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Dispersal and persistence traits inform long-term herbaceous plant community change in encroached savannas

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Abstract

Savanna plant communities are highly diverse, characterized by an open-canopy structure with rich herbaceous diversity, and maintained by frequent low-intensity fire and grazing. Due to habitat loss and fragmentation, savannas are globally threatened, with less than 1% of former oak savanna land cover found in the Midwestern United States remaining. In remnant oak savannas, loss of fire and grazing has led to woody encroachment and canopy closure over the past century with cascading consequences for the taxonomic composition. Whether these taxonomic changes can be broadly predicted using species functional traits (morpho-physio-phenological characteristics that impact the fitness of a species) is a key question. We ask whether the impacts of woody encroachment on herbaceous species can be predicted from species' abilities to persist (avoid extinction) and disperse (colonize new areas). Specifically, we pair persistence traits (e.g., clonality, belowground storage) and dispersal traits (e.g., seed mass, dispersal mode, flowering height) with a rare 60-year dataset from oak savannas in Wisconsin, USA to understand how the representation of these traits has changed in the herbaceous community over time. Over 60 years, change in species composition was explained both by dispersal abilities and persistence traits; small-seeded species reliant on unassisted dispersal and moderately clonal species experienced the greatest losses. These changes in functional composition are likely due to increased woody encroachment, which may impede propagule production and movement. Restoration efforts need to prioritize species that are dispersal limited and those that create fine fuels, which aid the persistence of fire-maintained open habitat savannas.

Keywords Dispersal · Persistence · Woody encroachment · Colonization · Local extinction · Temperate oak savanna

Introduction

Savannas historically covered 20 percent of Earth's land area in temperate and tropical zones (Scholes and Archer 1997). They are maintained by frequent, low-intensity disturbance like fire and/or grazing that facilitate the co-existence of grasses and trees (Bond et al. 2005; Higgins et al. 2003) and result in often highly diverse ecosystems (Aleman and Staver 2018; Lehmann et al. 2011). Today, savannas occupy a fraction of their former extent due to land use changes and the loss of routine disturbances (Rhemtulla et al. 2007; Hoffmann et al. 2012). As a result, savannas in North America now occur in small, isolated fragments (Nuzzo 1986) where the plant communities are changing due to encroachment by woody species and resulting canopy closure (Fig. 1a) (Ratajczak et al. 2012). Indeed, substantial species loss and turnover has occurred in Wisconsin savannas where tree density has nearly doubled since 1950 and there has been considerable loss of prairie and savanna specialist species

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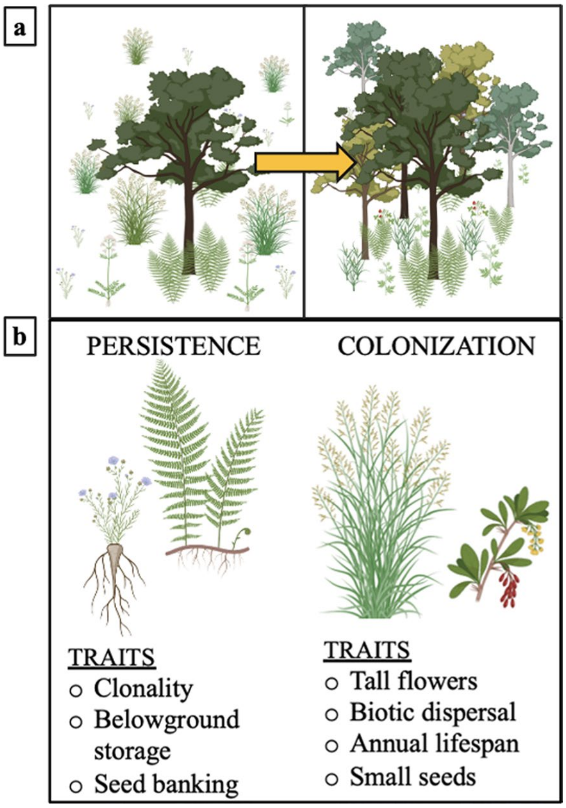

Fig. 1 Conceptual figure depicting **a** increased canopy cover in savannas due to woody encroachment and **b** two suits of traits, persistence or colonization, that enable herbaceous species to remain in savanna understories

with an increase in woodland and non-native species (Ladwig et al. 2018). Given these taxonomic changes, a useful next step is to determine if there are commonalities in the life histories of the species that are being lost and gained to better understand the processes responsible for change (Purschke et al. 2013).

One way to determine the ecological mechanisms underpinning changes to community structure is to use functional traits – morpho-physio-phenological attributes that affect the fitness of a species in a landscape (Grime 1977; Lavorel and Garnier 2002; Funk et al. 2017; Kunstler et al. 2016). In encroached oak savannas, functional traits associated with species' abilities to persist (avoid extinction) and colonize (disperse to new areas) will be particularly useful for isolating mechanisms driving changes in species diversity and community resilience and determining effective restoration practices (Fig. 1b) (Levin et al. 2003). Most trait-based studies have focused on resource acquisition traits (Reich et al. 1999; Wright et al. 2004; Osnas et al. 2013), while traits related to colonization ability and belowground investment have received far less attention (Larson and Funk 2016; Klimešová et al. 2016; Weigelt et al. 2021). Separating causal drivers using species traits is complicated by the fact that traits do not arise independently and are often correlated with each other (Shipley et al. 2009; Funk et al. 2017; Flores-Moreno et al. 2019). Given this, we expect suites of traits to change together, suggesting general plant life histories that may be particularly resilient or susceptible to woody encroachment in fire adapted systems (Keeley et al. 2011). Our goal here is not to determine casual trait drivers nor "spectra" of related traits, but rather groups of traits that suggest particular plant life histories that are more or less susceptible to woody encroachment of Midwestern oak savannas.

Traits that predict if species will remain in a site over time are those associated with surviving or recolonizing a local area following disturbance, so examining traits associated with these two processes help us understand community change. In the case of oak savannas, historical disturbance regimes of frequent low-intensity fires and grazing selected for species with belowground storage structures and buds that facilitate regrowth after aboveground biomass is removed (Klimešová and Klimeš, 2007; Clarke et al. 2013; Fidelis et al. 2014; Pausas et al. 2018). These resprouting traits can promote species persistence and community resilience (Pausas and Keeley 2014; Ottaviani et al. 2017; Zheng et al. 2019; Li et al. 2021). With the loss of disturbance and canopy closure, long-lived resprouting species may be able to maintain their presence in the short term but lose out to more competitive species in the long term (e.g., shrubs). Fournier et al. (2020) found that species diversity was highest following fire, with rarefication of fire-adapted species driving diminishing richness in fire-adapted systems. Even if individual plants are unable to persist, species dispersal ability may promote recolonization and rescue effects to allow the species to remain at the site (Brown and Kodric-Brown 1977; Vittoz and Engler 2007). Recolonizations can occur in both space (e.g., seed inter-patch movement) and time (e.g., soil seed bank dormancy and emergence). The latter can be predicted by seed mass whereby lighter, smaller seeds often persist longer in the soil seed bank (Thomson and Grime 1977; Thompson et al. 1993; Moles et al. 2000). One mechanism facilitating seed bank persistence of smaller seeds is the ease of seed burial which prevents granivory (Thompson 1987). Although seed size and shape also influence persistence, results vary across systems (Funes et al. 1999; Moles et al. 2000). Larson and Suding (2022) found that seed bank communities were biased towards species with smaller seed mass compared to the standing vegetation. We, therefore, predict that species with resprouting capacity and belowground storage organs (persistence *within* a generation), or the ability to disperse seed and seed bank (persistence *across* generations) will persist over time due to their ability to survive canopy closure. Species extinctions will, therefore, be driven by the inability to survive or recolonize local habitats.

Changes to disturbance regimes that result in woody encroachment can also allow new species to enter the community. Traits that predict colonization of local sites by new species are those associated with dispersal ability, including plant height, dispersal mode, and seed mass. Taller plants release seeds at a greater height, allowing seeds to move farther away from the parent plant (Thomson et al. 2011). The vector by which seeds disperse (hereafter "dispersal mode") also influences how far seeds disperse. In closed-canopy systems such as encroached savannas, seeds moved by animals (e.g., birds and mammals) travel farther than those dispersed by wind (Sorensen 1986; Aslan et al. 2013). Finally, seed mass also affects the distance a seed travels, with lighter seeds traveling farther than heavier seeds (Greene and Johnson 1993; Pérez-Harguindeguy et al. 2013). We predict that species gains (colonizations) will be more likely for species with taller flowering heights, animal-dispersed seeds, and lightweight seeds.

Evaluating the drivers of community change can be difficult due to the lack of historical baselines that can be used to document species persistence, losses, and gains. Historical data, especially that include species identities and abundances, are particularly important in this regard, though rare. Here, we use a historical, long-term plant community dataset paired with contemporary data to ask whether functional traits can predict species persistence and colonizations after 60 years of woody encroachment in Midwestern oak savannas. We predict that: (1) herbaceous species with traits that promote persistence—resprouting and belowground storage abilities, or annual life cycles that facilitate recolonization—will increase, while those without these traits will decrease (Fig. 1b); and (2) species with traits that facilitate dispersal—greater flowering height, smaller and lighter seeds, and seeds dispersed by animals—will increase while those with the opposite set of traits will decrease.

Materials and methods

Study system—temperate oak savannas and woodlands

The savannas of the Midwestern USA are dominated by oak trees, most often by bur oak (*Quercus macrocarpa*) with white oak (*Q. alba*) and black oak (*Q. velutina*) at lower abundances (Curtis, 1959). Oak savannas often share species with neighboring deciduous forests and tallgrass prairies which all occur in a mosaic across the landscape (Anderson 1987). In addition, there are several unique community types within or closely related to oak savannas, based on soil moisture availability, soil properties, and overstory tree composition (Curtis, 1959). For example, on the wet end of this gradient are oak woodlands, historically dominated by swamp white oak (*Q. bicolor*) and bur oak (*Q. macrocarpa*) (Curtis, 1959), and on the dry end of this gradient are cedar glades, which are dominated by red cedar (*Juniperus virginiana*) (Curtis, 1959). Woody encroachment has affected all of these community types, regardless of their environmental differences (Mills 2008; Ladwig et al. 2018). Here, we use "oak savannas" to refer to oak woodlands, oak barrens, and other fire-maintained communities with sparse canopies and grassland understories.

Reduced fire frequency and intensity plus altered grazing has facilitated the encroachment of woody species into prairies and savannas (Fig. 1a) (Cottam 1949; Heisler et al. 2003; Briggs et al. 2005; Peterson et al. 2007; Stevens et al. 2016; Wilcox et al. 2018). In fire- or grazing-maintained savannas, scattered and sparse trees generate light gradients (Bray 1955; Leach and Givnish 1999; Brudvig and Asbjornsen 2009) that promote a rich herbaceous understory and high plant diversity due to heterogeneous fine-grained microclimatic conditions (Leach and Givnish 1999). Shady conditions near the sparse trees also allows shade-tolerant and fire-sensitive species to establish in savannas (Kreye et al. 2013). When woody encroachment occurs, the canopy of the savanna closes and microsite variation in nutrients, soil moisture, and light becomes more homogenous (Breshears 2006), reducing plant species diversity (Anderson, 1998). This homogenization in structure is true for Wisconsin oak savannas as well; Ladwig et al. (2018) found that tree cover in these savannas nearly doubled between the 1950s and 2014.

Vegetation sampling

We used vegetation survey data from 1951 to 1954 (hereafter referred to as the 1950s) collected from oak savannas across southern Wisconsin (42–45° N, 88–93° W; Bray, 1960) that were surveyed as part of larger project to classify the vegetation of Wisconsin (Curtis 1959; Waller et al. 2012). Sites surveyed in the 1950s were chosen because they retained sparse, open-grown trees and understories dominated by native grasses and forbs (Bray, 1960).

In the summer of 2014, we resampled 16 of these savanna sites following the same methods as the initial 1950s survey (Ladwig et al. 2018). We surveyed at least 20 sampling points located > 10 m from each other for understory vegetation at each site. We placed a 1 × 1 m quadrat North and center of each sampling point and assessed the presence of all species occurring in the quadrat. See Ladwig et al. (2018) for additional sampling details. Taxonomic resolution was kept consistent between survey times. In the original surveys, most plants were identified to species, but some were identified to genus (e.g., *Carex* spp.). When there was a mismatch in nomenclature between the 1950s and 2010s, we updated nomenclature to match modern flora (Chadde

2019). Across both survey times, a total of 261 plant taxa were identified in savanna understories.

Functional traits

To test how functional traits were associated with plant response to woody encroachment in savannas, we measured functional traits related to persistence and dispersal for all understory forbs, grasses, and vines, excluding shrubs and tree seedlings. We used regional floras or online databases detailed below to define categorical traits. We followed methods described by Pérez-Harguindeguy et al. (2013) to measure continuous quantitative traits (e.g., plant height & seed mass)—we collected tissue from 10 individuals from three populations (30 individuals total) from remnant grasslands and savannas in central WI during the 2014 to 2019 growing seasons. For missing trait data, we filled gaps with comparably collected trait data from other sites in Wisconsin (Waller et al. 2021) and other midwestern states (Zirbel et al. 2017). We filled any remaining gaps with identically collected data from the same species in southeastern United States longleaf pine savannas (Damschen et al. 2019; Orrock et al. In Press). Traits used in analyses are taxon averages of all measurements.

To characterize persistence ability, we assigned all species persistence categories based on the presence of belowground structures and life history characteristics (Miller et al. 2017). Persistence categories ranged from 1 to 5, corresponding to the least to most persistence capacity as follows: (1) annual and biennial species; (2) perennials without root storage structures or rhizomes; (3) perennials with storage structures such as tubers, taproots, corms, or bulbs; (4) species with short rhizomes; and (5) species with long rhizomes. Annual or biennial species with storage structurers (e.g., the taproot of *Melilotus* developed during its first year) were included in Category 1 because these species still have a lifespan limited to one or two years, and in the scope of 60 years of change, these species do not warrant their own category. In addition, we split rhizomatous species into two categories because of the increased clonal spread and size that comes with having long rhizomes over short rhizomes. To assign species to these persistence categories, we determined the plant lifespan and types of belowground tissue present from a regional flora (Chadde 2019).

To characterize dispersal ability, we used dispersal mode category, inflorescence height (cm), and seed mass (mg). We categorized dispersal mode as: unassisted (no specialized dispersal structures), wind dispersed (with pappi or wings), or animal dispersed (with fleshy fruits or adhesive dispersal structures) (Bullock et al. 2006) using the USDA Plant Database (USDA, NRCS 2022; http://plants.usda.gov) and primary literature. We measured plant height in the field and seed mass in the lab using standard methods (Pérez-Harguindeguy et al. 2013).

Statistical analysis

To compare changes in functional traits independent of their impact on species abundance, we used a separate t test (using the function ‘t.test’ in the stats package) for each trait to test for differences in the mean trait values of all species present between the two time periods. We also used a t test (using the function ‘t.test’ in the stats package) to determine change in overall community abundance.

We used trait averages in all analyses. To test whether species abundances (percentage of plots occupied) are influenced by persistence or colonization abilities, we evaluated the influence of traits and time on species abundances by fitting a generalized linear-mixed model for each trait using ‘glmmTMB’ (Brooks et al. 2017). We used the frequency of plots occupied out of the total sampled at each site as a measure of species abundance for each site. We used logit-normal binomial generalized linear-mixed models (GLMM) following Jamil et al. (2013), Brooks et al. (2017) and Miller et al. (2018) with the abundance of each species at each site as the response variable and species’ trait values and time (1950s and 2014) as fixed effect predictor variables. We included seed mass and inflorescence height as continuous traits and persistence category and dispersal mode as categorical traits. Although persistence is ordinal, with category 1 species having the least persistence ability and category 5 species having the greatest, we were most interested in changes within categories (i.e., if certain persistence categories are being lost or gained) and less in community-wide change in persistence strategy (e.g., this community had an average persistence value of 3.2) since this is less informative. The model also included independent random effects of species taxonomic identity, species-dependent random effects of time, and included an additional zero-inflation parameter. Specifically, the models were fit as follows:

$$\begin{aligned}&\text{glmmTMB}\big(\text{abundance} \sim \text{trait} + \text{time} + \text{trait:time}\\&+ (1|\text{species}) + (0 + \text{time}|\text{species}),\ \text{ziformula} =\sim 1,\\&\text{family} = \text{"binomial" (link} = \text{"logit")}\big)\end{aligned}$$

The significance of each fixed effect, including interactions, was determined from asymptotic Wald tests.

We ran linear regressions between continuous traits to test for correlations. All statistical tests were conducted in R version 4.1.1 (R core team 2021) with an alpha of 0.05.

Results

Overall, herbaceous plant abundance decreased from the 1950s to 2014 ($t_{788.79} = -2.48$, $p = 0.01$); there were fewer presence observations across sites in 2014. Several significant trait-by-time interactions indicate that changes in abundance are not uniform and driven by different trait compositions (Table 1).

Regardless of time period, species with greater persistence traits (e.g., categories 4 and 5, species with rhizomes) are more common in savanna understories than those that do not have these traits (e.g., categories 1–2, species that are annuals or biennials or perennials without storage organs) (Fig. 2a). Between time periods, the relative abundance of short-persisting species (categories 1–2) has increased from the 1950s to 2014 whereas long-persisting species (categories 4–5) have maintained a constant relative abundance (Fig. 2a); there was an overall loss of species in category 3. Our model indicates that probability of occurrence was not significantly different between any of the persistence categories in the 1950s. Each persistence category interacted significantly with time (Table 1; Fig. 2b), with all categories having lower probabilities of occurrence in 2014. The probability of occurrence did differ significantly across persistence categories in 2014, with category 3 having significantly lower occurrence probabilities than either short or long persisting species (i.e., categories 1 and 5) (See Table S1 for pairwise comparisons between persistence categories). This indicates that although all persistence categories decreased, category 3 experienced the greatest change.

Some, but not all, traits related to dispersal ability predicted change in abundance over time. The greatest change in the dispersal modes of species within the plant community over time was an increase in animal dispersal and simultaneous decline in species that had unassisted or wind dispersal modes (Fig. 3a). The probability of occurrence was not significantly different between any dispersal modes in the 1950s. Each dispersal mode interacted significantly with time (Table 1; Fig. 3b), with all modes having lower probabilities of occurrence 2014. The probability of occurrence significantly differed between dispersal modes in 2014—animal dispersed species were significantly more likely to occur than both unassisted and wind dispersed species (Fig. 3B; See Table S2 for pairwise comparisons between dispersal modes). While all dispersal modes decreased, unassisted and wind dispersed species experienced the greatest change.

Table 1 Generalized linear mixed model (Eq. 1) results for occurrence probability of savanna understory species

Variable	Estimate	Standard Error	P-value
Time: Category 1	**−2.540**	**0.785**	**<0.001**
Time: Category 2	**−3.821**	**0.972**	**<0.001**
Time: Category 3	**−6.214**	**0.816**	**<0.001**
Time: Category 4	**−4.011**	**0.469**	**<0.001**
Time: Category 5	**−2.852**	**0.561**	**<0.001**
Seed Mass	0.026	0.073	0.469
Time: Seed Mass	**0.593**	**0.138**	**<0.001**
Inflorescence Height	−0.111	0.436	0.307
Time: Inflorescence Height	0.486	0.389	0.211
Time: Animal Dispersal	**−1.740**	**0.461**	**<0.001**
Time: Wind Dispersal	**−4.240**	**0.550**	**<0.001**
Time: Unassisted Dispersal	**−5.010**	**0.517**	**<0.001**

A separate model was run for each trait. Significant interactions are bolded ($p < 0.05$). Each trait and its interaction with time are included

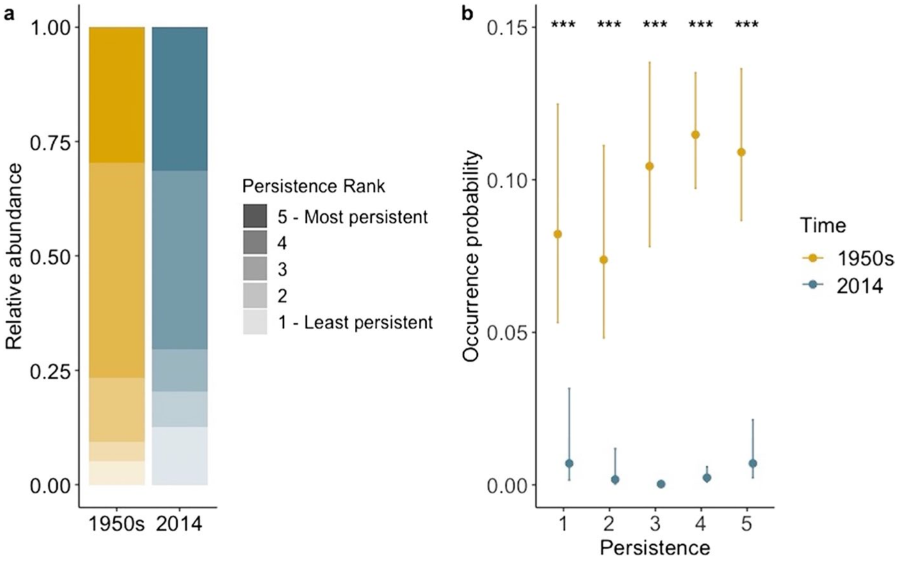

Fig. 2 **a** Comparison of persistence distributions between the 1950s and 2014. **b** Generalized linear mixed model of occurrence probabilities of persistence category in the 1950s (yellow) and 2014 (blue). Significant interactions are marked with asterisks (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

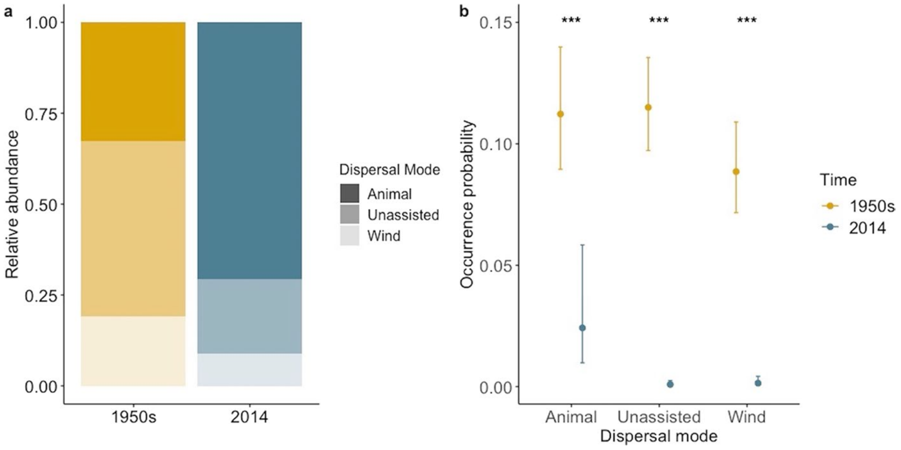

Fig. 3 **a** Comparison of relative dispersal mode distributions between the 1950s and 2014. **b** Generalized linear mixed effects model of occurrence probabilities of dispersal modes in the 1950s (yellow) and 2014 (blue). Significant interactions are marked with asterisks (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

Average seed mass increased from an average of 5.51 mg to 8.28 mg ($t_{259.4} = -2.03$, $p = 0.04$; Fig. 4a) from the 1950s to 2014. Seed mass significantly interacted with time to predict species abundance (Fig. 4b; Table 1), resulting in a lower abundance of species with small, lightweight seeds in 2014. Inflorescence height, however, did not change significantly between the two time periods (average of 62.76 cm and 66.37 cm for the 1950s and 2014, respectively; Fig. 4c; Table 1) and inflorescence height nor its interaction with time predicted species frequencies (Fig. 4d; Table 1). There was a weak but significant correlation between

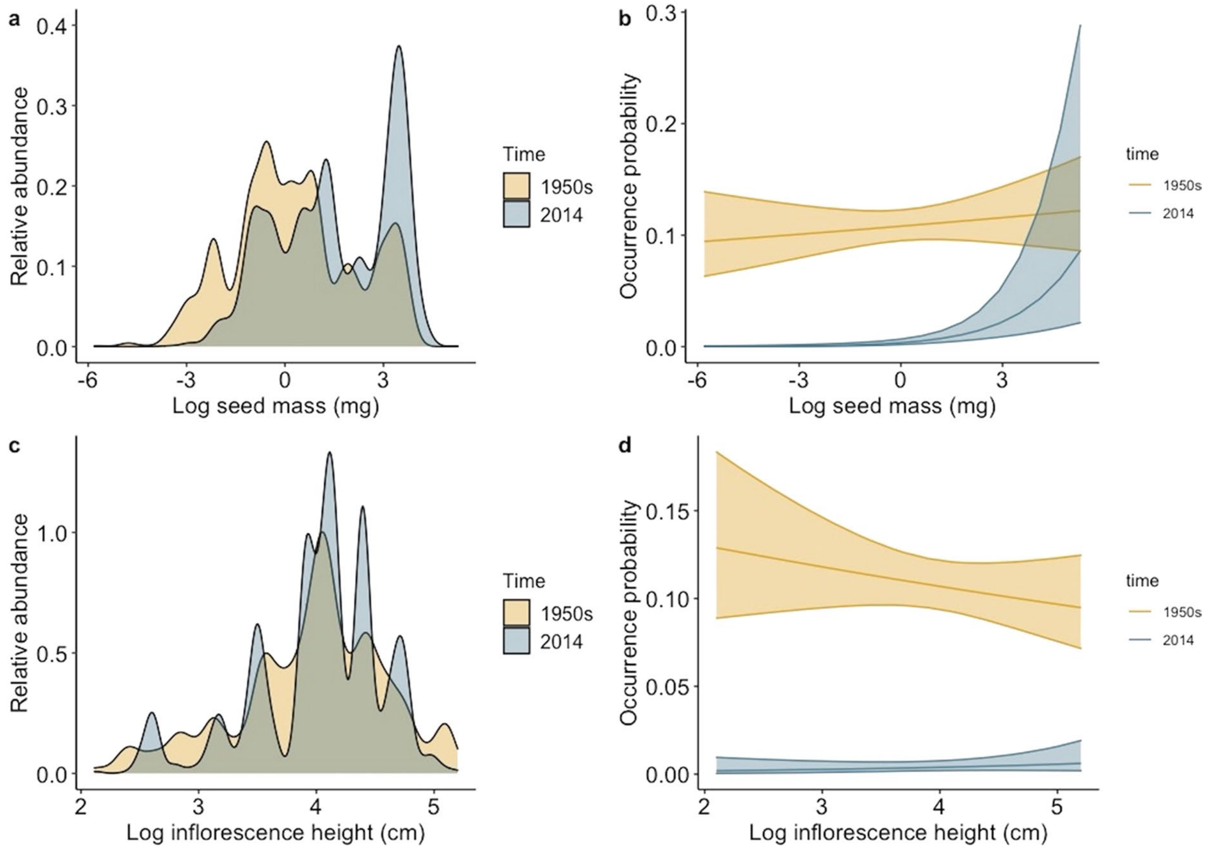

Fig. 4 **a** Comparison of seed mass distributions between the 1950s (yellow) and 2014 (blue) and **b** generalized linear mixed effects model of occurrence probabilities of seed mass in the 1950s (yellow) and 2014 (blue). **c** Comparison of inflorescence height distributions between the 1950s (yellow) and 2014 (blue) and **d** generalized linear mixed effects model of occurrence probabilities of inflorescence height in the 1950s (yellow) and 2014 (blue). Seed mass was the only continuous trait with a significant interaction with time ($p < 0.001$)

inflorescence height and seed mass ($R^2 = 0.12$, $p < 0.01$; Figure S1).

Discussion

The savannas of Wisconsin have undergone significant change in species composition and structure. These systems have experienced a significant increase in woody encroachment (Ladwig et al. 2018), altering the light and moisture patterns of what were historically open and heterogeneous systems. Our results indicate that change in functional composition captures potential mechanisms for community change in response to increased woody encroachment and canopy closure that is missing from analyses focusing on taxonomic changes alone.

We predicted that species with greater investment in belowground persistence structures (e.g., clonality, storage organs) in the 1950s would persist into the 2010s. We found that more persistent species (categories 4–5) indeed remained the dominant growth forms, but also that short-persisting species increased their relative abundance (categories 1–2); annual plants often produce many small seeds (Baker 1972; Silvertown, 1981; Hodgson et al. 2020), making persistence more likely if habitat preferences continue to be met facilitating recolonization success. The greatest losses were observed for non-clonal perennial species with investment in storage organs (category 3), implying a weak bi-modal distribution of persisting species. While the abundance of perennial species non-clonal has decreased, the few that have persisted have high abundances and are primarily woodland species (e.g., *Circaea lutetiana*). This suggests that remaining species belonging to this category of our persistence categories are those adapted to shady conditions now common in savannas. Shade tolerance could enable these intermediate-persisting species to compensate for their lack of clonality.

There was an overall decrease in species abundances between the two time periods, but steady relative abundance of highly clonal prairie species (categories 4–5) (e.g., *Coreopsis palmata*, *Monarda fistulosa*, *Comandra umbellata*) which may be harbingers of an extinction debt; persistence facilitated because of their long life-spans and clonal growth (de Witte and Stöcklin 2010). If encroachment continues, however, and new individuals of these species are unable to successfully establish before older individuals die, long-living, clonal species may also be lost from savanna understories given enough time. The continued presence of highly clonal species provides rationale for actively reopening savanna canopies which have become closed. Individuals that vegetatively remain may increase flowering and seed production if light availability increases because of restoration management (Turley et al. 2017). Additionally, highly persistent woodland savanna species (e.g., *Parthenocissus quinquefolia*, *Pteridium aquilinum*) have increased in abundance likely because they have and continue to thrive in shady environmental conditions, so creating a more open canopy could allow additional species to compete and coexist with these successful shade-adapted species.

Seed dispersal also influenced species abundance, as animal dispersed species became more abundant while species with unassisted and wind seed dispersal decreased with time, supporting our hypothesis. This change in the composition of dispersal traits is expected with a transition towards closed-canopy systems. Seeds of many prairie and savanna species are either unassisted or wind dispersed, whereas closed-canopy woodland species are typically animal dispersed (Takahashi and Kamitani 2004; Vittoz and Engler 2007). The abundance of animal-dispersed species increased over the past 60 years in Wisconsin savannas while unassisted species have decreased, likely driven by an increase in both fleshy-fruited woodland herbs (e.g., *Actaea spp.*) and species with adhesive seeds (e.g., *Desmodium spp.*, *Agrimonia spp.*, *Osmorhiza spp.)* (Sorensen 1986). Seed mass increased with time as a result of a loss of small-, lightweight-seeded species and an increase in large-seeded species. Although plant height has greater implications for dispersal than seed mass (Thomson et al. 2011), smaller seeds generally disperse farther than larger, heavier seeds. However, heavier seeds tend to be animal dispersed, which likely ameliorates the negative impact of being heavy and smaller seeds likely have unassisted dispersal. To test for the potential changes in seed mass within dispersal modes, we ran additional models testing for three-way interactions between time, dispersal mode, and seed mass, but this interaction was not statistically significant (Table S3). The change in dispersal mode at the community-level indicates a functional change in the savanna understory towards species with larger, animal-assisted seeds that are better dispersers than the unassisted, small-seeded species present in the 1950s. This increased dispersal ability could be a result of animal dispersers traveling greater distances than the seeds would alone (e.g., birds flying between savanna sites) and increased occurrences of animal dispersers, namely birds, in encroached savannas (Stanton et al. 2018, 2020).

The seedbank provides an additional potential mechanism for species persistence. Species with smaller, lighter seeds can persist longer in the seed bank because they become embedded in the soil more easily than larger seeds (Thomson and Grimes 1977). Despite the savanna understory now containing larger-seeded species, there is potential that the seedbank still contains propagules of many smaller-seeded species. For example, *Scutellaria parvula*, a short-statured forb with unassisted small seeds, disappeared from the savannas but could still be present in the soil seedbank. If a more open canopy structure is reinstated via management, these seeds may have the proper conditions for germination and (re)establishment. Additional traits worth considering include seed coat thickness, which—like seed mass—relates to a seed's ability to persist in the seed bank (Gardarin et al. 2010) and seed mass index, which may more directly affect persistence over mass alone. These trait would expand our understanding of persistence beyond individual plants to the persistence of seeds; data coverage in our dataset was too low to be included in these analyses.

Different functional traits are often correlated (Grime 1977; Westoby 1998; Wright et al. 2004; Reich 2014), making it difficult to ascertain which traits actually drive observed community patterns. Globally, plant height correlates with seed size (Díaz et al. 2015), but the correlation can be weak or absent at local scales (Herben et al. 2012). We found a very weak but significant correlation between the inflorescence height and seed mass in our data (Figure S1). Our observed change in seed size, with large-seeded species becoming more abundant, would indicate a likely increase in plant height as well, which we did not observe. This indicates that our observed changes in persistence traits and dispersal traits may be occurring independently. Failing to account for potential functional correlations and tradeoffs when assessing long-term community change can hide potential mechanisms for this change.

Over the past 60 years of savanna community change, there was a loss of moderately clonal, small seeded, and short-statured herbaceous species. Continued woody encroachment will presumably drive continued community change, particularly the loss of highly clonal savanna and prairies species that have been able to resist complete extirpation thus far. Our results suggest that using restoration management practices such as burning and thinning to create a more open canopy structure may promote the recovery of the herbaceous community. In addition, restoration efforts could prioritize seeding species that have: (1) been lost from the aboveground community completely and may not be in the seedbank, and (2) have functional traits that may promote a routine, low-intensity fire regime (e.g., high flammability and litter production).

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Declarations

Conflict of interest The authors declare that they have no known competing personal relationships or financial interests that could have appeared to influence the work reported in this paper.

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