimens reveal regional patterns of tallgrass prairie invasion and changing species abundance across 130 years

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Summary

- The spread of non-native species is an acute threat to global biodiversity. However, a lack of long-term, spatially widespread occurrence data has prevented investigation of how multi-species invasions affect native assemblages.
- We harnessed >65,000 digitized herbarium specimens across 522 species to study how relative abundances of native and non-native species have changed since the 1890s in tallgrass prairies in three ecoregions of Missouri, USA. To validate specimen-based relative abundances against standardized field surveys, we compiled 65 paired field-herbarium datasets and tested whether native percent cover positively correlates with relative abundance of native specimens.
- Non-native species were more likely to have increased in the Interior Plain and Interior Highland ecoregions, while species that changed in abundance in the Atlantic Plain were more likely to have decreased regardless of native status. Native percent cover and relative abundance of native specimens were positively correlated and trends were robust to overall sample size through time.
- Our results support the use of herbarium specimens for investigating patterns of relative abundance shifts of native and non-native species. Specimen-based relative abundance shifts have scientific value for providing quick, taxonomically- and spatially-broad overviews of how non-native species have affected native assemblages, which can guide more precise, fine-scale investigations.

Keywords: collector bias; global change; grasslands; invasive species; museum records; natural history collections; prairie restoration; species-abundance distribution

Introduction

Biodiversity loss is threatening ecosystems worldwide, with human activity driving population declines and resultant local and global extinctions (Cardinale et al. 2012). Plants are a particularly threatened group, with 40% of species at risk of extinction (Antonelli et al. 2023). Among myriad anthropogenic drivers threatening plant diversity, the spread of non-native species is a critical stressor (Wilcove et al. 1998; Powell et al 2011). Over the past 200 years, the number of introductions has increased globally, with 37% occurring since 1970 (Seebens et al. 2017) and the number of established alien species projected to increase by 36% by 2050 (Seebens et al. 2021). The negative consequence of non-native species on native populations is often described as an abundance-impact relationship, where higher non-native abundance drives declines of native populations with greater magnitude (Bradley et al. 2019; Soafer et al. 2018). While this relationship indicates that the expansion of non-native species should decrease native abundance, we know comparatively little about how multi-species introductions affect native species assemblages at broad spatial scales and over long (multi-decadal) timescales.

Specimens from natural history collections offer the potential to fill this gap. Newly digitized specimens are revolutionizing global change research by providing long-term, global species occurrence data that can be used to track how species have changed through time (Davis 2023; Daru 2025; Iwanycki Ahlstrand et al. 2025). Indeed, herbarium specimens have already been extremely useful in documenting the effects of global change. Plant specimens collected since the 1800s have been used to document changes to flowering time (e.g., Davis et al. 2015), species range shifts (e.g., D'Andrea et al. 2009), and a variety of other responses such as plant diseases or plant-herbivore interactions (reviewed in Lavoie 2013; Soltis 2017; Meineke & Davies 2018; Meineke et al. 2018; Lang et al. 2019). It is estimated that as of 2024, the world's herbaria hold more than 396 million plant specimens (Thiers 2024), making herbaria well suited for investigating not only how individual species, but also entire assemblages, have changed through time (Austin et al. 2024). Accordingly, herbaria offer the potential to document the trajectory of multi-species introductions, their effect on native species assemblages, and how these patterns vary across space.

Despite their promise, patterns observed in herbarium specimens are subject to collector sampling preferences and online mobilization of specimens that can introduce biases (ter Steege et al. 2011; Meyer et al. 2016; Daru et al. 2018). As a result, validating herbarium-based estimates of assemblage patterns against those from the field is necessary to assess the effect of this bias. If herbarium specimens can be used to provide a coarse picture of how non-native and native species have changed in relative abundance through time, this work could guide future investigations into the consequences of species invasions at the local scale.

As one of the most endangered ecosystems in North America, tallgrass prairies are a vitally important system for investigating the impacts of non-native species expansion (Samson et al. 2004). Tallgrass prairies are the native grasslands of North America that occur at the eastern extent of the Great Plains, where precipitation, productivity, and species diversity are the highest (Rickletts 1999). Before European colonization, tallgrass prairies were maintained by indigenous peoples as well as by natural fires and grazing by bison and elk (Schroeder 1981). This system once covered over 160 million hectares, and since 1830, has declined in area by 82-99% (Samson & Knopf 1994). The decline is even more acute in certain areas, such as the state of Missouri, USA, which contained approximately 4.7 - 5.7 million hectares of prairie pre-settlement, and now less than 1% of that historic coverage remains (Schroeder 1981, Samson & Knopf 1994). Tallgrass prairies primarily declined due to land conversion to agriculture, with additional modern drivers threatening their long-term persistence (Leahy et al. 2020). Non-native plant species are primary among these contemporary threats to both remnant, and reconstructed prairies (Cully et al. 2003; Rowe 2013; Kaul & Wilsey 2021).

Missouri has a long history of human inhabitation, starting with the arrival of Native Americans 12-10 Kybp, followed by European exploration in the late 1600s, increasing European-derived immigration and farming from the 1800s onward, and eventually conversion to industrialized agriculture and animal husbandry from the mid-20th century. Since 1890, the statewide population has increased from ~2.6 to ~6.2 million (US Census Bureau 2025). While we cannot assess non-native spread by pre-colonial inhabitants, the past two centuries of human land use and disturbance provided many opportunities for non-natives to establish and spread.

In recent decades, there has been growing interest in prairie conservation and restoration, with land-management agencies, conservation organizations, and private landowners working to protect and restore remaining prairie remnants and reconstruct tallgrass prairie ecosystems across their range (Packard & Mutel 1997; Samson et al. 2004). In Missouri, reconstructed tallgrass prairies have been established throughout the state, but despite these efforts, it remains a threatened ecosystem due to continued land conversion, non-native species, climate change, nutrient deposition, and other factors (Nelson 2010, Newbold et al. 2019, Leahy et al. 2020). Long-term data on how the rise of non-native species have affected native prairie assemblages could be used to inform ongoing conservation efforts including where to prioritize conservation and restoration efforts, and helping to establish targets of native species for conservation efforts.

Here, we use herbarium specimens to explore how native and non-native species assemblages have changed in relative abundance across the past century in tallgrass prairies in Missouri, a state with a diverse prairie flora and long history of active collecting of herbarium specimens, especially since the founding of the Missouri Botanical Garden and its herbarium (MO) in 1859 (Steyermark & Yatskievych 1999). To accomplish this, we use a newly developed statistical method for quantifying relative abundance from natural history collections that handles biases introduced by uneven collection patterns from year-to-year (Gotelli et al. 2023). This method – validated across multiple taxa and locations – utilizes museum specimens to reconstruct relative abundance of target taxa (Gotelli et al. 2023). We use herbarium specimens to ask the following questions: (1) Are non-native species more likely to have increased over time in relative abundance than native species? (2) Do patterns of change in the relative abundance of native and non-native species vary between physiographic ecoregions? (3) Is relative abundance of native and non-native species derived from herbarium specimens consistent with percent cover data obtained from field surveys? Here, we use “relative abundance” to mean “abundance relative to other species” (versus, say, an index correlated with abundance of a focal species, regardless of abundances of other species). Our results suggest regional differences in the expansion of non-native species in Missouri prairies, and support the use of herbarium specimens for documenting coarse-scale patterns of invasion.

Materials and Methods

Study system

We restricted our study area to the state of Missouri, in the central USA, due to its abundance and accessibility of herbarium specimens, relatively long history of intensive botanical collection, and historic prairie coverage. The state is subdivided into three physiographic ecoregions (Missouri Geological Survey): (1) Interior Plain, (2) Interior Highland, and (3) Atlantic Plain (Fig. 1). Prior to European settlement of the region, prairies covered approximately one-third of Missouri, primarily the Interior Plain, and the western portion of the Interior Highland (Schroeder 1981). Only scattered locations of prairie occurred in the rest of the Interior Highland in south-central Missouri, and the Atlantic Plain in southeast Missouri.

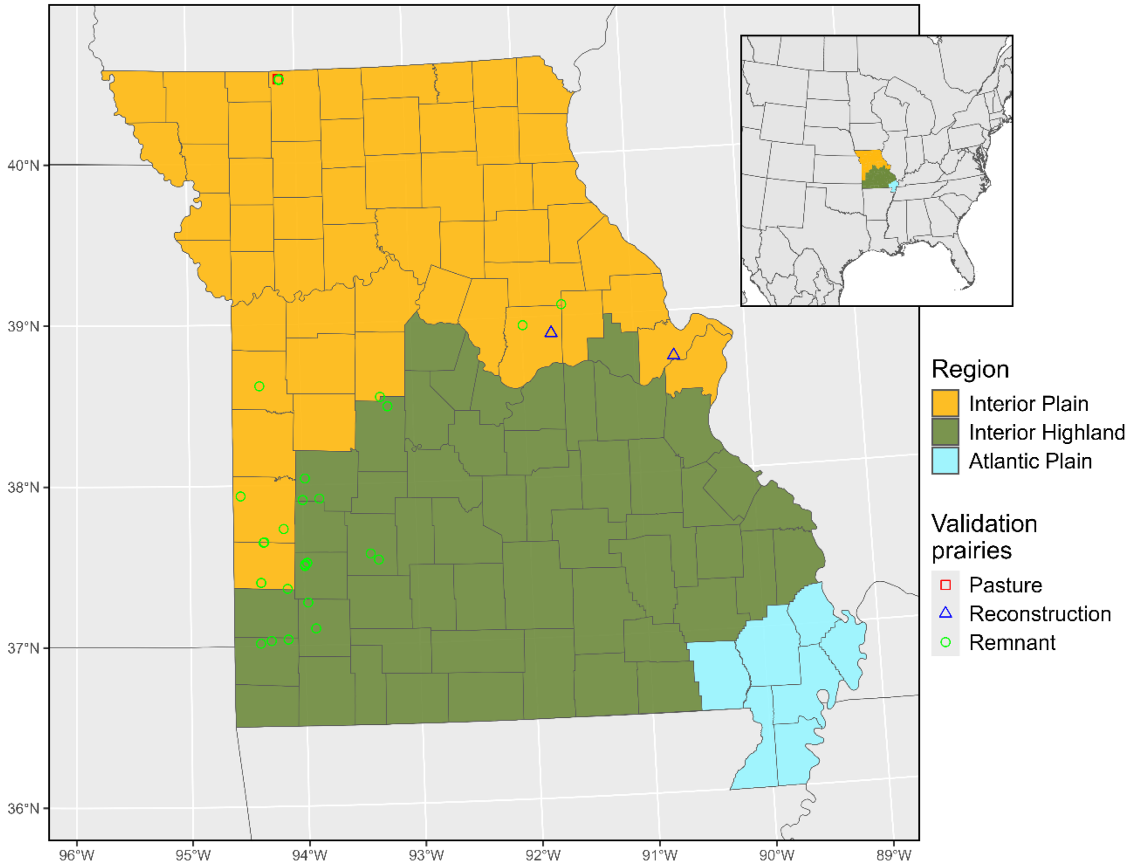

Figure 1. Physiographic regions of Missouri. Counties are colored according to the region in which the majority of the county occurs. Prairies used to validate specimen-based relative abundance given as points.

Data collection

We assembled a species list by compiling data from the Missouri Prairie Foundation (MPF) network on species occurrences across 22 remnant Missouri prairies (Missouri Prairie Foundation 2024). This list contained 847 species that were observed at least once across any site. To remove species that only occur sporadically in Missouri prairies, we restricted this list to species that occurred in $\geq$3 sites. We standardized names by matching species to a static copy of the World Flora Online (WFO) taxonomic backbone (WFO 2023) using the *WorldFlora* R package (Kindt 2020). This resulted in a final list of 536 species. We categorized each species as either native or non-native according to the ecological checklist of Missouri flora (Ladd & Thomas 2015). Accordingly, this list is a representative – but non-comprehensive – pool of species that occur in Missouri prairies, including native and non-native species, as well as habitat generalists. It is not a list of highly conservative indicator species of intact prairies.

We obtained specimen data for these species from Tropicos.org (2024), an online database maintained by the Missouri Botanical Garden (MO), which contains metadata on specimens from MO and non-MO institutions and constitutes one of the largest online repositories of primary plant data in the world (>7.47 million specimens as of May 2025). Prior to analysis, we subset these data to specimens that were collected in Missouri and have a recorded year of collection. We further subset these data to remove duplicate specimens by retaining only one specimen per unique combination of senior collector and collection number. The only exception to this were specimens lacking a collection number (i.e., ‘s.n.’), for which we did not attempt to remove duplicates.

To evaluate our ability to estimate trends in relative abundance from herbarium data, we obtained validation data from field estimates of abundance for these species, by combining datasets from surveys of 34 remnant and reconstructed Missouri prairies. Seventeen sites are MPF remnant prairie preserves (Missouri Prairie Foundation 2025), and the other seventeen were found in published research articles. Five sites (all remnants) are from Briggler et al. (2017), eight sites (two remnant; six reconstruction) are from Newbold et al. (2020), and four sites (two remnant; two reconstruction) are from Leahy et al. (2020) (Table S1). Each site documented by Briggler et al. (2017), was sampled in each year from 2005-2008 and each Leahy site was sampled in five different years spanning 1996-2017. Accordingly, our field data consist of 65 unique site-year combinations (hereafter referred to as unique field datasets; Table S1). The MPF, Newbold, and Leahy datasets consist of percent cover data, while the Briggler dataset consists of percent cover data divided into seven different cover classes. We matched each species in these field data to the WFO taxonomic backbone using the *WorldFlora* package (Kindt et al. 2020). Whenever multiple species within a unique field dataset matched to the same WFO ID, we took the sum of their percent cover data.

Testing for temporal shifts in species relative abundance

Temporal trends in native vs. non-native species: To examine species-level shifts in relative abundance across time, we first divided the specimen data into Missouri's three physiographic ecoregions. We accomplished this by assigning each specimen to one region based on its county of collection; when a county overlapped with multiple regions, we assigned the specimen to the physiographic region in which the majority of the county occurred. We further subdivided specimen data within each region into thirteen 10-year temporal bins ranging from 1891 to 2020 (i.e., bin 1: 1891-1900, bin 2: 1901-1910, etc.; cf. Booher et al. 2023). In each temporal bin of each physiographic region, we used the *gtools* package (Warnes et al. 2015) to estimate the relative abundance of each species with the Dirichlet distribution. Using the Dirichlet distribution to estimate relative abundance of species in biological collections has been recently demonstrated as a novel statistical approach that can estimate relative abundance while effectively accommodating biases present in opportunistically collected specimen data (Gotelli et al. 2023). As opposed to the frequentist approach of estimating relative abundance as $p = n/N$ – where n is the number of individuals of a given species and N is the total number of individuals across species – the Dirichlet distribution always estimates relative abundance as a non-zero value, even in periods with zero occurrence (Booher et al. 2023). For species with zero occurrences in a given period, the Dirichlet distribution accounts for sampling intensity by estimating relative abundance as a smaller value when the overall sample size across species is larger (Booher et al. 2023). By always returning a non-zero relative abundance estimate, this approach assumes no extinction or colonization (Booher et al. 2023).

We tested for long-term shifts in relative abundance by using the *betareg* package (Cribari-Neto & Zeileis 2010) to run a beta-regression for each species in each physiographic region, which set the minimum year of each bin as the predictor and estimated relative abundance as the response. These analyses estimated relative abundance by taking the abundance of each species relative to the sum of abundances of the all taxa in our species list. To evaluate whether estimates of temporal shifts in relative abundance are affected by the size of the species pool (Ries et al. 2019; Wepprich 2019), we repeated these analyses by taking the abundance of each species in our species list relative to the sum of abundances of all plant specimen data in Tropicos collected from Missouri.

Temporal trends in community-abundance distributions: To analyze species evenness and changes to community structure over time, we also evaluated shifts in relative abundance at the community level by examining shifts in rank-abundance distributions (RADs) within each ecoregion and decade across native, non-native, and all species. Among the broken stick, geometric, lognormal, Zipf, and Zipf-Mandelbrot models, we selected the best fitting model using AIC evaluated with the radfit function in the *vegan* package version 2.6-10 (Oksanen et al. 2025) for R (R Core Team 2024).

Testing for temporal shifts in relative abundance of native specimens

In addition to testing for temporal changes to species-level relative abundance, we tested for changes to the abundance of native specimens relative to non-native specimens, while being agnostic to species identity. Similar to the species-level analysis, we accomplished this by first dividing specimen data into each physiographic ecoregion and then subdividing the data into thirteen 10-year bins from 1891 to 2020. In each temporal bin of each region, we calculated the relative abundance of native specimens relative to all specimens using the Dirichlet distribution. To test for long-term shifts in the relative abundance of native specimens, we then ran a beta-regression for each physiographic region, which set the minimum year of each bin as the predictor and the estimated relative abundance of native specimens as the response. Accordingly, this analysis tests whether specimen data reveal coarse patterns of non-native plant expansion across species, when not accounting for taxonomic identity.

Phylogenetic signal

We tested whether relative abundance shifts exhibit statistical dependency on phylogenetic relationships by assessing species-level beta-regression slopes for phylogenetic signal, regardless of native/non-native status. To accomplish this, we tested for phylogenetic signal in each physiographic region using Blomberg's *K* (Blomberg et al. 2003) via the phylosig function in the *phytools* package (Revell 2012). Blomberg's *K* follows a Brownian motion model of character evolution; $K = 1$ indicates that a trait is statistically dependent on phylogenetic relationships, $K = 0$ indicates that a trait is not statistically dependent on phylogeny. To determine the statistical significance of *K*, we compared the observed *K* to 10,000 *K* values simulated from 10,000 randomizations. We used the GBOTB.extended.WP.tre plant megatree (Jin & Qian 2019, 2022) pruned to our species list for all phylogenetic signal analyses.

Correspondence between specimen data and field surveys

We tested for correspondence between specimen data and field surveys using two methods. The first method tested whether rank abundances derived from specimen data positively correlate with rank abundances derived from field surveys. To accomplish this, we grouped specimen data into the thirteen 10-year temporal bins per physiographic region, as described above. We then paired each field dataset with the thirteen temporal bins from the physiographic region in which the field site occurred. For each field dataset, we calculated the Spearman rank correlation coefficient (ρ) between the rank abundances of species from the field and specimen data. As a proxy for the correspondence between field and specimen data in each temporal bin, we calculated the mean ρ across sites separately for remnant and reconstructed prairies. Calculating ρ for every paired field-herbarium dataset across all temporal bins allows us to test whether reconstructed sites show greater correspondence to contemporary specimen data and whether remnant sites show greater correspondence to historic specimen data.

The second method tested for a correlation between the proportion of native specimens and the proportion of native plant cover across field sites. For this analysis, we paired each field dataset with the specimen data in the temporal bin and physiographic region in which the field sampling occurred. We then used the Dirichlet distribution to estimate the relative abundance of native specimens, while being agnostic to species identity. We calculated the proportion of native plant cover in each field dataset by taking the sum of percent cover data across native species. We then ran a linear regression that tested whether the proportion of native plant cover predicts the relative abundance of native specimens. Prior to analysis, we logit transformed the proportion of native plant cover and the relative abundance of native specimens. The field sites derived from Briggler et al. (2017) use percent cover classes, instead of raw percent cover data. Accordingly, we removed the Briggler sites from this analysis.

Evaluating collector bias

Native vs. non-native species: We evaluated whether any collectors in our specimen dataset exhibited biases toward collecting or avoiding non-native species. To accomplish this, we used the glmer function from the *lme4* package (Bates et al. 2015) to run a general linear mixed effects model with a logit link function, where the response was a binary variable indicating a specimen's native status (1 = native, 0 = non-native). We set collection year – centered and scaled – as a fixed effect, and collector as a random intercept and random slope. We considered a collector to have potentially exhibited collection biases if the 95% CI of their random intercept and/or slope did not overlap with 0. We restricted this model to collectors with a minimum of 100 specimens to ensure reliable estimation of random effects for all collectors included in the model.

Temporal trends in native vs. non-native species: We also evaluated the effect of artifacts arising from the total number of specimens collected in each region and decade by repeating analysis of abundances using a subsampling procedure. Specifically, we first calculated the total number of specimens in each decade in each physiographic ecoregion and then quantified the lower 10th quantile across decades and ecoregions, which we selected because smaller quantiles (especially for the Atlantic Plain) would have resulted in very small communities. We subsequently iterated the beta-regression analyses for each ecoregion and decade 1,000 times, with the specimens randomly sampled to the sample size of the 10th quantile prior to analysis. If the sample size of a decade was already smaller than the 10th quantile, we did not subsample the decade. As with the observed dataset, we evaluated trends in the increase or decrease in native versus non-native species.

Temporal trends in species-abundance distributions: To assess how the analysis of best-fit RAD model may have been influenced by the total number of specimens collected in each ecoregion and decade, we identified the best-fit RAD model for each of the subsampled datasets.

The proportion of times each RAD model was selected was tallied, and compared to the observed best-fit RAD model.

Reproducibility

All analyses were conducted in R version 4.3.1 (R Core Team 2024).

Results

Species sampling

Specimen data were available for 522 of the 536 species on our species list. Of these 522 species, 89.8% (n = 469) are native and the remainder 10.2% (n = 53) are non-native to Missouri. Percentages within each ecoregion are very similar (~90% native, ~10% non-native). After filtering the specimen data to remove duplicates and restrict to specimens collected from Missouri with a recorded year of collection, we had a total of 65,920 specimens that we used in downstream analysis. Across ecoregions, collection effort generally increased across decades (Fig. S1).

Temporal shifts in species relative abundance

Temporal trends in native vs. non-native species: We observed regional differences in changes to the relative abundance of native and non-native species in Missouri from 1891 to 2020. In the Interior Plain and Interior Highland, non-native species are more likely to have increased in relative abundance than native species; 31.4% and 20.4% of non-native species have significantly increased in relative abundance in the Interior Plain and Interior Highland respectively, compared to 12.5% and 13.4% of native species (Table 1; Fig. 2A,B). Similarly, native species are more likely to have significantly declined in these regions than non-native species; 9.8% and 14.2% of native species have declined in the Interior Plain and Interior Highland respectively, compared to 5.9% and 4.1% of non-native species (Table 1; Fig. 2A,B). In the Interior Plain, 77.7% of native and 62.7% of non-native species have not significantly changed relative abundance (Table 1). In the Interior Highland, 72.4% of native and 75.5% of non-native species have not significantly changed relative abundance (Table 1).

Table 1. Beta-regression results giving the number and percent of species exhibiting significant and non-significant changes to relative abundance from 1891 to 2020. Integers give the number of species; percentages are in parentheses.

Region	Total number species		Number species significantly increasing		Number species significantly decreasing		Number species no significant change	
	Native	Non-Native	Native	Non-Native	Native	Non-Native	Native	Non-Native
Interior Plain	448	51	56 (12.5%)	16 (31.4%)	44 (9.8%)	3 (5.9%)	348 (77.7%)	32 (62.7%)
Interior Highland	463	49	62 (13.4%)	10 (20.4%)	66 (14.2%)	2 (4.1%)	335 (72.4%)	37 (75.5%)
Atlantic Plain	355	44	14 (3.9%)	1 (2.3%)	51 (14.4%)	5 (11.4%)	290 (81.7%)	38 (86.4%)

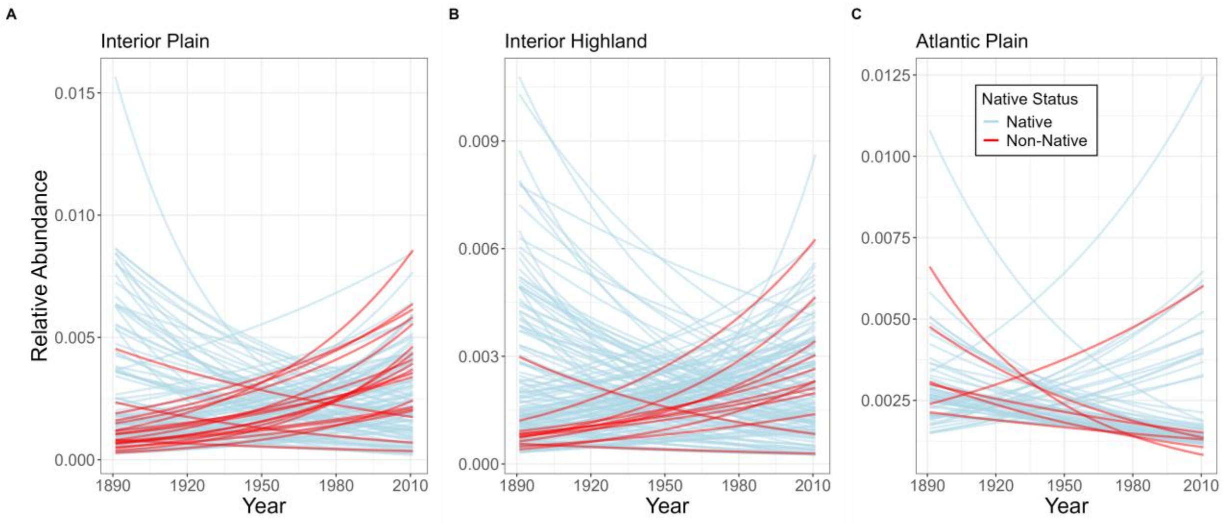

Figure 2. Significant shifts ($P < 0.05$) in species relative abundance through time in each physiographic region: (A) Interior Plain, (B) Interior Highland, (C) Atlantic Plain. Each line represents a species. Trendlines for species with non-significant changes are not shown.

In contrast, the Atlantic Plain is characterized by prairie species being more than three times as likely to have significantly decreased in relative abundance than to have significantly increased in relative abundance, regardless of native status. In this region, 14.4% of native species and 11.4% of non-native species have significantly decreased in relative abundance, compared to 3.9% and 2.3% respectively that have significantly increased (Table 1; Fig. 2C); 81.7% of native species and 86.4% of non-native species have not significantly changed relative abundance in the Atlantic Plain. Note that both native and non-native species can be more likely to have significantly decreased in this region, than to have significantly increased, if a substantial number of other prairie species exhibited non-significant increases in relative abundance or a few species experience very large, significant increases.

Echinochloa crus-galli (barnyard grass) – the only non-native species to have significantly increased in the Atlantic Plain – has also significantly increased in the Interior Plain and Interior Highland (Fig. 3). Seven additional non-native species have also significantly increased in both the Interior Plain and Interior Highland: *Arenaria serpyllifolia* (thyme-leaved sandwort), *Barbarea vulgaris* (yellow rocketcress), *Commelina communis* (common dayflower), *Hypericum perforatum* (common St John's wort), *Lespedeza cuneata* (Chinese bushclover), *Rosa multiflora* (multiflora rose), and *Setaria faberi* (giant foxtail grass) (Fig. 3A,B). No non-native species have significantly decreased in all three physiographic regions.

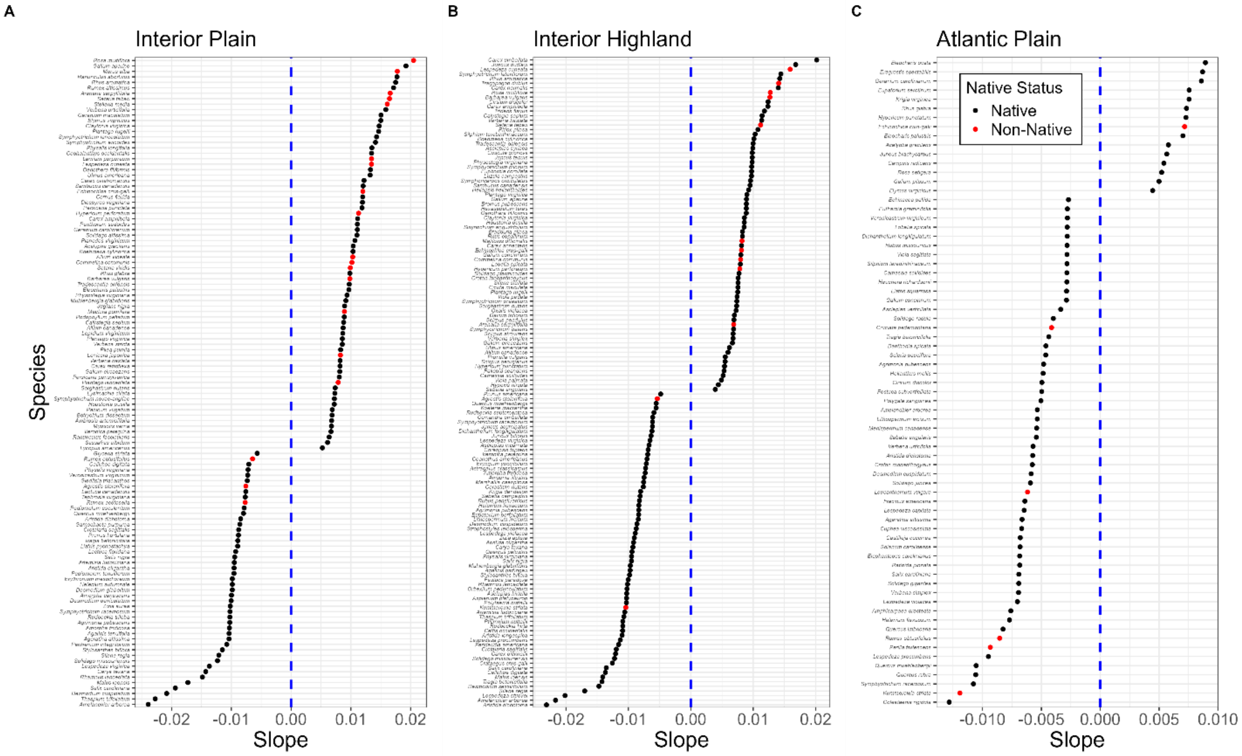

Figure 3. Beta-regression slopes of species exhibiting significant ($P < 0.05$) changes to relative abundance through time in each physiographic region: (A) Interior Plain, (B) Interior Highland, (C) Atlantic Plain. Positive values indicate increases in relative abundance; negative values indicate decreases in relative abundance. Red dots indicate non-native species.

Eight native species have significantly decreased in all three physiographic regions: *Agrimonia pubescens* (soft agrimony), *Amelanchier arborea* (shadbush), *Aristida dichotoma* (churchmouse three-awn grass), *Desmodium cuspidatum* (bracted tick trefoil), *Quercus muehlenbergii* (Chinkapin oak), *Salix caroliniana* (Ward's willow), *Symphyotrichum racemosum* (small white aster), and *Tragia betonicifolia* (noseburn) (Fig. 3). In contrast, no native species have significantly increased in all three physiographic regions.

Regional differences in changes to the relative abundance of native and non-native species are robust to the different methods of defining the species pool. When standardizing abundance estimates against all plant specimen data, the Interior Plain and Interior Highland are still characterized by non-native species being more likely to have increased in relative abundance than native species, while the Atlantic Plain is still characterized by prairie species being more likely to have significantly decreased in relative abundance than to have significantly increased in relative abundance, regardless of native status (Figs. S2 & S3).

Temporal trends in species-abundance distributions: The most parsimonious RAD model varied by ecoregion, decade, and type of species (native, non-native, or all combined; Fig. 4). The best models for native species and all species combined were nearly always the same, with the Zipf-Mandelbrot model strongly favored for both with most exceptions occurring in the Atlantic Plain where occasionally the Zipf distribution was more parsimonious. For non-native species, there was a general temporal trend in the best model within ecoregions. Within the Atlantic Plain, the Zipf distribution was best until the 1960s, after which it generally alternated with the Zipf-Mandelbrot distribution. Within the Interior Highlands, the Zipf-Mandelbrot was initially strongly favored, switching to the lognormal in the 1970s. A similar pattern was observed within the Interior Plain.

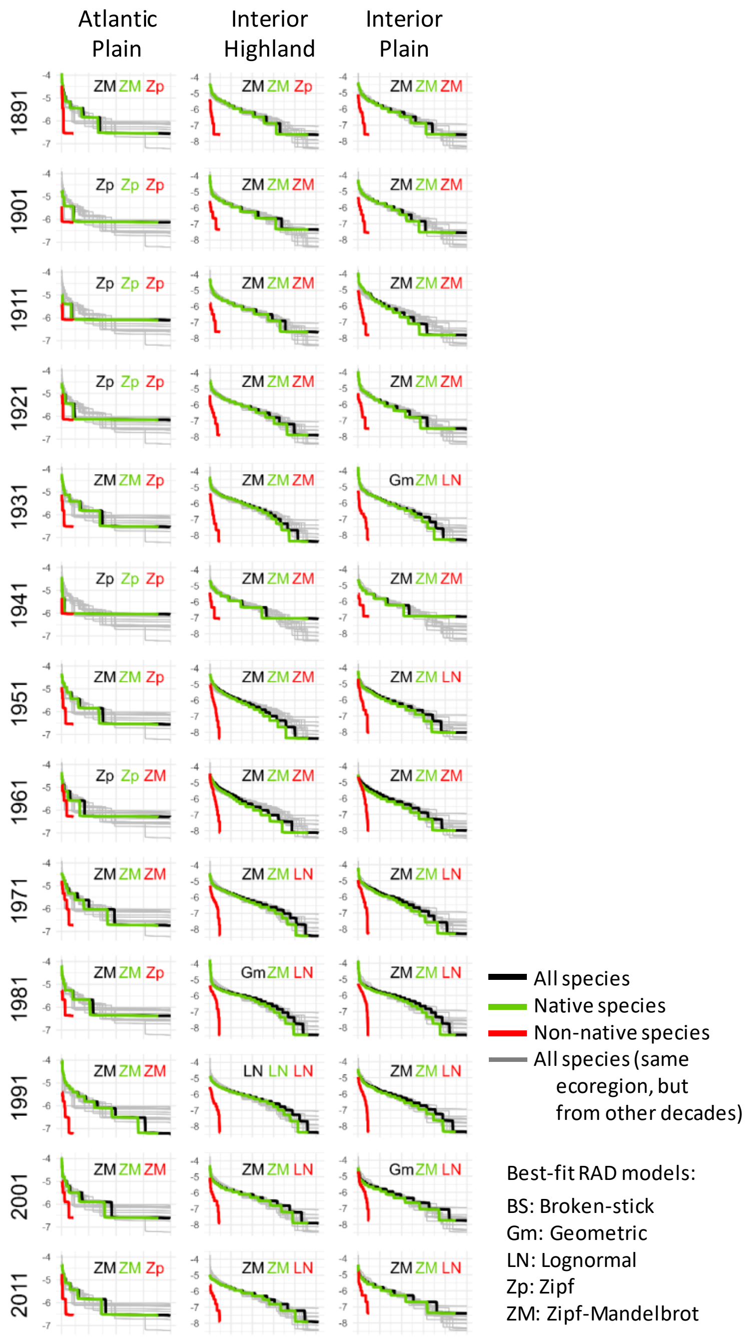

Figure 4. Rank-abundance distributions (RADs) for each ecoregion, decade, and type of species (natives, non-natives, and all combined). In each panel, the *x*-axis is species' rank (from most to least abundant from left to right) and the *y*-axis the $\log_{10}$ of relative abundance. The most parsimonious RAD model is indicated in each panel by colored letters corresponding to each species type. To aid visual comparison, the RADs for all species combined within the given ecoregion across all decades are plotted in gray.

Temporal shifts in relative abundance of native specimens

The abundance of native relative to non-native specimens has significantly decreased through time in the Interior Plain (beta regression between time period and total native relative abundance: $P < 0.0005$) and Interior Highland ($P < 0.05$), but has not significantly changed through time in the Atlantic Plain ($P = 0.26$) (Fig. 5). This suggests regional differences in the expansion of non-native prairie plants across the 20th century, with the Interior Plain and Interior Highland – but not the Atlantic Plain – being characterized by increases in non-native plant abundance.

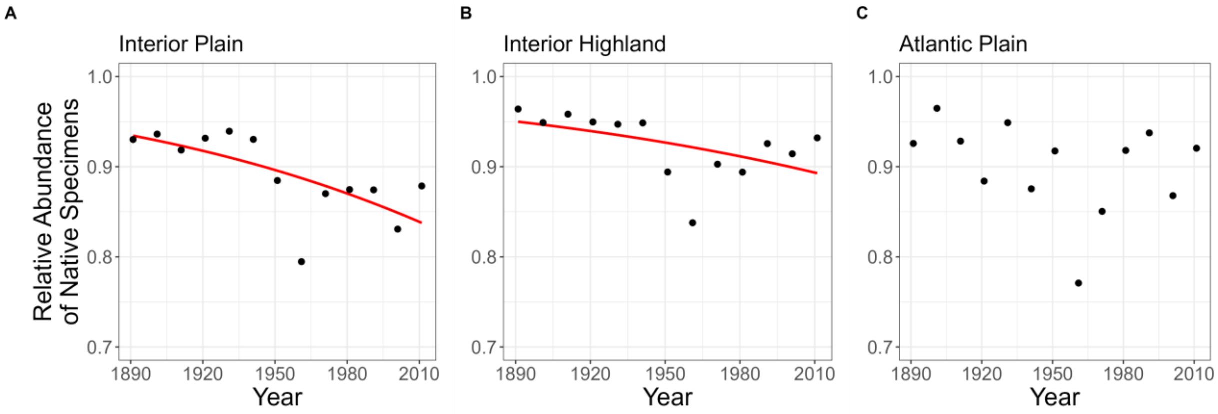

Figure 5. Change to relative abundance of all native specimens combined through time in each physiographic region: (A) Interior Plain, (B) Interior Highland, (C) Atlantic Plain. Red lines give significant beta-regression trends ($P < 0.05$). Non-natives abundances are the complement of the values shown.

Phylogenetic signal

Species-level beta-regression slopes did not exhibit phylogenetic signal in any physiographic ecoregion (all $K < 0.004$ and $P > 0.35$). This suggests that changes to relative abundance across the past century are not dependent on phylogenetic relationships for species in Missouri prairies.

Correspondence between specimen data and field surveys

The majority of mean ρ values were modestly positive, suggesting a weak correspondence between rank abundances derived from specimen and field data (Fig. 6). There was no apparent effect of decade or site type on mean ρ values, suggesting that reconstructed and remnant sites do not show greater correspondence to contemporary and historic specimen data, respectively.

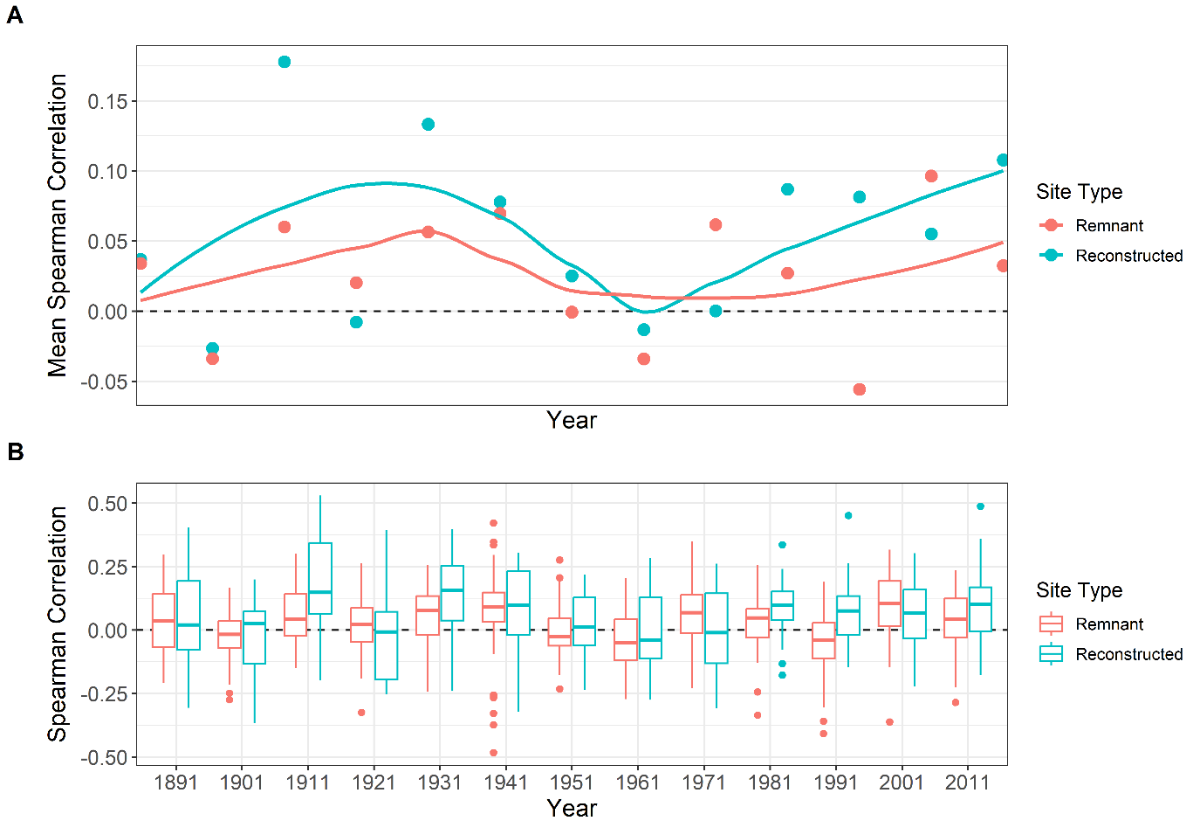

Figure 6. Spearman correlation coefficients (ρ) of paired field-herbarium datasets across temporal bins. (A) Mean spearman correlation coefficients. Lines give loess curves for remnant and restored sites separately. (B) Raw Spearman correlation coefficients. Remnant (red) and reconstructed (blue) sites shown separately.

There was a significant positive association ($P < 0.005$; slope = 0.065; $R^2 = 0.175$) between the logit transformed proportion of native specimens and proportion of native plant cover from field surveys (Figs. 7 & S4). This suggests that – when being agnostic to species identity – sites with a greater proportion of native percent cover generally correspond to herbarium data with a greater proportion of native specimens. Accordingly, species relative abundance based on herbarium specimens generally gives a reasonable first approximation of the abundance of species in the field.

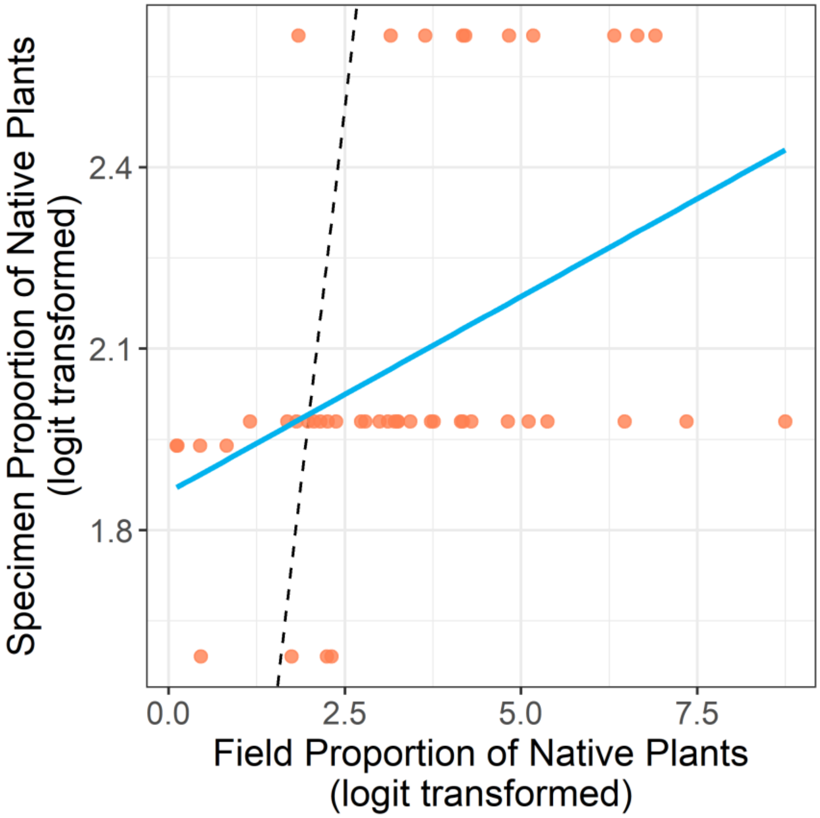

Figure 7. Correspondence between the proportion of native specimens and the proportion of native percent cover from field surveys. Each point is a paired field-herbarium dataset following logit transformation. The dashed black line is a one-to-one line; the solid blue line is the regression line ($P < 0.005$; slope = 0.065).

Collector biases

Native vs. non-native species: We found evidence of collection biases for 18 collectors in our specimen dataset (out of 103 collectors who collected $\geq$100 specimens; 17.5%), based on the 95% CI of their random effect for the intercept and/or slope not overlapping with 0 (Fig. S5). Together, these collectors account for 34.2% of our specimen data (22,574 specimens). Of these collectors, the random effect for the intercept was negative for 10 and positive for 6 collectors, which indicate baseline biases toward collecting non-natives or natives respectively. Additionally, the random effect for the slope was negative for 2 and positive for 3 collectors, which indicate temporal shifts toward collecting non-natives or natives respectively, which deviate from the overall trend across collectors. When re-running our analysis of temporal shifts in species relative abundance with these 18 collectors removed, we still find the same qualitative results; i.e., non-native species are more likely to have increased in relative abundance than native species in the Interior Plain and Interior Highland, while prairie species are more likely to have significantly decreased in relative abundance, regardless of native status, in the Atlantic Plain (Figs. S6 & S7). This suggests that the biases of these 18 collectors did not affect our results.

Temporal trends in native vs. non-native species: The subsampling analyses revealed comparable results to temporal trends observed in the full data. When subsampling each decade per ecoregion to the lower 10th quantile sample size (n = 117 specimens), non-native species in the Interior Plain and Interior Highland are more likely to have significantly increased in relative abundance than to have significantly decreased, while native species are roughly equally likely to have significantly increased or decreased (Fig. S8A,B). In the Atlantic Plain, both native and non-native species are still characterized by being more likely to have significantly decreased than to have significantly increased in relative abundance (Fig. S8C).

Temporal trends in community-abundance distributions: For native and all species in each ecoregion, the observed most parsimonious RAD model matched the one most commonly selected across the 1,000 subsamples in most cases, ranging from matches in 9 to 13 of 13 decades (Table S2). In the Atlantic Plain, non-native observed RAD also matched the most commonly selected RAD among the samples in 11 of 13 decades. However, among the Interior Plain and Interior Highland, match rates were low, with only 1 or 2 decades showing a match, respectively. Within these ecoregions, the Zipf RAD was most commonly selected across subsamples.

Discussion

Harnessing >65,000 specimens across 522 species collected over a 130-yr timespan, we find evidence of regional changes to the relative abundance of native and non-native species which characterize the flora of tallgrass prairies in Missouri. Non-native species were more likely than natives to have increased in relative abundance in the Interior Plain and Interior Highland, while native and non-native prairie species tended to decline in the Atlantic Plain regardless of native status (Figs. 2 & 3). These patterns were corroborated by the change in relative abundance of native specimens in each ecoregion agnostic to species identity (Fig. 5). Comparisons between herbarium-derived and field-based abundances support the use of herbarium specimens for investigating coarse patterns of how the expansion of non-native species have affected native assemblages. In an age where non-native species are continuing to be introduced, become established, and spread across the globe (Seebens et al. 2017, 2021), it is critical to document how multi-species introductions affect native species assemblages across large spatial scales.

We found that trends in native versus non-native abundance varied across ecoregions. The Interior Plain and Interior Highland are characterized by increasing non-native species abundance, while the Atlantic Plain is characterized by declines in both native and non-native prairie species, trends that correspond with historic prairie coverage in the state. Namely, the tallgrass prairie that occurred in Missouri prior to European settlement was concentrated in the Interior Plain and the western portion of the Interior Highland, while the Atlantic Plain has historically been dominated by cypress swamp (Schroeder 1981). This suggests that across the past century, non-native prairie species abundance has tended to increase in areas historically suited for prairie growth, regardless of whether prairies in those regions have since been cleared due to changes in land use (e.g., agriculture, urbanization). In contrast, the physiographic characteristics of the Atlantic Plain appear to have not supported spread of prairie species, even those that are non-native and may have a competitive edge over their native prairie counterparts.

Certain species showed consistent responses across ecoregions. Some common and aggressive invasive species – such as multiflora rose (*Rosa multiflora*) and Chinese bushclover (*Lespedeza cuneata*) – increased in both the Interior Plain and Interior Highland, consistent with their known impacts on North American tallgrass prairies (Evans 1983, Ohlenbusch 2007). Barnyard grass (*Echinochloa crus-galli*) – a particularly noxious weed, which poses a serious agricultural threat due to evolved herbicide resistance (Bajwa et al. 2015) – was the only native or non-native species found to have significantly increased in all three ecoregions. These consistent increases in the relative abundance of known invasive species suggests that herbarium specimens may be used to identify species that are becoming problematically invasive, but whose impact may not yet be fully realized. Conversely, by revealing native species that have consistently decreased in relative abundance across ecoregions (e.g., bracted tick trefoil (*Desmodium cuspidatum*), Chinkapin oak (*Quercus muehlenbergii*), Ward's willow (*Salix caroliniana*)) it might be possible to use herbarium specimens as early warning indicators for native population declines. It would be informative to further investigate the native species that exhibited consistent decreases in relative abundance, to determine if these decreases are indicative of a broader threat to long-term stability of these species.

The distributions of abundances of species are the product of all of the factors shaping communities, including environmental filtering and biotic interactions, random fluctuations of population size, dispersal, and extirpation (Vellend 2010). Across 130 years, the most parsimonious rank-abundance distribution (RAD) model varied by ecoregion, decade, and type of species (native, non-native, and all combined), but displayed some notable temporal trends indicative of a changing community. RADs for natives and all species together were generally best-described by the Zipf and Zipf-Mandelbrot models, in which a few species dominate community abundance and the others are very rare. These distributions are generally indicative of communities experiencing disturbance and/or transition (Magurran 2004; McGill et al. 2007). Since European-derived settlers arrived, prairies have indeed undergone dramatic change from transformation to agricultural lands, fire suppression, and loss of changes in herbivore presence and identity, and invasion. Concurrently, the non-native species in the Interior Highland and Interior Plain have transitioned from the Zipf to a lognormal distribution, in which most species have "intermediate" abundance (but are still not common), which is associated with more "mature" communities (Magurran 2004; McGill et al. 2007). Trends in non-native community abundance distributions in the Interior Highland and Interior Plain were more susceptible to sampling biases, however (Table S2), so this temporal trend in best-fit RAD should only be interpreted provisionally. Overall, patterns in the shape of the RADs agree with expectations we have for this highly disturbed flora.

Despite finding that non-natives are increasing relative to natives in large portions of the state, prairies overall seem to be less colonized by non-natives than ecosystems across the state as a whole. At the state level, the second edition of the *Steyermark's Flora of Missouri* (Yatskievych 1999) lists ~3,000 native or naturalized species, of which approximately one-third are non-native. In contrast, only 10% of the 522 prairie-related species for which we could find specimens were non-native. This discrepancy could be due in part to our data filters. For example, we did not include species occurring in fewer than three remnant sites, and given that most species are rare, this may have excluded many non-natives. However, this filter would have excluded very rare native prairie species, as well. Potential biases notwithstanding, the relatively low prevalence of non-natives in prairies compared to the state at large is rather remarkable, given that tallgrass prairies have been one of the most exploited and diminished in areal extent. The reasons for this deserve further inquiry, but may be related to differences in the rate of arrival and introduction (i.e., propagule pressure; Simberloff 2009) of non-native prairie species versus those favoring other Missouri ecosystems, the retarding effect of high native diversity on establishment and spread of non-natives (Cheng et al. 2024), and interplay with fire and large herbivores (which were once prominent but now diminished) (Andersen 2006). In contrast, perhaps other ecosystems in Missouri are more easily colonized by non-natives and are more interdispersed with human population centers and their associated non-native plants species, especially concentrations of ornamental plants.

This study is one of the first to compare relative abundance of species in natural history collections to their abundance in paired field datasets. Notably, the positive correlation revealed between the relative proportion of native plant cover and the relative abundance of native specimens (Fig. 7) is consistent with other studies that have found positive correlations between specimen- and field-based relative abundances across taxa (Gotelli et al. 2023; Booher et al. 2023). Collectively, this work supports using curated natural history collections for estimating species relative abundance, at least when aggregating specimen records at coarse spatial scales. When pursuing this work, it is important to be mindful of biases in digitized specimen records, which are inherent in natural history collection data due to collector preferences and collections that are not completely digitized (Marcer et al. 2022; Daru et al. 2018). Such biases have been found to cause very rare species to be overrepresented in museum collections, and very common species to be underrepresented in museum collections. Use of the Dirichlet distribution for estimating relative abundance – which we employed here – can help account for such biases but not eliminate them (Gotelli et al. 2023). We found evidence of bias in the collection of native versus non-native species for 18 collectors in the specimen dataset (Fig. S5). Notably, however, after removing these collectors and rerunning analysis of how species relative abundances have changed through time, the same qualitative results are found as when including these collectors in analysis (Figs. S6 & S7).

Beyond collector biases, there are additional artifacts of specimen data that may affect estimates of specimen-based relative abundance. One of these is uneven collection intensity across time. We found that collection intensity has generally increased across decades, albeit with considerable variance across decades and ecoregions (Fig. S1). However, our subsampling analyses reveal that the same qualitative patterns of change in the relative abundance of native and non-native species are found when collection intensity is similar across decades, as when using the full dataset (Fig. S8). We also found that the analyses at the species-level (Figs. 2 & 3), and those that are agnostic to species identity (Fig. 5), both reveal the same qualitative patterns of how non-native and native species have changed in relative abundance through time. Collectively, these results support the use of the Dirichlet distribution for estimating relative abundance from specimen records, which can then be used for testing how relative abundances have changed through time. Accordingly, this study suggests that natural history collections can be used to document coarse spatiotemporal patterns of how multi-species introductions have affected native species assemblages.

Although our findings are largely consistent with overall global trends of increases in non-native species at the expense of native species, the unstandardized nature of specimen collection makes estimation of trends from them inherently imprecise. Rather than accepting estimates of specimen-based relative abundance shifts at face value, we encourage scientists to view this technique as another tool in their methodological toolbelt. That is, specimen-based estimates provide a quick, taxonomically- and spatially-broad overview of how changes to non-native species abundance have affected native assemblages. These fast, coarse analyses can then be used to identify species and regions that warrant further investigation using more standardized types of field-based data. For example, we found that it would be informative to investigate how control of the non-native barnyard grass (*E. crus-galli*) in reconstructed prairies in the Interior Plain and Interior Highland affect native species diversity, and whether mitigation techniques might vary between these regions and the Atlantic Plain. Likewise, prairies in the Atlantic Plain may need special conservation attention, as they were historically rare and remain rare, and thus prone to suffer attrition of both native and non-native species (Fig. 3C). As native species continue to be threatened by anthropogenic global change, it is increasingly important to harness natural history collections as sources of long-term data that can be used to study how multi-species assemblages have changed through time.

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Author Contributions

M.W.A. – Conceptualization, Methodology, Data collection, Data curation, Formal analysis, Writing (original draft), Writing (review & editing)

A.D.K. – Conceptualization, Methodology, Data collection, Data curation, Formal analysis, Writing (review & editing)

A.B.S. – Conceptualization, Methodology, Data curation, Formal analysis, Writing (review & editing)

M.R. – Conceptualization, Methodology, Data collection, Data curation, Writing (review & editing)

R.B.P. – Conceptualization, Methodology, Data collection, Writing (review & editing)

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Supporting Information

Title: Herbarium specimens reveal regional patterns of tallgrass prairie invasion and changing species abundance across 130 years

Authors: Matthew W. Austin, Andrew D. Kaul, Adam B. Smith, Matthew Rothendler, Richard B. Primack

The following Supporting Information is available for this article:

Fig. S1. Sample size per decade in each of the three physiographic ecoregions.

Fig. S2. Significant species-level shifts when standardizing to all plant specimen data.

Fig. S3. Significant beta-regression slopes when standardizing to all plant specimen data.

Fig. S4. Correspondence between specimen and field data, using raw non-logit transformed data.

Fig. S5. Random effects for intercepts and slopes of collectors.

Fig. S6. Significant species-level shifts when removing biased collectors.

Fig. S7. Significant beta-regression slopes when removing biased collectors.

Fig. S8. Percent of species exhibiting significant changes to relative abundance following an iterative subsampling procedure.

Table S1. The 65 unique site-year combinations compiled from field surveys of 34 remnant and restored Missouri prairies.

Table S2. Rank-abundance model fits to subsampled communities.

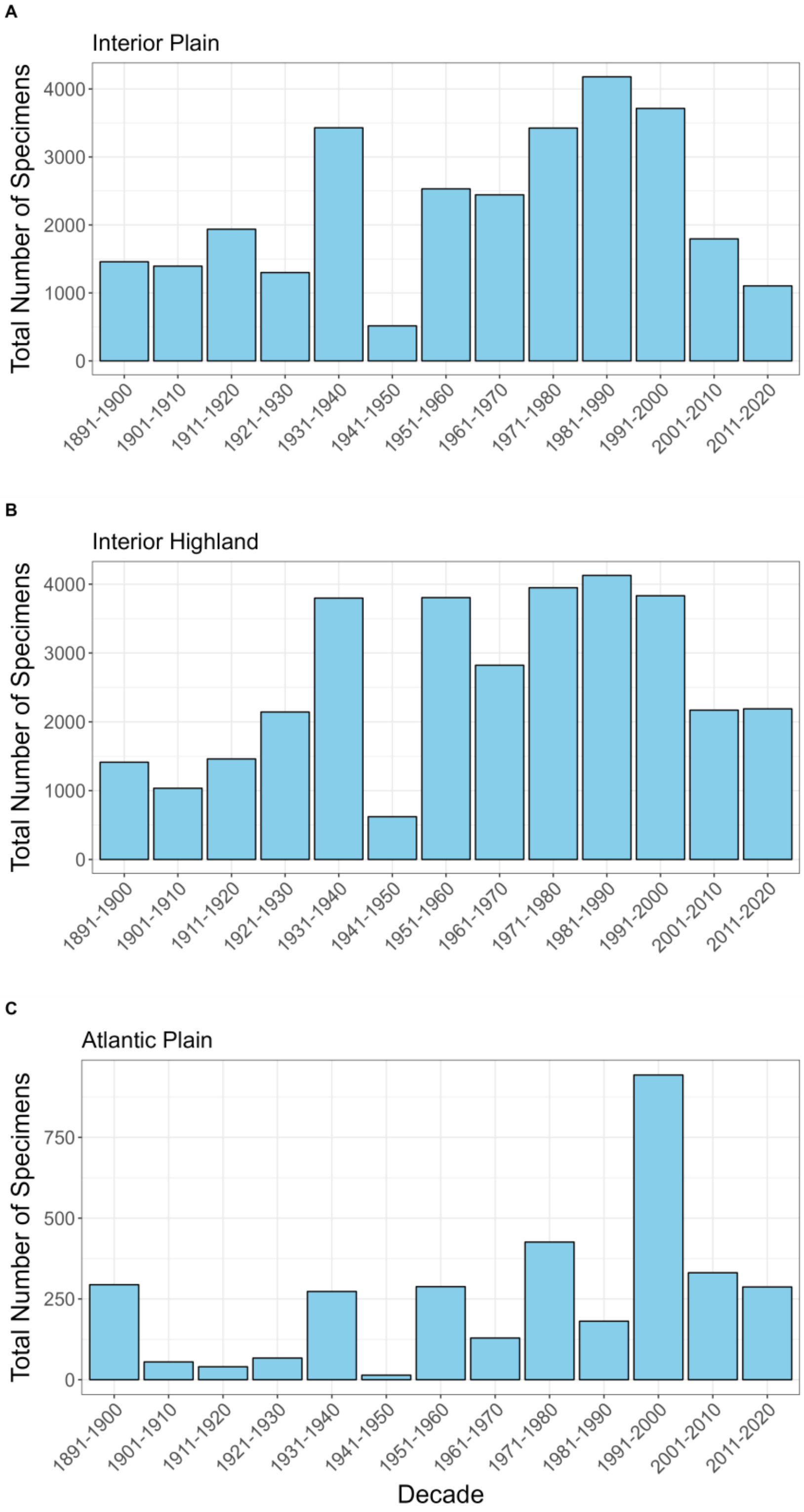

Figure S1. Sample size per decade in each of the three physiographic ecoregions: (A) Interior Plain, (B) Interior Highland, and (C) Atlantic Plain.

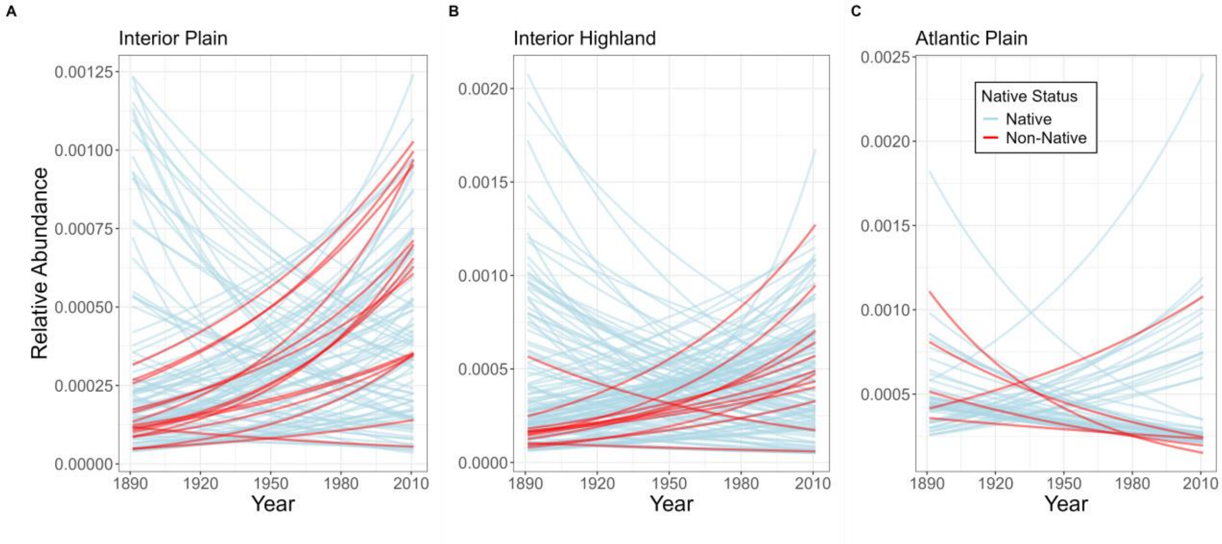

Figure S2. Significant shifts (*P* < 0.05) in relative abundance through time in each physiographic region, when abundance estimates are standardized to all plant specimen data.

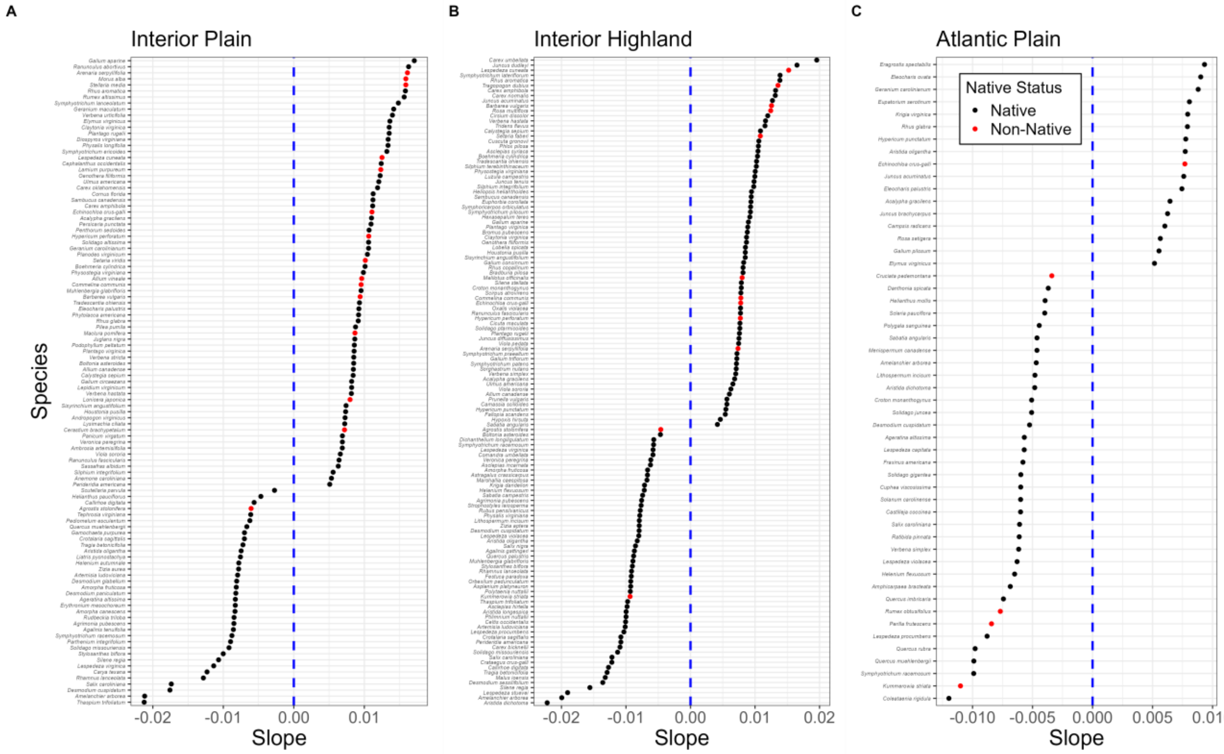

Figure S3. Beta-regression slopes of species exhibiting significant ($P < 0.05$) changes to relative abundance through time in each physiographic region, when abundance estimates are standardized to all plant specimen data. Positive value indicate increases in relative abundance; negative values indicate decreases in relative abundance. Red dots indicate non-native species.

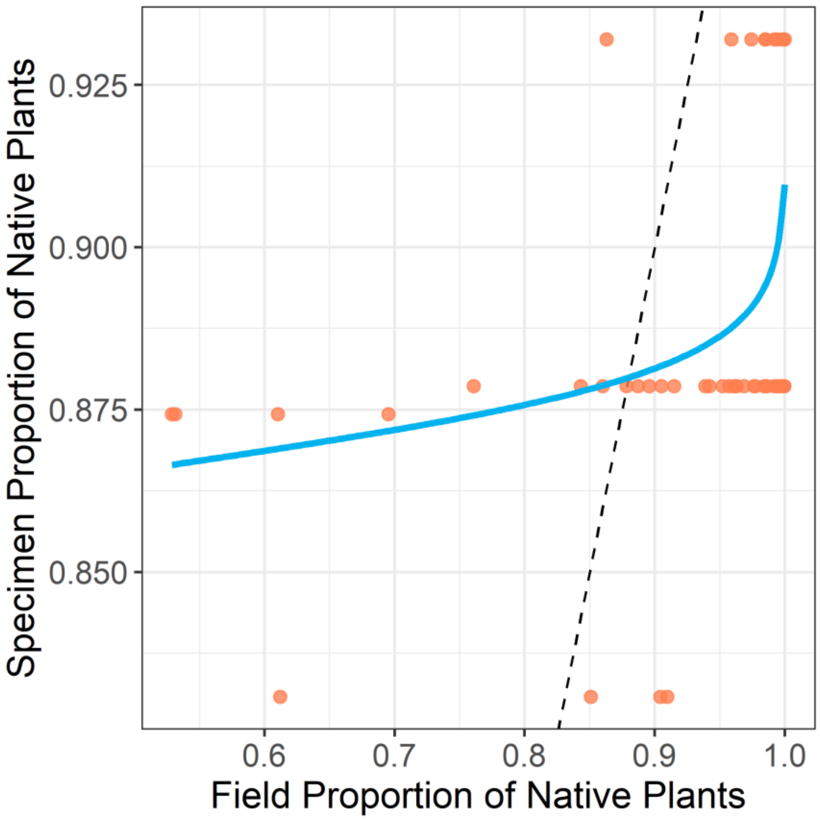

Figure S4. Correspondence between the proportion of native specimens and the proportion of native percent cover from field surveys, using raw data that is not logit transformed. Each point is a paired field-herbarium dataset. The dashed black line is a one-to-one line; the solid blue line is the regression line from the model ($P < 0.005$; slope = 0.065).

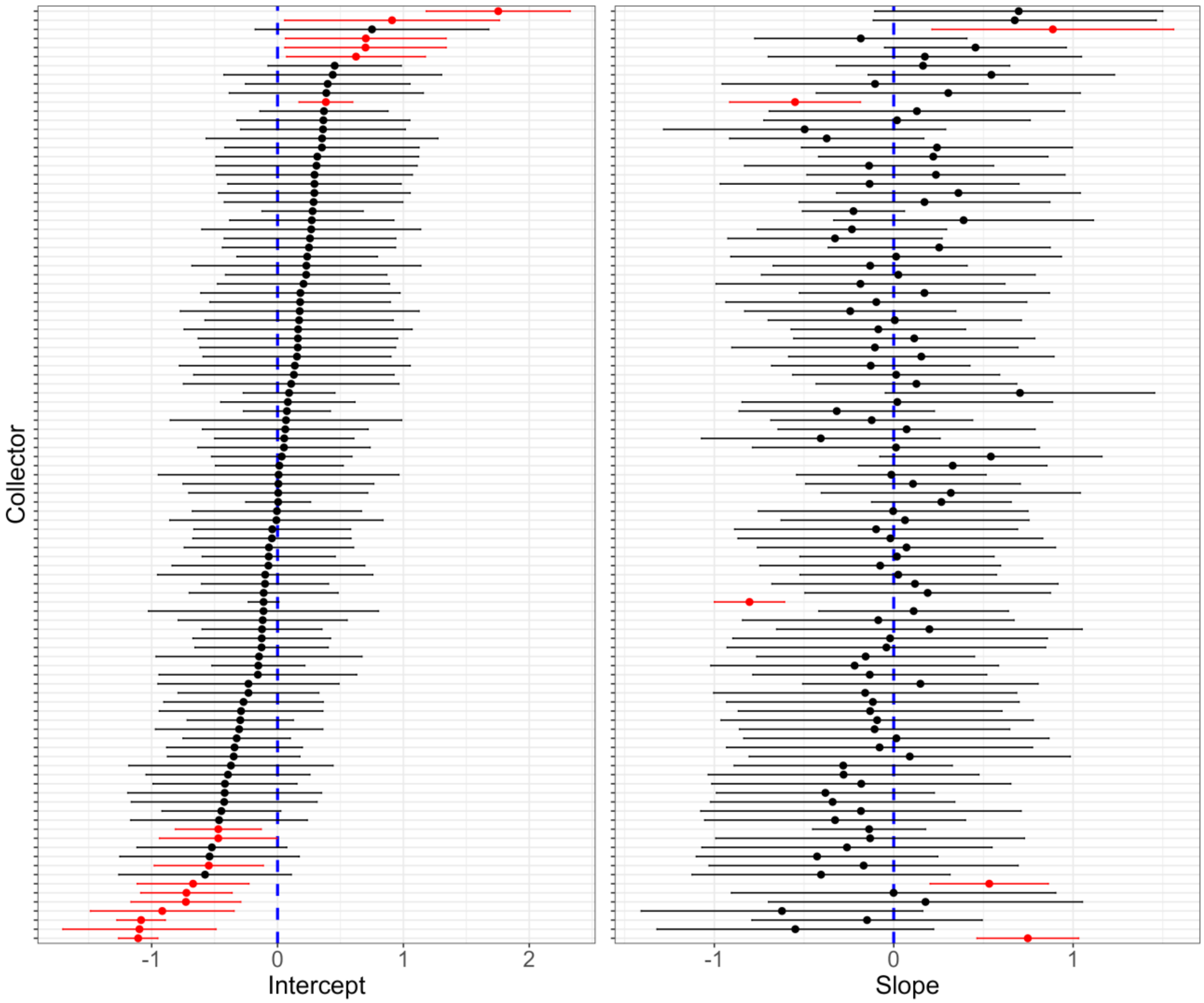

Figure S5. Random effects for intercepts (left) and slopes (right) of collectors in the general linear mixed effects model. Error bars are 95% CIs. Red points have 95% CIs that do not overlap with 0 and may reflect collection biases.

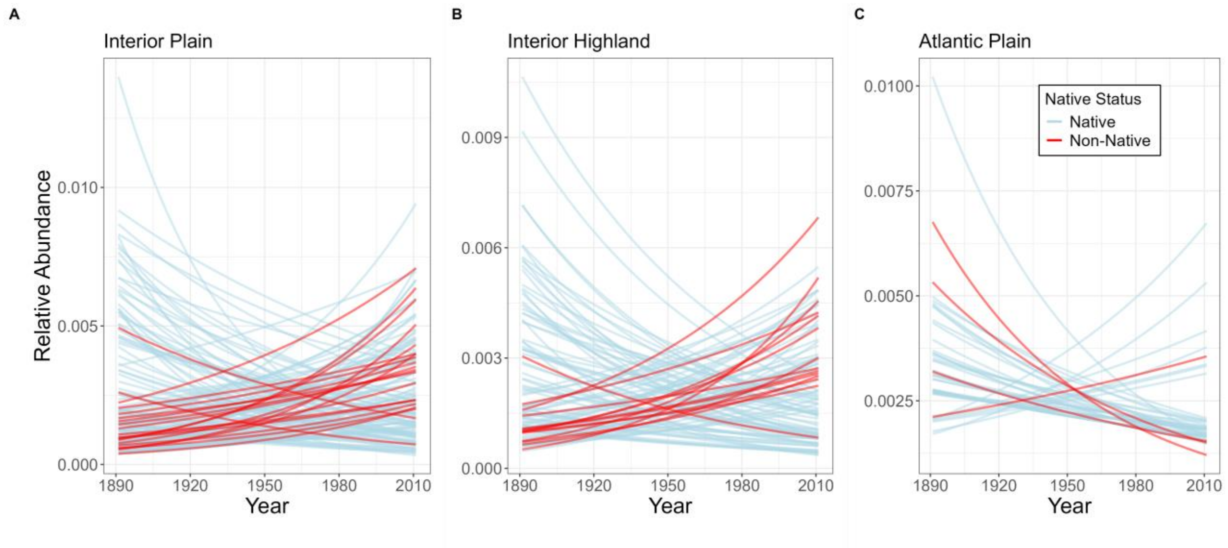

Figure S6. Significant shifts (*P* < 0.05) in relative abundance through time in each physiographic region, when collectors that exhibit collection biases are removed.

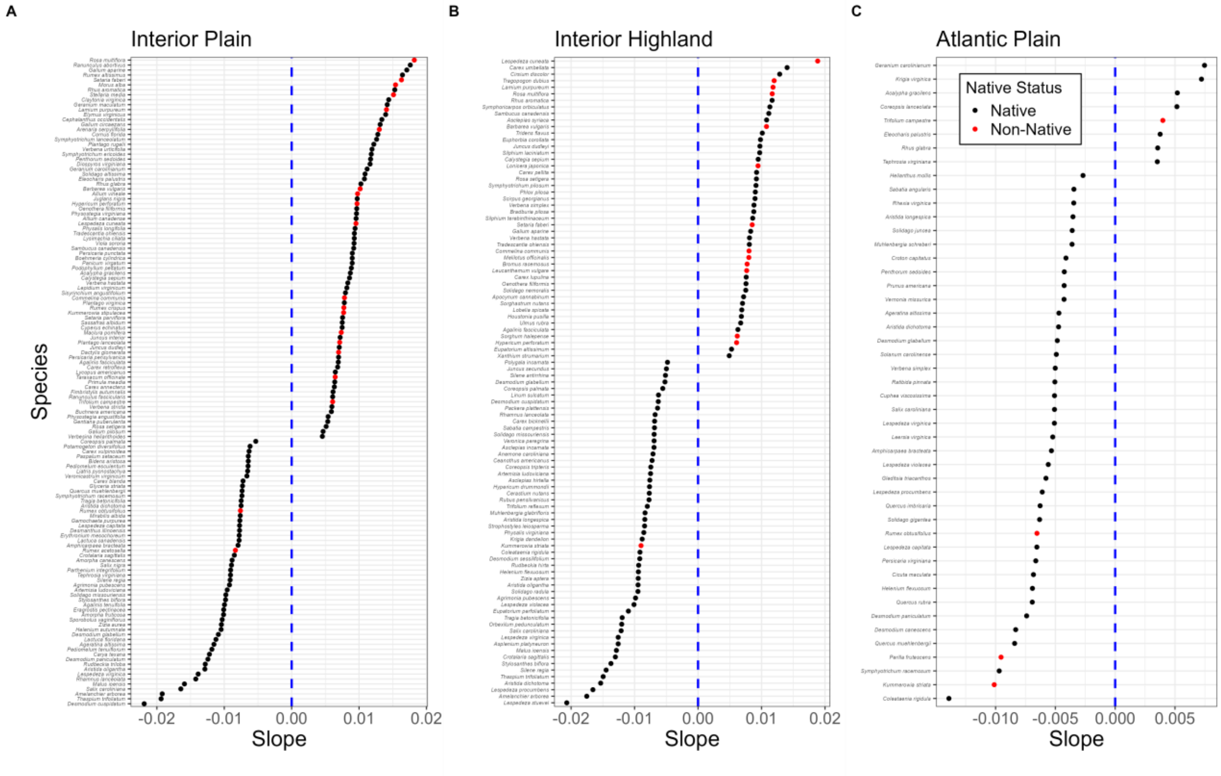

Figure S7. Beta-regression slopes of species exhibiting significant ($P < 0.05$) changes to relative abundance through time in each physiographic region, when collectors that exhibit collection biases are removed. Positive value indicate increases in relative abundance; negative values indicate decreases in relative abundance. Red dots indicate non-native species.

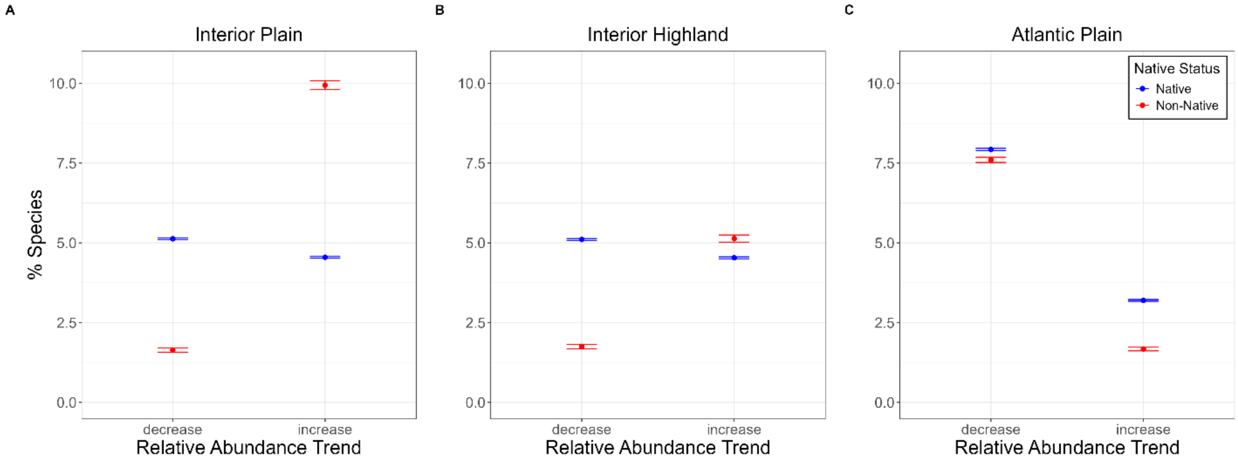

Figure S8. Percent of species exhibiting significant ($P < 0.05$) changes to relative abundance following an iterative subsampling procedure in each of the three physiographic ecoregions: (A) Interior Plain, (B) Interior Highland, and (C) Atlantic Plain. Points are the mean ± SE.

Table S1. The 65 unique site-year combinations compiled from field surveys of 34 remnant and restored Missouri prairies.

Site	Site-Year	Name	Site Type	Years	County	Source	Sample Type	Area in acres	Latitude	Longitude
1	1	Carver	remnant	2016, 2021	Newton	MPF report	cover	65	37.02	-94.39
2	2	Coyne	remnant	2017, 2018, 2020	Dade	MPF report	cover	80	37.51	-93.99
3	3	Denison	remnant	2017	Barton	MPF report	cover	320	37.65	-94.35
4	4	Gayfeather	remnant	2019	Vernon	MPF report	cover	76	37.73	-94.17
5	5	Golden	remnant	2020	Barton	MPF report	cover	320	37.36	-94.15
6	6	Linden	remnant	2016, 2020	Lawrence	MPF report	cover	171	37.11	-93.91
7	7	Lordi Marker	remnant	2021	Pettis	MPF report	cover	100	38.54	-93.29
8	8	La Petite Gemme	remnant	2016	Polk	MPF report	cover	37	37.56	-93.41
9	9	Noah Brown	remnant	2017	Newton	MPF report	cover	19	37.03	-94.30
10	10	Northwest Lawrence	remnant	2019	Lawrence	MPF report	cover	34	37.27	-93.97
11	11	Pleasant Run Creek	remnant	2016	Vernon	MPF report	cover	84	37.65	-94.35
12	12	Penn-Sylvania	remnant	2016, 2018	Dade	MPF report	cover	160	37.50	-93.99
13	13	Rae Letsinger	remnant	2020	Newton	MPF report	cover	68	37.04	-94.15
14	14	Schuette	remnant	2021	Polk	MPF report	cover	40	37.52	-93.34
15	15	Schwartz	remnant	2018	St. Clair	MPF report	cover	240	37.91	-93.85
16	16	Snowball Hill	remnant	2017, 2018	Cass	MPF report	cover	22	38.62	-94.37
17	17	Stilwell	remnant	2019	Vernon	MPF report	cover	117	37.94	-94.55
18	18	Diggs	remnant	2017	Audrain & Montgomery	Newbold et al. 2020	cover	9	39.07	-91.63
19	19	Tucker	remnant	2017	Calloway	Newbold et al. 2020	cover	145	38.95	-91.99
20	20	A1-3_crop	reconstruction	2017	Calloway	Newbold et al. 2020	cover	911	38.89	-91.74
21	21	A1-3_grass	reconstruction	2017	Calloway	Newbold et al. 2020	cover	911	38.89	-91.74
22	22	A4-7_crop	reconstruction	2017	Calloway	Newbold et al. 2020	cover	911	38.89	-91.74
23	23	A4-7_grass	reconstruction	2017	Calloway	Newbold et al. 2020	cover	911	38.89	-91.74
24	24	A8+_crop	reconstruction	2017	Calloway	Newbold et al. 2020	cover	911	38.89	-91.74
25	26	A8+_grass	reconstruction	2017	Calloway	Newbold et al. 2020	cover	911	38.89	-91.74
26	26	Hi Lonesome	remnant	2005	Benton	Briggler et al. 2017	cover classes	655	38.48	-93.23
26	27	Hi Lonesome	remnant	2006	Benton	Briggler et al. 2017	cover classes	655	38.48	-93.23
26	28	Hi Lonesome	remnant	2007	Benton	Briggler et al. 2017	cover classes	655	38.48	-93.23
26	29	Hi Lonesome	remnant	2008	Benton	Briggler et al. 2017	cover classes	655	38.48	-93.23
27	30	Bethel	remnant	2005	Barton	Briggler et al. 2017	cover classes	260	37.40	-94.38
27	31	Bethel	remnant	2006	Barton	Briggler et al. 2017	cover classes	260	37.40	-94.38
27	32	Bethel	remnant	2007	Barton	Briggler et al. 2017	cover classes	260	37.40	-94.38

27	33	Bethel	remnant	2008	Barton	Briggler et al. 2017	cover classes	260	37.40	-94.38
28	34	Niawathe	remnant	2005	Dade	Briggler et al. 2017	cover classes	319.5	37.52	-93.97
28	35	Niawathe	remnant	2006	Dade	Briggler et al. 2017	cover classes	319.5	37.52	-93.97
28	36	Niawathe	remnant	2007	Dade	Briggler et al. 2017	cover classes	319.5	37.52	-93.97
28	37	Niawathe	remnant	2008	Dade	Briggler et al. 2017	cover classes	319.5	37.52	-93.97
29	38	Taberville	remnant	2005	St. Clair	Briggler et al. 2017	cover classes	1680	38.04	-93.98
29	39	Taberville	remnant	2006	St. Clair	Briggler et al. 2017	cover classes	1680	38.04	-93.98
29	40	Taberville	remnant	2007	St. Clair	Briggler et al. 2017	cover classes	1680	38.04	-93.98
29	41	Taberville	remnant	2008	St. Clair	Briggler et al. 2017	cover classes	1680	38.04	-93.98
30	42	Wah’Kon-Tah	remnant	2005	Cedar	Briggler et al. 2017	cover classes	3350.5	37.91	-94.00
30	43	Wah’Kon-Tah	remnant	2006	Cedar	Briggler et al. 2017	cover classes	3350.5	37.91	-94.00
30	44	Wah’Kon-Tah	remnant	2007	Cedar	Briggler et al. 2017	cover classes	3350.5	37.91	-94.00
30	45	Wah’Kon-Tah	remnant	2008	Cedar	Briggler et al. 2017	cover classes	3350.5	37.91	-94.00
31	46	Pawnee fescue pasture 1	pasture	1996	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
31	47	Pawnee fescue pasture 1	pasture	2001	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
31	48	Pawnee fescue pasture 1	pasture	2013	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
31	49	Pawnee fescue pasture 1	pasture	2015	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
31	50	Pawnee fescue pasture 1	pasture	2017	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
32	51	Pawnee fescue pasture 2	pasture	1996	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
32	52	Pawnee fescue pasture 2	pasture	2001	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
32	53	Pawnee fescue pasture 2	pasture	2013	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
32	54	Pawnee fescue pasture 2	pasture	2015	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
32	55	Pawnee fescue pasture 2	pasture	2017	Harrison	Leahy et al. 2020	cover	476	40.52	-94.15
33	56	Pawnee remnant 1	remnant	1996	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14
33	57	Pawnee remnant 1	remnant	2001	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14
33	58	Pawnee remnant 1	remnant	2013	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14
33	59	Pawnee remnant 1	remnant	2015	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14
33	60	Pawnee remnant 1	remnant	2017	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14
34	61	Pawnee remnant 2	remnant	1996	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14
34	62	Pawnee remnant 2	remnant	2001	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14
34	63	Pawnee remnant 2	remnant	2013	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14
34	64	Pawnee remnant 2	remnant	2015	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14
34	65	Pawnee remnant 2	remnant	2017	Harrison	Leahy et al. 2020	cover	476	40.52	-94.14

Table S2. Rank-abundance distribution (RAD) model fits to subsampled communities. The columns under "Proportion of times RAD model was selected" represent the proportion out of the 1,000 subsamples each model was most parsimonious. The observed best fit model is also listed, along with whether it was also the most frequently selected among the subsamples.

a) Atlantic Plain			Proportion of times RAD model was selected					Observed best-fit model	
Region	**Species**	**Decade**	**Broken Stick**	**Geometric**	**Lognormal**	**Zipf-Mandelbrot**	**Zipf**	**Model**	**Fit**
Atlantic Plain	all	1891	0.000	0.000	0.000	0.389	0.611	Zipf-Mandelbrot	FALSE
Atlantic Plain	all	1901	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	all	1911	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	all	1921	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	all	1931	0.000	0.000	0.000	0.814	0.186	Zipf-Mandelbrot	TRUE
Atlantic Plain	all	1941	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	all	1951	0.000	0.000	0.000	0.873	0.127	Zipf-Mandelbrot	TRUE
Atlantic Plain	all	1961	0.000	0.000	0.000	0.484	0.516	Zipf	TRUE
Atlantic Plain	all	1971	0.000	0.000	0.000	0.930	0.070	Zipf-Mandelbrot	TRUE
Atlantic Plain	all	1981	0.000	0.000	0.000	0.608	0.392	Zipf-Mandelbrot	TRUE
Atlantic Plain	all	1991	0.000	0.000	0.000	0.922	0.078	Zipf-Mandelbrot	TRUE
Atlantic Plain	all	2001	0.000	0.000	0.000	0.723	0.277	Zipf-Mandelbrot	TRUE
Atlantic Plain	all	2011	0.000	0.000	0.000	0.821	0.179	Zipf-Mandelbrot	TRUE
Atlantic Plain	native	1891	0.000	0.000	0.000	0.524	0.476	Zipf-Mandelbrot	TRUE
Atlantic Plain	native	1901	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	native	1911	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	native	1921	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	native	1931	0.000	0.000	0.000	0.892	0.108	Zipf-Mandelbrot	TRUE
Atlantic Plain	native	1941	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	native	1951	0.000	0.000	0.000	0.885	0.115	Zipf-Mandelbrot	TRUE
Atlantic Plain	native	1961	0.000	0.000	0.000	0.006	0.994	Zipf	TRUE
Atlantic Plain	native	1971	0.000	0.000	0.000	0.771	0.229	Zipf-Mandelbrot	TRUE
Atlantic Plain	native	1981	0.000	0.000	0.000	0.634	0.366	Zipf-Mandelbrot	TRUE
Atlantic Plain	native	1991	0.000	0.000	0.000	0.944	0.056	Zipf-Mandelbrot	TRUE
Atlantic Plain	native	2001	0.000	0.000	0.000	0.556	0.444	Zipf-Mandelbrot	TRUE
Atlantic Plain	native	2011	0.000	0.000	0.000	0.850	0.150	Zipf-Mandelbrot	TRUE
Atlantic Plain	non-native	1891	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	non-native	1901	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	non-native	1911	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	non-native	1921	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	non-native	1931	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	non-native	1941	0.000	0.000	0.000	0.000	1.000	Zipf	TRUE
Atlantic Plain	non-native	1951	0.000	0.000	0.000	0.009	0.991	Zipf	TRUE
Atlantic Plain	non-native	1961	0.000	0.000	0.000	0.999	0.001	Zipf-Mandelbrot	TRUE
Atlantic Plain	non-native	1971	0.000	0.000	0.000	0.564	0.436	Zipf-Mandelbrot	TRUE
Atlantic Plain	non-native	1981	0.000	0.000	0.000	0.087	0.913	Zipf	TRUE
Atlantic Plain	non-native	1991	0.000	0.000	0.000	0.024	0.976	Zipf-Mandelbrot	FALSE
Atlantic Plain	non-native	2001	0.000	0.000	0.000	0.474	0.526	Zipf-Mandelbrot	FALSE
Atlantic Plain	non-native	2011	0.000	0.000	0.000	0.016	0.984	Zipf	TRUE

b) Interior Highland			**Proportion of times RAD model was selected**					**Observed best-fit model**	
Region	**Species**	**Decade**	**Broken Stick**	**Geometric**	**Lognormal**	**Zipf-Mandelbrot**	**Zipf**	**Model**	**Fit**
Interior Highland	all	1891	0.000	0.000	0.000	0.636	0.364	Zipf-Mandelbrot	TRUE
Interior Highland	all	1901	0.000	0.000	0.000	0.498	0.502	Zipf-Mandelbrot	FALSE
Interior Highland	all	1911	0.000	0.000	0.000	0.687	0.313	Zipf-Mandelbrot	TRUE
Interior Highland	all	1921	0.000	0.000	0.000	0.793	0.207	Zipf-Mandelbrot	TRUE
Interior Highland	all	1931	0.000	0.000	0.000	0.848	0.152	Zipf-Mandelbrot	TRUE
Interior Highland	all	1941	0.000	0.000	0.000	0.713	0.287	Zipf-Mandelbrot	TRUE
Interior Highland	all	1951	0.000	0.000	0.000	0.641	0.359	Zipf-Mandelbrot	TRUE
Interior Highland	all	1961	0.000	0.000	0.000	0.597	0.403	Zipf-Mandelbrot	TRUE
Interior Highland	all	1971	0.000	0.000	0.000	0.915	0.085	Zipf-Mandelbrot	TRUE
Interior Highland	all	1981	0.000	0.000	0.000	0.636	0.364	Geometric	FALSE
Interior Highland	all	1991	0.000	0.000	0.000	0.955	0.045	Lognormal	FALSE
Interior Highland	all	2001	0.000	0.000	0.000	0.863	0.137	Zipf-Mandelbrot	TRUE
Interior Highland	all	2011	0.000	0.000	0.000	0.973	0.027	Zipf-Mandelbrot	TRUE
Interior Highland	native	1891	0.000	0.000	0.000	0.761	0.239	Zipf-Mandelbrot	TRUE
Interior Highland	native	1901	0.000	0.000	0.000	0.559	0.441	Zipf-Mandelbrot	TRUE
Interior Highland	native	1911	0.000	0.000	0.000	0.760	0.240	Zipf-Mandelbrot	TRUE
Interior Highland	native	1921	0.000	0.000	0.000	0.841	0.159	Zipf-Mandelbrot	TRUE
Interior Highland	native	1931	0.000	0.000	0.000	0.885	0.115	Zipf-Mandelbrot	TRUE
Interior Highland	native	1941	0.000	0.000	0.000	0.792	0.208	Zipf-Mandelbrot	TRUE
Interior Highland	native	1951	0.000	0.000	0.000	0.545	0.455	Zipf-Mandelbrot	TRUE
Interior Highland	native	1961	0.000	0.000	0.000	0.357	0.643	Zipf-Mandelbrot	FALSE
Interior Highland	native	1971	0.000	0.000	0.000	0.854	0.146	Zipf-Mandelbrot	TRUE
Interior Highland	native	1981	0.000	0.000	0.000	0.524	0.476	Zipf-Mandelbrot	TRUE
Interior Highland	native	1991	0.000	0.000	0.000	0.947	0.053	Lognormal	FALSE
Interior Highland	native	2001	0.000	0.000	0.000	0.841	0.159	Zipf-Mandelbrot	TRUE
Interior Highland	native	2011	0.000	0.000	0.000	0.965	0.035	Zipf-Mandelbrot	TRUE
Interior Highland	non-native	1891	0.000	0.000	0.011	0.001	0.988	Zipf	TRUE
Interior Highland	non-native	1901	0.000	0.000	0.001	0.013	0.986	Zipf-Mandelbrot	FALSE
Interior Highland	non-native	1911	0.000	0.000	0.004	0.003	0.993	Zipf-Mandelbrot	FALSE
Interior Highland	non-native	1921	0.000	0.000	0.001	0.013	0.986	Zipf-Mandelbrot	FALSE
Interior Highland	non-native	1931	0.000	0.000	0.001	0.012	0.987	Zipf-Mandelbrot	FALSE
Interior Highland	non-native	1941	0.000	0.000	0.002	0.011	0.987	Zipf-Mandelbrot	FALSE
Interior Highland	non-native	1951	0.000	0.000	0.000	0.170	0.830	Zipf-Mandelbrot	FALSE
Interior Highland	non-native	1961	0.000	0.000	0.000	0.543	0.457	Zipf-Mandelbrot	TRUE
Interior Highland	non-native	1971	0.000	0.000	0.000	0.220	0.780	Lognormal	FALSE
Interior Highland	non-native	1981	0.000	0.000	0.000	0.275	0.725	Lognormal	FALSE
Interior Highland	non-native	1991	0.000	0.000	0.000	0.087	0.913	Lognormal	FALSE
Interior Highland	non-native	2001	0.000	0.000	0.000	0.122	0.878	Lognormal	FALSE
Interior Highland	non-native	2011	0.000	0.000	0.000	0.066	0.934	Lognormal	FALSE

c) Interior Plains			Proportion of times RAD model was selected					Observed best-fit model	
Region	Species	Decade	Broken Stick	Geometric	Lognormal	Zipf-Mandelbrot	Zipf	Model	Fit
Interior Plain	all	1891	0.000	0.000	0.000	0.696	0.304	Zipf-Mandelbrot	TRUE
Interior Plain	all	1901	0.000	0.000	0.000	0.726	0.274	Zipf-Mandelbrot	TRUE
Interior Plain	all	1911	0.000	0.000	0.000	0.351	0.649	Zipf-Mandelbrot	FALSE
Interior Plain	all	1921	0.000	0.000	0.000	0.463	0.537	Zipf-Mandelbrot	FALSE
Interior Plain	all	1931	0.000	0.000	0.000	0.598	0.402	Geometric	FALSE
Interior Plain	all	1941	0.000	0.000	0.000	0.800	0.200	Zipf-Mandelbrot	TRUE
Interior Plain	all	1951	0.000	0.000	0.000	0.787	0.213	Zipf-Mandelbrot	TRUE
Interior Plain	all	1961	0.000	0.000	0.000	0.844	0.156	Zipf-Mandelbrot	TRUE
Interior Plain	all	1971	0.000	0.000	0.000	0.815	0.185	Zipf-Mandelbrot	TRUE
Interior Plain	all	1981	0.000	0.000	0.000	0.769	0.231	Zipf-Mandelbrot	TRUE
Interior Plain	all	1991	0.000	0.000	0.000	0.905	0.095	Zipf-Mandelbrot	TRUE
Interior Plain	all	2001	0.000	0.000	0.000	0.919	0.081	Geometric	FALSE
Interior Plain	all	2011	0.000	0.000	0.000	0.922	0.078	Zipf-Mandelbrot	TRUE
Interior Plain	native	1891	0.000	0.000	0.000	0.721	0.279	Zipf-Mandelbrot	TRUE
Interior Plain	native	1901	0.000	0.000	0.000	0.782	0.218	Zipf-Mandelbrot	TRUE
Interior Plain	native	1911	0.000	0.000	0.000	0.347	0.653	Zipf-Mandelbrot	FALSE
Interior Plain	native	1921	0.000	0.000	0.000	0.501	0.499	Zipf-Mandelbrot	TRUE
Interior Plain	native	1931	0.000	0.000	0.000	0.652	0.348	Zipf-Mandelbrot	TRUE
Interior Plain	native	1941	0.000	0.000	0.000	0.814	0.186	Zipf-Mandelbrot	TRUE
Interior Plain	native	1951	0.000	0.000	0.000	0.685	0.315	Zipf-Mandelbrot	TRUE
Interior Plain	native	1961	0.000	0.000	0.000	0.560	0.440	Zipf-Mandelbrot	TRUE
Interior Plain	native	1971	0.000	0.000	0.000	0.685	0.315	Zipf-Mandelbrot	TRUE
Interior Plain	native	1981	0.000	0.000	0.000	0.631	0.369	Zipf-Mandelbrot	TRUE
Interior Plain	native	1991	0.000	0.000	0.000	0.811	0.189	Zipf-Mandelbrot	TRUE
Interior Plain	native	2001	0.000	0.000	0.000	0.791	0.209	Zipf-Mandelbrot	TRUE
Interior Plain	native	2011	0.000	0.000	0.000	0.839	0.161	Zipf-Mandelbrot	TRUE
Interior Plain	non-native	1891	0.000	0.000	0.000	0.018	0.982	Zipf-Mandelbrot	FALSE
Interior Plain	non-native	1901	0.000	0.000	0.000	0.015	0.985	Zipf-Mandelbrot	FALSE
Interior Plain	non-native	1911	0.000	0.000	0.000	0.037	0.963	Zipf-Mandelbrot	FALSE
Interior Plain	non-native	1921	0.000	0.000	0.000	0.041	0.959	Zipf-Mandelbrot	FALSE
Interior Plain	non-native	1931	0.000	0.000	0.001	0.024	0.975	Lognormal	FALSE
Interior Plain	non-native	1941	0.000	0.000	0.000	0.041	0.959	Zipf-Mandelbrot	FALSE
Interior Plain	non-native	1951	0.000	0.000	0.000	0.193	0.807	Lognormal	FALSE
Interior Plain	non-native	1961	0.000	0.000	0.000	0.793	0.207	Zipf-Mandelbrot	TRUE
Interior Plain	non-native	1971	0.000	0.000	0.000	0.336	0.664	Lognormal	FALSE
Interior Plain	non-native	1981	0.000	0.000	0.000	0.350	0.650	Lognormal	FALSE
Interior Plain	non-native	1991	0.000	0.000	0.000	0.338	0.662	Lognormal	FALSE
Interior Plain	non-native	2001	0.000	0.000	0.000	0.634	0.366	Lognormal	FALSE
Interior Plain	non-native	2011	0.000	0.000	0.000	0.260	0.740	Lognormal	FALSE