Long-term trends in the understory communities of Wisconsin forests: 50 years of climate change and species' distribution patterns

By

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A dissertation submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

(Botany)

at the

UNIVERSITY OF WISCONSIN-MADISON

2016

Date of final oral examination: 07/25/2016

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For Lia and Rowan

Acknowledgements

Completing this dissertation is a direct outcome of the support, guidance, friendship and encouragement of many people.

I am grateful to my advisor, Don Waller, for welcoming me into the lab and opening up the treasure trove of resources he and his students have amassed over the years. He has always made himself available and I consider myself fortunate to have been one of his students. Don gave me the freedom to explore a range of scientific questions and helped me express the results by editing my writing for clarity and meaning. Many thanks for everything.

My committee has been incredibly generous with their time, feedback and expertise over the course of my program. Tom Givnish shared his extensive insights into the vegetation of Wisconsin and challenged me to think about ecological questions in fundamental terms. I am very grateful to Sara Hotchkiss for the thoughtfulness and perspective she has provided throughout all stages of my PhD. Bret Larget's expertise and enthusiasm for rigorous statistical analyses has motivated me to pursue a strong analytical foundation. Jack Williams has shared feedback, methods and scientific insights that have greatly influenced the work presented here.

I initially began my PhD at the University of Florida and although my time there was short, my advisor, Jack Putz, was highly influential in shaping my scientific viewpoint. I am ever grateful for his mentorship, support and advice.

I am particularly grateful for the support and encouragement of many current and previous members of the Waller lab: Bil Alverson, Katie Frerker, Daijiang Li, Sara Souther, Greg Sonnier, Lauren Bradshaw, Ali Paulson, Shiteng Kang, Rachel Toczydlowski, Jeannine Richards, as well as others. Specifically, I want to thank my

officemates Ali and Daijiang. It has been a privilege to be in graduate school with you both and to know that I can always count on you for encouragement and support.

I have been extremely fortunate to have access to several high quality datasets that made this work possible. Chris Kucharik generously provided the climate data used in each of my chapters. Dave Rogers, Shannon Wiegmann, Sarah Johnson, Tom Rooney and Daijiang Li all spent extensive time and energy collecting the resurvey data. The above people along with Bil Alverson, Chengke Bai, Katie Amatangelo and Greg Sonnier were involved in collecting the trait data, for which I am very grateful. This list is likely much longer, including all of the field assistants and lab technicians who participated in collecting the data. To everyone involved, I express my sincere gratitude.

Don and the other PIs (Tom Givnish, Ken Cameron and Ken Sytsma) generously supported me through their Dimensions of Biodiversity grant (DEB-1046355). Additionally, I greatly appreciate the Botany Department staff for facilitating all of the daily aspects of being in the Department.

Both the Ash and Coleman families have provided untold support throughout my program. Most of all, I am grateful to my parents for fostering my interest in science and being a constant source of encouragement.

Above all, I dedicate this work to my family. Lia, your partnership and friendship mean everything to me. I could not have done this without your constant love and support. Rowan, you keep me grounded. As I watch you get older, I am reminded every day about what is most important in life.

Statement of author contributions

For Chapter 1, Jeremy Ash and Donald Waller conceived of research. Jeremy Ash developed and conducted analyses, and wrote the first draft of the manuscript. Jeremy Ash, Donald Waller and Tom Givnish all contributed to the hypotheses being tested and revising the manuscript.

For Chapter 2, Jeremy Ash, Daijiang Li and Donald Waller conceived of research. Jeremy Ash developed and conducted analyses, and wrote the first draft of the manuscript. Jeremy Ash, Daijiang Li, Sarah Johnson, Dave Rogers and Donald Waller all contributed to revising the manuscript.

For Chapter 3, Jeremy Ash and Donald Waller conceived of research. Jeremy Ash developed and conducted analyses, and wrote the first draft of the manuscript. Jeremy Ash, Daijiang Li, Sarah Johnson, Dave Rogers, Gregory Sonnier and Donald Waller all contributed to revising the manuscript.

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Abstract

Long-term trends in the understory communities of Wisconsin forests: 50 years of climate change and species' distribution patterns

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The effects of climate change on ecological systems are complex and difficult to ascertain. Our ability to detect the influence of climate drivers is limited in part by the availability of baseline data. Long-term studies provide an essential component to understand the degree to which climate change has influenced the ecology of species and communities. These studies can be used to fill the gap between understanding recent ecological responses to climate change and predicting future scenarios. Using historical forest surveys from the 1950s and resurveys of these same sites in the 2000s, I investigate the environmental drivers that structure the distribution of forest understory species over space and time. I quantify shifts in the abundance and distribution of understory species over the 50-year time period and relate species' patterns to equivalent spatial shifts in climate conditions. I additionally test how species-environment relationships are mediated by life history and functional traits. Lastly, I explore whether accounting for species' interactions improves the predictive ability of species' distribution models.

Understory species' distributions have shifted primarily to the northwest over the 50-year interval, largely paralleling but lagging shifts in climatic conditions. The extent of these lags is related to species' ability to colonize new sites, but only weakly related to their functional traits. While broader scale geographic shifts appear unrelated to species' traits, they do strongly mediate species-environment relationships across the network of survey sites. Species' distributions at individual time periods appear to be strongly structured by soil variation, overstory dynamics, and climatic gradients. However, changes in species' abundance at the site level appear unrelated to climate change and overstory dynamics. Additionally, species' interactions appear secondary to environmental variables for structuring species' distributions, though the importance of these processes varies widely across species and over time. Collectively, understory species show highly individualistic responses to climatic gradients, environmental conditions and species' interactions. Our ability to forecast future responses appears challenged by our limited ability to predict changes in species' abundance patterns. Nonetheless, the research presented here provides a quantitative measure of recent responses to ecological change and a foundation for predicting future scenarios.

Introduction

A central challenge in ecology is to understand and predict the responses of species, communities and ecosystems to global climate change. Considerable evidence now exists that recent and accelerating rates of climate change (Stocker et al. 2013) have caused ecological impacts at a variety of scales. Ecological changes have been documented in the phenology (Ellwood *et al.*, 2013), elevation and latitudinal range (Lenoir *et al.*, 2008; Stocker *et al.*, 2013; Amano *et al.*, 2014) and extinction risks of species (Parmesan & Yohe, 2003; Ellwood *et al.*, 2013). Historical surveys afford insight into evaluating the impacts of climate change and other environmental drivers (Tingley & Beissinger, 2009; Vellend *et al.*, 2013). Resurvey efforts have identified marked changes over time to local and regional patterns of diversity, species' distribution shifts and occupancy patterns (Leach & Givnish, 1996; Moritz *et al.*, 2008; Tingley *et al.*, 2009; Damschen *et al.*, 2010; Crimmins *et al.*, 2011; Waller *et al.*, 2012; Johnson *et al.*, 2014; Li & Waller, 2015; McCune & Vellend, 2015), with a number of identified causal agents. These datasets can be used as a foundation for disentangling environmental and anthropogenic drivers of ecological change and forecasting possible future impacts.

Original survey efforts by Curtis (1959) and resurveys by Waller and colleagues (2012) provide a unique perspective into recent changes to the flora of Wisconsin. These datasets provide a baseline by which to measure the rate and magnitude of ecological change in the flora. Efforts to date have shown strong patterns of biotic homogenization throughout the state (Rooney *et al.*, 2004; Rogers *et al.*, 2008; Johnson *et al.*, 2014; Li & Waller, 2015), but also that species are responding in an individualistic manner with clearly defined "winners" and "losers" (Wiegmann & Waller, 2006). Collectively, forest understory communities have shown strong changes over this time period. While there are many possible drivers of change (i.e., fire suppression, succession, deer herbivory, nitrogen deposition, habitat fragmentation, etc.), systematic climate change throughout the state may also be playing a role in influencing the distribution and abundance of understory species.

The U.S. Midwest is projected to experience some of the most pronounced rates of local climate change and highest spatial velocities of climate movement (WICCI, 2011; Dobrowski *et al.*, 2013; Ordonez *et al.*, 2014). There are already evident trends in the last 50 years of climate patterns in Wisconsin: winter and springtime temperatures have increased, particularly in the northwest, minimum temperatures have increased in the summer months, and both drought and wetter conditions have occurred throughout the state (Kucharik *et al.*, 2010; WICCI, 2011). Future projections include a pronounced warming by the middle of the century and a general increase in the mean and variance of precipitation events (WICCI, 2011).

Herbaceous communities are thought to be particularly susceptible to climate change, given limited dispersal ability and lagged responses in distributional shifts (Van der Veken *et al.*, 2007), although see De Frenne *et al.* (2013). Within Wisconsin, there is already some evidence that plants have responded to climate change. Phenological data gathered by Aldo and Nina Leopold combined with community resampling data have shown that many spring flowering species have advanced their phenology by as much as 2 weeks (Bradley *et al.*, 1999; Ellwood *et al.*, 2013). While some species show climatic niche conservatism through shifting phenologies, others may track climate change by shifting their spatial distributions (Amano *et al.*, 2014).

The climate of Wisconsin has changed considerably over time (Kucharik *et al.*, 2010) and space (Dobrowski *et al.*, 2013). As such, it is expected that species' responses to climate change will also be spatially variable. While the classic hypothesis is for species to track rising temperatures by moving northward or up in elevation (Thomas *et al.*, 2004; Hickling *et al.*, 2006; Parmesan, 2006), the realized response is often more complex (Crimmins *et al.*, 2011; Tingley *et al.*, 2012). Species have been shown to track temperature changes (Parmesan & Yohe, 2003; Normand *et al.*, 2009; Chen *et al.*, 2011), but interactive effects of precipitation and temperature (as well as more nuanced climate variables, such as seasonal-based measures) will also determine the extent of species' responses to climate change (Crimmins *et al.*, 2011). For instance, temperature and precipitation seasonality are likely to influence the spatial responses of species (Easterling, 2000; Parmesan *et al.*, 2000). Microclimate changes that drive individual-level responses, such as flowering and leaf phenology, may influence large scale spatial responses of species (Amano *et al.*, 2014). With such individualistic and complex patterns, a fundamental challenge is to identify general trends in the responses of species to environmental change. One promising avenue for generalizing across the landscape of species-level responses is through the use of species' traits.

Functional traits provide insight into the ecological and life history mechanisms by which species respond to dynamic environments, as they represent the interface between an organism and its environment (Buckley & Kingsolver, 2012). Additionally, geographic traits, such as a species' area of occurrence, can be useful when comparing how widespread versus narrowly distributed species differ in spatial responses. When coupled with long-term survey data, traits provide a powerful approach for quantifying ecological change (Damschen *et al.*, 2012; Soudzilovskaia *et al.*, 2013; Auer & King, 2014; Boucek & Rehage, 2014; Pearson *et al.*, 2014). For instance, traits have been used as a predictive tool in local and regional community assembly processes (Shipley *et al.*, 2006; Xing *et al.*, 2014) and have been shown to vary across large scale climate gradients (Wright *et al.*, 2005). Despite these documented trait-environment relationships, less is understood about how traits might be involved in predicting species' responses to climate change. Additionally, some of the most widely implemented climate change vulnerability assessments are based upon a set of traits hypothesized to reflect susceptibility to climate change (i.e., NatureServe Climate Change Vulnerability Index, http://www.natureserve.org/conservation-tools/climate-change-vulnerability-index).

Species' traits hold a larger appeal not only in providing a more mechanistic understanding of drivers of change, but also in their ability to identify shared patterns among functionally similar species (Buckley & Kingsolver, 2012). Additionally, an enhanced understanding of how traits interact with spatial gradients to structure species' distribution patterns is essential for our ability to predict future outcomes of climate change (Pollock *et al.*, 2012). Trait-based approaches have been used in understanding the role of climatic constraints in community assembly (Laughlin *et al.*, 2011; Frenette-Dussault *et al.*, 2012), however these studies use snapshot data to infer temporal dynamics and are largely focused at localized scales. Strong spatial scale dependence has been demonstrated in studies on trait-based community assembly processes (Cavender-Bares *et al.*, 2006; Swenson & Enquist, 2009; Kraft & Ackerly, 2010; Xing *et al.*, 2014), necessitating an explicit consideration of scale and spatial domain. The main drivers of assembly differ at localized scales (i.e., biotic interactions) to more regional scales (i.e., climate and edaphic factors), so studies testing the role of traits in the distribution of species need to consider the spatial scale variance in trait-based processes (Smith *et al.*, 2013). Approaches developed by Jamil et al. (2013) and Pollock et al. (2012) consider the role of traits in structuring species' occupancy patterns and the interactive influence of traits and climate (or other environmental variables) in structuring species' distribution patterns. The integration of the species-trait-environment relationship pushes the boundaries of inference afforded by the classical species distribution modeling (SDM) approach.

Species distribution modeling is a powerful tool that couples with species occurrence data with environmental gradients to develop predictive distribution models (Franklin, 2010). While SDM has formed one of the core areas for understanding how species respond in geographic space, it can be limited in scope and predictive power (Ibanez *et al.*, 2006). Often, these models abstract species from the biotic processes that also shape their distribution. Proper application of these models can be effectively utilized as a tool for understanding species' sensitivity to climate change (Araujo & Peterson, 2012), however other dynamic ecological processes shape the current and future distribution of species. While climatic controls operate over large scales of species' distributions, local forces such as competition and other species' interactions may exert a strong influence on local abundance and occupancy. New integrative approaches have been developed that incorporate analytical tools from community ecology (i.e., co-occurrence patterns) into multi-species distribution models to more fully depict the conditions under which distribution patterns might change (Kissling *et al.*, 2012). Using these models to characterize existing changes and parameterizing predictive models can thus capture more of the biological determinants of species' distributions. Although co-occurrence patterns have a contentious history in ecology (see Gotelli & McCabe, 2002 for a summary), they can provide a surrogate for biotic interactions by identifying non-random species' associations. Additionally, residual variation in the co-occurrence patterns can be analyzed using functional traits to provide a more mechanistic understanding of species' co-occurrence patterns and their shared response to environmental gradients (Pollock *et al.*, 2014).

Within this context, I investigate how climate change has driven changes in the abundance and distribution of forest understory species in Wisconsin over the past 50 years. Specifically, my main objective is to link the often-separate veins of research in community ecology (both species and trait-based methods) with species' distribution modeling to fully characterize changes in the understory flora of Wisconsin. In Chapter 1, I investigate how state-level shifts in species' distributions are correlated with equivalent spatial shifts in climatic conditions. By comparing shifts in species' distributions and climate conditions, I quantify species' ability to track climate changes (i.e., the migratory lag). I then decompose species' variation in their lags into the underlying population-level processes (colonization, extirpation and change in abundance) and their functional traits. In Chapter 2, I consider site-level dynamics by modeling static species' distributions at each time period, as well as the change in species' abundances over time. The models integrate the main effects of environmental variables and interactions with their functional traits to understand how variation in species' life history controls species' distribution patterns over space and time. In Chapter 3, I consider the importance of biotic interactions in shaping species' distributions and community-level patterns. I relate species' co-occurrence patterns to shared environmental responses and biotic interactions in a joint species distribution model. Collectively, these analyses indicate the degree to which understory communities in Wisconsin have responded to recent climate change and provide a foundation for forecasting future scenarios.

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Chapter 1 - Tracking lags in historical plant species' shifts in relation to regional climate change

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Citation:

Ash JD, Givnish TJ, Waller DM. *in press*. Tracking lags in historical plant species' shifts in relation to regional climate change. *Global Change Biology*.

Abstract

Can species shift their distributions fast enough to track changes in climate? We used abundance data from the 1950s and the 2000s in Wisconsin to measure shifts in the distribution and abundance of 78 forest-understory plant species over the last half-century and compare these shifts to changes in climate. We estimated temporal shifts in the geographic distribution of each species using vectors to connect abundance-weighted centroids from the 1950s and 2000s. These shifts in distribution reflect colonization, extirpation, and changes in abundance within sites, separately quantified here. We then applied climate analog analyses to compute vectors representing the climate change that each species experienced. Species shifted mostly to the northwest (mean: 49 ± 29 km) primarily reflecting processes of colonization and changes in local abundance. Analog climates for these species shifted even further to the northwest, however, exceeding species' shifts by an average of 90 ± 40 km. Most species thus failed to match recent rates of climate change. These lags decline in species that have colonized more sites and those with broader site occupancy, larger seed mass, and higher habitat fidelity. Thus, species' traits appear to affect their responses to climate change, but relationships are weak. As climate change accelerates, these lags will likely increase, potentially threatening the persistence of species lacking the capacity to disperse to new sites or locally adapt. However, species with greater lags have not yet declined more in abundance. The extent of these threats will likely depend on how other drivers of ecological change and interactions among species affect their responses to climate change.

Keywords: forest understory; climate analog; geographic centroid; functional traits; migratory lag

Introduction

Climate change is affecting ecological communities by shifting patterns of species' phenology (Ellwood *et al.*, 2013), elevational and latitudinal ranges (Lenoir *et al.*, 2008; Amano *et al.*, 2014), risks of local extinction (Parmesan & Yohe, 2003), and the nature of local adaptation and evolution (Aitken *et al.*, 2008). Species' migrations are expected to lag climate change given limitations associated with dispersal ability, generation time, and interactions with other taxa (Corlett & Westcott, 2013). While migration lags have been observed across a broad range of taxa (Bertrand *et al.*, 2011; Chen *et al.*, 2011; Devictor *et al.*, 2012; La Sorte & Jetz, 2012; Schloss & Nuñez, 2012; Sunday *et al.*, 2015), our understanding of the processes that affect the differential ability of species to track climate change remains incomplete. Most climate-impact studies to date have focused on assessing how species respond to large-scale shifts in climate, limiting our understanding of how species may differ in their responses to local shifts in climate (Dawson *et al.*, 2011). Herbaceous communities may be particularly susceptible to climate change given that many species lack the capability to disperse long distances, limiting their ability to closely track shifts in climate (Van der Veken *et al.*, 2007). However, shaded forest understories can also ameliorate local environmental conditions in ways that could delay impacts of climate change (De Frenne *et al.*, 2013). Nevertheless, biological signals of climate change are still evident in the phenology of herbaceous plants, like those in central Wisconsin that now flower weeks earlier than they did earlier in the 20th century in apparent response to early-season warming (Bradley *et al.*, 1999; Wright & Bradley, 2009; Ellwood *et al.*, 2013).

Because the mechanisms by which plant species respond to climate change remain obscure, it is worth exploring whether species' functional traits affect these responses.

Functional traits reflect how organisms interact with their environment (McGill *et al.*, 2006). We therefore expect them to affect how plant species respond to climatic factors and future climate change (Buckley & Kingsolver, 2012; Pollock *et al.*, 2012). Traits vary in response to broad climate gradients (Wright *et al.*, 2005) and affect local and regional processes of community assembly (Shipley *et al.*, 2006; Xing *et al.*, 2014). Fewer studies, however, use life history and functional traits to assess species' responses to climate change. Life history traits and range characteristics served to predict extinction risk due to climate change in some regions (Pearson *et al.*, 2014), but these responses are complex and rarely generalize to predict range shifts across a broad range of taxa (Angert *et al.*, 2011). In studies resurveying multiple species across many sites, species' traits can help to disentangle diverse drivers of ecological change (Leach & Givnish, 1996; Damschen *et al.*, 2010; Crimmins *et al.*, 2011; Soudzilovskaia *et al.*, 2013; Amatangelo *et al.*, 2014; Savage & Vellend, 2014). It is thus reasonable to suppose that traits might help explain the complex responses of individual species to climate change.

Site resurveys have identified marked changes in local and regional patterns of diversity and species' incidence and abundance in the latter 20th century (Leach & Givnish, 1996; Damschen *et al.*, 2010; Crimmins *et al.*, 2011). The extensive ecological surveys made by J. T. Curtis and his students in the 1950s at more than 1000 sites (Curtis, 1959) provide a particularly useful baseline for evaluating the rate, nature, and extent of ecological change. Resurveys of forested sites in the 2000s (Waller *et al.*, 2012) reveal frequent declines in local species richness (α diversity) and pervasive declines in compositional differences among sites (β diversity, reflecting "biotic homogenization", Rooney *et al.*, 2004; Rogers *et al.*, 2008). Upland forests in northern Wisconsin lost an average of 15% of native plant species, with conspicuous declines in taxa susceptible to deer herbivory, and increases in exotic species and those avoiding or tolerating herbivory by deer (Rooney *et al.*, 2004; Wiegmann & Waller, 2006). The upland forests of southern Wisconsin saw sharper declines in α and β diversity and more invasion by exotic species related to habitat fragmentation (Rogers *et al.*, 2009). Sandy barrens dominated by open canopies of pines and oaks in the 1950s underwent succession in response to fire suppression, gaining some α diversity as they lost β diversity (Li & Waller, 2015).

Plant distributions in the upper Midwest are sensitive to climate as shown by the alignment of major ecotones along climatic gradients like the "tension zone" in Wisconsin, Michigan and Minnesota, where many species reach northern or southern range limits (Curtis, 1959). Cooler, moister, and snowier conditions prevail north of the tension zone. Over the past 50 years, winter and spring temperatures have increased, especially in northwestern Wisconsin (Kucharik *et al.*, 2010). In summer, minimum temperatures have increased while drought and extreme precipitation events have become more frequent throughout the state. Climate models predict pronounced warming by mid-century, with increases in both the mean and variance of annual precipitation and accelerating rates of local climate change (WICCI, 2011; Ordonez *et al.*, 2014).

Here we explore shifts in the distributions of 78 understory plant species over the past 50 years in Wisconsin and how these relate to shifts in local climatic conditions. We expect climate change to have affected plant distributions given the systematic climate changes that have occurred (WICCI, 2011). We hypothesize that shifts in species' distributions have paralleled shifts in climatic conditions. However, we also appreciate that the ability of species to shift in distribution may be limited by various factors including limited dispersal (especially in fragmented or heavily modified habitats), competition with other species (in which established plants have an inherent advantage), herbivory (e.g., by white-tailed deer), and other environmental factors. Using extensive resurvey data (Waller *et al.*, 2012), we estimate shifts in species' distributions using vectors connecting abundance-weighted centroids of the distribution of each species across 274 sites in Wisconsin surveyed in both the 1950s and 2000s. We further decompose these centroid shifts into vectors representing the underlying processes (local extirpation, colonization and changes in abundance) and relate them to the centroid shift vectors to understand which processes structure species' responses. To estimate how climates have shifted over this interval for each species, we apply climate analog analyses (Williams & Jackson, 2007; Veloz *et al.*, 2011; Ordonez & Williams, 2013a). These allow us to compare the average climatic conditions species experienced in the 1950s to those experienced in the early 2000s by weighting the observed climate shifts by species' abundances at each site. Using climate analog vectors for each species allows us to directly compare shifts in species' distribution and abundance to the changes in climate that species has experienced. These comparisons reveal that shifts in species' distributions have generally paralleled shifts in climate, but often fell short. We therefore ask whether variation in the magnitude of these lags is related to key life history and functional traits to learn more about the factors that may limit species' responses.

Methods

Field sampling

We analyzed changes across 274 study sites distributed across Wisconsin among three community types: southern upland forest (SUF), northern upland forest (NUF) and the central sand plains (CSP). These communities are compositionally distinct, with differing types and rates of ecological change over the last 50 years (Waller *et al.*, 2012). Wisconsin Plant Ecology Laboratory staff surveyed the vegetation of Wisconsin at approximately 1000 sites between 1942 and 1958 to characterize community composition and species' responses to environmental gradients (Curtis, 1959; Waller *et al.*, 2012). They relied on plotless methods to characterize the overstory and sampled the understory using 20 – 50 spaced 1m^2 quadrats placed along a U-shaped or box-shaped transect. Within each quadrat, they noted all species present (herbs, shrubs and tree seedlings), producing estimates of abundance based on their frequency across these 20 – 50 quadrats. Resurveys of the forested sites began in the 2000s using similar but more intensive sampling (80-120 quadrats) at 136 SUF sites (Rogers *et al.*, 2008), 108 NUF sites (Rooney *et al.*, 2004; Wiegmann & Waller, 2006), and 30 CSP sites (Li & Waller, 2015), for 274 sites in all (**Fig. 1**). Sampling design varied across community types (see citations above for specifics), but involved either replicating the original survey technique including more quadrats (SUF) or by using a series of evenly spaced quadrats along parallel transects (CSP and NUF). Here we focus on more abundant species to ensure adequate sample sizes, including only native species found in at least 5 sites and 50 quadrats. This yielded an initial pool of 117 species.

Climate Variables

We relied on 8 km gridded climate data of daily precipitation and minimum and maximum temperature between 1950 and 2006, spatially interpolated from an extensive network of weather stations to characterize historical climates (Kucharik *et al.*, 2010). We computed seasonal summary variables from these data for each of our 274 sites using mean daily temperature and precipitation for fall, winter, spring and summer; mean annual temperature and precipitation; annual temperature seasonality (coefficient of variation of mean monthly temperatures); and annual precipitation seasonality (standard deviation of mean monthly precipitation totals). We chose these summary variables to reflect a broad range of seasonal and annual aspects of climate change (Ordonez & Williams, 2013a).

Data Analysis

Centroid Shifts

Unlike many other studies that examine shifts in species' ranges or distributions in terms of presence-absence data, we used abundance-weighted measures to depict species' responses. These more accurately portray shifts in distribution, particularly in the short term as shifts in site incidence tend to lag behind shifts in climate (Chamberlain & Fuller, 2001; Virkkala & Lehikoinen, 2014). To measure shifts in geographic distribution, we calculated the abundance-weighted geographic centroid for each species in both the 1950s and 2000s. We weighted the mean latitude and longitude for each species at each site by its abundance (frequency) at that site, combining data across all sites. We then computed the bearing and distance for the shift in centroid for each species. These centroid shift vectors efficiently summarize changes in the distribution and abundance of each species across all the sites it occupied in the state. We then applied Rayleigh's Test of Uniformity to compare these bearings to a uniform circular distribution reflecting the null hypothesis of random centroid shifts. Rayleigh's statistic, *r*, quantifies the angular dispersion among the vectors from 0 (representing uniform dispersion) to 1 (indicating complete concentration in a single direction). We tested directionality of the centroid shifts by comparing the number of northward versus southward shifts using a binomial test. We also compared the distances moved between these two groups using a two-sample t-test. Seven species were highly unusual in showing centroid shifts greater than 3 standard deviations beyond the shifts of other species. These outliers are so extreme that we considered it likely they reflected some artifact. To be conservative, we excluded them from further analysis leaving a pool of 110 species. In addition, our ability to track northward movements is restricted for species limited to northern Wisconsin as we could not track movements beyond its northern border. We therefore also excluded species whose Wisconsin distributional limits were confined to the northern two-thirds of the state (i.e., with a southern distributional limit above 43.5°). This further limited our species pool to 78 species, but reduced possible biases.

To assess how changes in overall abundance might affect the centroid shifts, we compared the distance and bearing of the centroid shifts to changes in abundance across and within community types. For each species, we calculated the regional proportional change in abundance over the last 50 years as the log of the ratio of total abundance across all sites in the 2000s divided by its corresponding abundance in the 1950s. We did the same for each species within each community type to understand whether the centroid shifts were being driven by loss or gains in particular habitats. These proportional changes in abundance were then used to predict centroid shift distances (via simple linear regression) and bearing (via circular regression). The circular regression model assumes the response variable has a von Mises distribution (Fisher & Lee, 1992), a circular analog of the Gaussian distribution (Lee, 2010).

Climate Analog Analyses

To estimate the climate shifts occurring at the sites where species occurred, we applied climate analog analyses. This approach generates output vectors comparable to the centroid shifts (Williams & Jackson, 2007; Veloz *et al.*, 2011; Ordonez & Williams, 2013a). We determined spatial displacements in climatic conditions at each site by comparing its climate between 1950 and 1954 with the climates present at all grid cells in 2001-2005. We then calculated Standardized Euclidean Distances (SED) to each of the 2000s cells to identify which grid cell had the most similar climate (minimum SED). We then calculated the distance and bearing between each of the 1950s sites and its contemporary (2000s) climate analog cell.

To construct species-specific climate analogs, we then calculated a weighted average of the climate analog shifts for each species. As with calculating species' centroid shifts, we summed the climate analog vectors across all sites that the species occupied in the 1950s, allowing us to calculate a weighted mean based on its original abundance there. The resulting vector provides a summary description of how climates have changed for each species across all occupied sites. We then compared these species-specific climate analog shifts to the corresponding centroid shift vectors for each species by calculating the difference between the two (hereafter referred to as the "lag" vector) and exploring the correlation between these vectors of change. We also calculated the unweighted mean climate analog change vector across all sites. The abundance-weighted climate analogs provided a stronger signal for predicting shifts in species' centroids than this overall vector of climate change (using dot products; see below for calculation). This suggests both that the climate signal is real and that species have responded individually to changes in climate. We acknowledge that our calculated lag vectors may not reflect the real migratory lag for each species. Species may be responding to very distinct sets of climate variables and their centroid vector may be highly dissimilar in direction from their climate analog vector. However, to facilitate comparison across species, we use this term regardless of whether species appear to be tracking climate change.

Vector Correlation

We compared species' centroid vectors and climate analog vectors using correlation methods. Although several directional statistics exist to express correlations between circular variables (Crosby & Breaker, 1993), few incorporate both vector magnitude and direction. We use the dot product here to compare species' centroid shift vectors to their corresponding climate analog shift vectors. The dot product provides a measure that incorporates divergence in the angle between the vectors as well as their magnitudes:

$$\mathbf{a} \cdot \mathbf{b} = \|\mathbf{a}\|\|\mathbf{b}\| \cos \boldsymbol{\theta}$$

Here, $\|\mathbf{a}\|$ and $\|\mathbf{b}\|$ are the magnitudes of the species' centroid and climate analog vector shifts and $\boldsymbol{\theta}$ is the angle between them. If the dot product is positive, the angle between the vectors is acute, while negative values reflect obtuse angles and zeros reflect orthogonal (independent) vectors. The dot product provides the mathematical basis of many correlation statistics, including the parametric Pearson's coefficient. Higher dot product values reflect stronger correlations between species' centroid shifts and corresponding climate analog shifts, especially when these are manifest as larger displacements.

We tested statistical significance of the dot products using a randomization procedure. We randomized species' abundances in the 2000s resurvey across all sites occupied during both time periods and calculated the resulting centroid shift and dot product. We repeated this procedure 1000 times to generate a distribution of dot products for each species and considered the observed dot product to be significant if it exceeded the 5th or 95th percentiles of the distribution. Species with significant negative dot products have centroids that are moving in a direction away from their vectors of climate change, while species with positive dot products indicate that shifts in species' movements are in the same direction as the changes in climate those species experienced.

Decomposing the Centroid Shift Vector

To better understand the processes underlying variation in species' centroid shifts, we decomposed the centroid shift vectors into three components reflecting the colonization of new sites in the 2000s, local extirpation at the 1950s sites, and changes in abundance at the sites where species persisted over the study period. The origin of each vector was the species' weighted centroid in the 1950s. For the colonization vector, the end point was an abundance-weighted centroid of all newly colonized sites in the 2000s. The local extirpation vector included the centroid for all sites where the species was lost over time. The change in abundance vector was an abundance-weighted centroid of all sites where the species persisted over the study period. As above, we used Rayleigh's Test of Uniformity to test for the existence of a mean bearing. We additionally computed dot products between the centroid shifts and the vectors reflecting the underlying processes (colonization, local extirpation and change in abundance). These allowed us to assess associations between these processes and overall shifts in species' distribution. If species' northward movement is driven by colonization and changes in abundance, we expect to find a positive correlation between the centroid vectors and the process vectors (i.e., a positive dot product). If the northward movement of centroid vectors is driven by local extirpation in southern sites, we expect to find the local extirpation vectors pointing in the opposite direction and a large proportion of negative dot products. Lastly, we used simple linear regression to relate the magnitudes of the process vectors and the lag vectors to estimate how the different processes predict species' capacity to track climate change.

Trait Analyses

We tested whether functional traits might account for differences among species in the extent of their centroid shifts and the degree to which their shifts lagged the observed climate analogs by measuring the association of these lags with 12 chemical, morphological and physiological traits characterizing each species: seed dispersal mode, leaf carbon content, leaf circularity, leaf dry matter content, leaf length, leaf nitrogen content, leaf thickness, leaf width, seed mass, vegetative height, specific leaf area and stem dry matter content. We measured each trait on at least 12 individuals (four individuals from each of three sites) following standardized protocols (Pérez-Harguindeguy *et al.*, 2013). We assume that mean trait values have not changed since the 1950s and confirmed that trait variation is much greater among than within these species (DMW, unpublished data). These functional traits are known to affect species establishment, survival, reproduction, and/or leaf economics (Weiher *et al.*, 1999; Westoby *et al.*, 2002). Individual traits can display complex relationships when compared to a set of univariate climate variables (Moles *et al.*, 2014). Since we track climate changes using a multivariate representation of climate space, we cannot make specific predictions about how individual traits affect potential species' responses to particular changes in climate.

We also compared species' centroid shifts and lags to three other variables: each species' initial area of occurrence (a convex hull drawn around the occupied sites in the 1950s), estimates of genome size for these taxa sampled in Wisconsin (Bai *et al.*, 2012), and each species' Coefficient of Conservatism (CC), an estimate of its habitat fidelity (Swink and Wilhelm 1994). Values of CC range from 0 (no fidelity) to 10 (rarer species confined to a specific, high-quality habitats). We expected that species with larger initial distributions would have more opportunities to respond to climate change through colonization/movement and therefore the lag between the movement of the species and its analog climate would be smaller. Larger genome sizes are associated with longer generation times and slower growth rates (Suda *et al.*, 2014), suggesting that species with larger genomes might show greater climate lags. Species with narrower ecological habitat requirements (i.e., high Coefficient of Conservatism) might show larger lags and be more vulnerable to climate change if they are mostly restricted to small, dispersed patches of suitable habitat. For continuous traits, we used regression to assess how the magnitude of species' centroid shifts and the lags between these shifts in centroids and climate analog vectors covaried with values of these traits. We applied ANOVA to compare the magnitude of the lags among three different seed dispersal modes: unassisted, animal and wind dispersal. We further evaluated the importance of dispersal traits using ANCOVA to relate the magnitude of lags to seed mass, dispersal mode and their interaction. We log-transformed traits that were highly skewed. Leaf dry matter content and stem dry mater content were highly correlated (Pearson’s correlation coefficient = 0.85), as were leaf length and log leaf width (Pearson’s correlation coefficient = 0.75). However, because we analyzed each trait separately, we included all traits in these analyses.

We used R (R Development Core Team) for all analyses, including the following packages: *circular* for circular regression (Agostinelli & Lund, 2013), *geosphere* for vector bearing and distance calculations (Hijmans *et al.*, 2015b), *ncdf4*, *raster* and *dismo* for processing climate variables (Pierce, 2014; Hijmans, 2015; Hijmans *et al.*, 2015a), and *ggplot2* for plotting (Wickham, 2009).

Results

Over the 50-year study period, distributions of most common understory plant species in Wisconsin shifted substantially (**Fig. 2a, Table S1**). The centroid shift vector for a species efficiently summarizes both its initial mean distribution and its subsequent movement, aggregating quantitative abundance data across hundreds of sites. Species show considerable variation in the distance and direction of their geographic movement, but clear trends are evident. About 78% (61) of the 78 species display northward shifts, while 17 moved south ($P < 0.001$, binomial test). Northward shifts are also larger: 52.6 ± 30.3 km vs. 35.9 ± 20.6 km for southward shifts (means and S.D.'s, Welch's t = 2.63, df = 38, $P = 0.01$). The average bearing of all centroid shifts was to the northwest (327°) and highly directional (P < 0.001 by Rayleigh's test). The overall strength of association among these vectors is intermediate ($r = 0.54$). The average distance of all centroid shifts is 48.9 ± 29.1 km. These centroid shifts were uncorrelated to the often conspicuous changes in species' regional abundance we observed in these communities (**Fig. S1**, but species that gained abundance at the SUF sites tended to shift slightly more towards the northwest - **Fig. S2f**). These centroid vector shifts in distribution parallel higher rates of colonization and differential changes in local abundance for species persisting at those sites, with 63 and 70 of 78 species, respectively, having positive dot products. Local extirpation did not appear to drive these centroid shifts despite 46 of the 78 species having a negative dot product (**Fig. S3**). The colonization and change in abundance vectors both trend toward the northwest (with bearings of 344° and 316°, respectively) and are highly directional ($P < 0.001$ by Rayleigh's test for both). In contrast, the local extirpation vectors varied in magnitude and lacked consistent directionality ($P > 0.05$ by Rayleigh's test).

The climate analog analyses reveal that Wisconsin climates have changed considerably, but in heterogeneous ways over the past 50 years (**Fig. S4**). The climate analogs shifted an average of 114.3 ± 66.3 km, aggregated around a mean bearing of 305° ($P<0.001$, Rayleigh's test). The species-specific shifts in analog climates are slightly shorter (99.7 ± 17.8 km), but more consistent in distance (compare S.D.'s) and highly concentrated in direction ($r = 0.93$), clustered around a mean bearing of 319° ($P < 0.001$, Rayleigh's test) (**Fig. 2b**).

Shifts in species' distributions over the past 50 years generally parallel the direction of shifts in analog climates (**Fig. 2a,b**). Three-quarters of the species (60 of 78) show a positive dot product between the species and climate-change vectors (mean = 0.19 ± 0.29), indicating an acute angle between the vectors (**Table S1**). Among these positive dot products, over half (32) show a significant dot product relative to the randomized expectation. Only 6 species had significantly negative dot products. None of the traits appear related to the magnitude of these species' centroid shifts (**Table S2**).

Although species' distribution shifts thus appear to be tracking recent shifts in climate, most species' centroid shifts seriously lag the estimated geographic shifts in climatic conditions (**Figs. 2c and 3**). Species' centroid shifts average only 52% of the observed climate shift distances without accounting for direction. Taking into account the magnitudes and directions of both vectors, climate changes lead changes in species' distributions by an average of 89.7 ± 40.4 km. Species' centroid shifts usually track the direction of the climate analogs but cover only about 12% of the distance expected based on the changes in climate. The lag vectors representing the difference between the geographic shifts in climate and species' centroid shifts are concentrated in direction ($r = 0.60$) with a mean bearing of 333° ($P<0.001$, Rayleigh's test) (**Fig. 2c**). We find no relationship between overall changes in species' regional abundance (log ratio of abundances) and the magnitude of the lags (linear regression: log ratio = 90.72 + 9.81*lag, $F = 3.60$, $df = 76$, $p = 0.06$, $R^2 = 0.04$) as might be expected if some systematic driver (e.g., deer browsing) is acting to block species' movements. However, species with greater seed mass, area of occupancy, and coefficient of conservatism all show slightly smaller lags (**Table 1**). None of these associations account for more than 10% of the variation in observed lags, however, and no other continuous trait shows any relation to the lags. The magnitude of the lags did not differ among seed dispersal mode (ANOVA: $F_{(2,69)} = 0.96$, $p = 0.39$) or the interaction between dispersal mode and seed mass (**Table S3**). Species with higher magnitude colonization vectors showed smaller lags (**Fig. 4a**), though the relationship is weak and noisy. The other process vectors were statistically unrelated to the lags, however the directions of the slope coefficients were in the predicted direction (**Figs. 4b, c**).

Discussion

The unusually extensive baseline and contemporary data on plant abundances in

Wisconsin allowed us to document 50-year changes in the distributions of 78 understory plant species and relate these to the corresponding shifts in climatic conditions observed across the state. Vectors reflecting shits in the distribution of these species are clustered and trend towards the northwest. The shifts in climate conditions we estimated for these species are also clustered and trend in the same direction, supporting the hypothesis that the shifts in plant distribution observed may reflect, at least in part, the changes in climatic conditions experienced by these species. These shifts in species' distributions are correlated with the corresponding climate shifts, but differ considerably in the extent to which they match in magnitude the climate shifts. Trends in both temperature and precipitation acted to drive the NW bearing of the climate analogs (**Fig. S5**) that often matched the direction of the species' centroid shifts we observed. These results make clear that we should look beyond simplistic characterizations of climate change based only on temperature and general predictions that species will move up in latitude and elevation.

Climates have changed episodically throughout the Quaternary with temperate plant species generally adapting by shifting their ranges in ways that allowed them to track these changes over broader spatial (subcontinental) and temporal scales (multiple centuries) (Davis & Shaw, 2001; Ordonez & Williams, 2013b). We observed that most of the species in this study seriously lag even the past half-century of climate change, albeit at finer spatiotemporal scales. Vectors of climate change outpaced those of species' change by an average of 89.7 km, suggesting that over the last 50-years, most plant species have not closely tracked the climatic conditions that supported them 50 years ago. No native plant species went extinct in Wisconsin during the study period but many have undergone considerable changes in regional abundance (Wiegmann & Waller, 2006; Rogers *et al.*, 2008). We did not find overall changes in species' abundance to be related to their respective lags, however we did find that species' ability to colonize new sites in the 2000s decreased the magnitude of the lags. Taken together, this suggests that while lags have not yet begun to substantially affect local species' abundance and persistence, colonization of new sites since the original survey is critically related to tracking climate change. Overall, the ability of these plant species to keep pace with climate change appears limited and may become more so, particularly if changes in climate are accelerating and barriers to colonization increase.

Species' lags were unrelated to extirpation and changes in abundance, further underscoring the difficulty in predicting population dynamics under future climate change and land use scenarios. Landscape context and habitat fragmentation have substantially influenced colonization events in the southern upland sites, but extirpation appears to be more stochastic (Rogers *et al.*, 2009). Southern sites face an extinction debt wherein smaller patches of forest surrounded by urbanization are experiencing higher risks of extinction (Rogers *et al.*, 2008; 2009). As climate change accelerates, these fragmentation effects could slow dispersal and thus the arrival of species better adapted to current climatic conditions. Species may also adapt to changing climates through phenotypic plasticity and/or local genetic adaptation. However, many understory species have long lifespans, limiting opportunities for selection. If the cooler and moister conditions present under forest canopies act to buffer these habitats against warm and dry conditions (De Frenne *et al.*, 2013), species may gain time to disperse and adapt. Thus, differences in dispersal, habitat occupancy, and other forces may cause extinction risks to vary, explaining the lack of consistent extirpation vectors related to distribution shifts in these species. McCune and Vellend (2015) also found 40-year extirpation events to vary greatly in ways unrelated to plant traits. With so many forces acting, extinction dynamics are likely to be complex and difficult to predict.

Climate changes vary geographically (Ackerly *et al.*, 2010). Likewise, species' shifts in apparent response to climate change are also spatially complex and individualistic (Grenouillet & Comte, 2014). Several factors appear related to the variation we observed in colonization and local changes in abundance among these species. Many species may lack the capacity (or opportunities) to disperse adequately to keep up with climate change, particularly in fragmented habitats (Pearson *et al.*, 1998; Verheyen *et al.*, 2004). Species that disperse ballistically, via ants (myrmechory), and those lacking adaptations for dispersal may have difficulty colonizing new sites, although we do not find evidence here (ANOVA comparing magnitude of colonization vectors among seed dispersal mode: $F_{(2,69)} = 2.74$, $p = 0.07$). We also expected those with larger seeds and habitat specialists with conservative life histories to be inefficient at colonizing new sites (Estrada *et al.*, 2015). We found that species with smaller areas of occupancy tended to lag shifts in analog climates more as might be expected if they are dispersal-limited. However, we also found that species with larger seeds and higher Coefficients of Conservatism (habitat specialists) exhibited lower lags, counter to expectations. Although smaller seeds generally enhance mobility (Thomson *et al.*, 2011), the dispersal of larger seeds could reflect fruit adapted for animal (bird or mammal) dispersal. Among our focal species, animal-dispersed species indeed had larger seeds on average (mean = 172 mg) than species with unassisted (24 mg) or wind-dispersed seeds (12 mg) (ANOVA: $F_{(2,66)} = 5.65$, $p = 0.005$, followed by Tukey HSD test). Widespread logging in northern Wisconsin could also limit suitable sites for colonization or rates of dispersal for shade-adapted species. Because logging also acts to boost local deer densities, it could also increase deer impacts on species palatable to deer, lowering their density, reproductive success, and opportunities for local recruitment (Waller, 2014).

Few studies have examined how functional traits may mediate how plant species respond to climate change. Soudziloskaia et al. (2013), however, noted in their study of alpine plants that species with larger seeds responded less to climate change, the opposite pattern from what we observed. It may be that environmental conditions and/or landscape context mediate how plants that differ in functional traits respond to changes in climate. In our study, the extent of climate change varied strongly with location, with higher rates of change in parts of northern Wisconsin. This may have created or increased the size of lags for species (and traits) particular to that area. Although functional trait studies have long examined how traits co-vary along environmental gradients, the literature on how traits affect changes in abundance is less developed. Li et al. (*in review*) found several traits associated with patterns of species' incidence among the CSP sites, but less related to differences in abundance. We only find weak evidence here of traits predicting geographic shifts over time, but this may reflect the spatial scale of the study and the fact that we aggregated abundance across sites rather than predicting changes within sites.

Several forces appear to be driving the changes observed in these Wisconsin plant communities over the past 50 years. Herbivory by white-tailed deer in northern Wisconsin has reduced the abundance of many understory species including many broad-leaved herbs, while enhancing the abundance of graminoids and some ferns that better avoid or tolerate deer herbivory (Frerker *et al.*, 2014). Many understory species also show declining rates of colonization, contributing to the species' declines and biotic homogenization observed in these communities (Wiegmann & Waller, 2006; Rogers *et* *al.*, 2009; Li & Waller, 2015). Yet despite these other strong drivers of ecological change, the results presented here strongly support the conclusion that changes in climate have already begun to alter the abundance and distributions of Wisconsin forest plants. The complex effects of these other drivers likely limit and modify how these plant species can respond to climate change, contributing to the complexity of patterns found and the apparent climate lags observed among these 78 species. We also note that these lags represent limited estimates of species' responses to climate change given that we lack data on shifts in abundance and distribution beyond Wisconsin. Given these effects, the ability of species to track changes in climate within the state seems likely to affect the future composition of local communities and perhaps the floristics of the state as a whole.

Species' distribution patterns reflect the effects of a complex mosaic of interacting biotic and abiotic factors (Sexton *et al.*, 2009). Although we expect shifts in plant distribution to lag shifts in climate (Corlett & Westcott, 2013), these lags vary greatly in size, and probably importance, among species. Increases in the size of these lags could increase downward pressures on (or the intensity of natural selection within) populations that are already declining for other reasons (e.g., biotic interactions). Many species appear to lack the traits necessary to keep up with recent rates of climate change and other shifts in ecological conditions. As the rates of change in climatic and landscape conditions accelerate, these species will become more vulnerable and additional species will likely become vulnerable as well. Being able to quantify the gap between species' current distributions and the climatic conditions they are adapted to will be of value for understanding the threats these species face and the ways diverse drivers of ecological change interact to threaten the persistence of many species.

Acknowledgements

The NSF Dimensions of Biodiversity program provided essential funding for this work (DEB-1046355). C. Kucharik, D. Rogers, D. Li , G. Sonnier and B. Alverson generously shared data for the analyses. We also thank P. de Frenne, S. Hotchkiss, A. Paulson and J. Williams for closely reading an earlier version of the manuscript. The manuscript benefited greatly from comments provided by anonymous reviewers. DMW thanks I. Olivieri, O. Ronce, the LABex program, and ISEM for support during his sabbatical stay at the University of Montpellier, France.

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Tables

Table 1. Regression summaries from simple linear models relating the lag (difference between each species' centroid shift and climate analog shift, Fig. 2c) to genome size (c-value), habitat fidelity (coefficient of conservatism) and the suite of functional traits listed below. Bolded values indicate statistical significance at an alpha level of 0.05.

Trait	**Intercept**	**β estimate**	**SE (β)**	***t* value**	***p* value**	**R²**	**n**
Area of occurrence	**90.05**	**-9.64**	**4.54**	**-2.12**	**0.04**	**0.06**	**77**
C-value	87.84	-7.66	4.86	-1.58	0.12	0.04	63
Coefficient of conservatism	**89.82**	**-12.25**	**4.43**	**-2.76**	**0.01**	**0.10**	**73**
Leaf carbon content (m^2 g^{-1})	88.80	-7.41	4.55	-1.63	0.11	0.04	71
Leaf circularity (no units)	89.36	0.06	4.71	0.01	0.99	0.00	72
Leaf dry matter content (mg g^{-1})	89.82	-3.42	4.65	-0.74	0.46	0.01	73
Leaf length (cm)	89.82	-5.78	4.61	-1.25	0.21	0.02	73
Leaf nitrogen content (m^2 g^{-1})	88.80	-5.06	4.60	-1.10	0.27	0.02	71
Log leaf thickness (mm)	89.82	-0.37	4.66	-0.08	0.94	0.00	73
Log leaf width (cm)	89.82	-7.45	4.58	-1.63	0.11	0.04	73
Log seed mass (g)	**91.21**	**-10.33**	**4.47**	**-2.31**	**0.02**	**0.07**	**70**
Log vegetative height (cm)	89.82	0.45	4.66	0.10	0.92	0.00	73
Specific leaf area (m^2 kg^{-1})	89.82	1.84	4.66	0.40	0.69	0.00	73
Stem dry matter content (mg g^{-1})	89.82	-1.14	4.66	-0.24	0.81	0.00	73

Figure Captions

Figure 1. Locations and community types of the 274 sites resampled across Wisconsin. Sites are colored by community types: northern upland forest (NUF), southern upland forest (SUF), and pine barrens of the central sand plains (CSP). The historical location of the tension zone designated by Curtis (1959) is shown in gray.

Figure 2. Vector fields showing the species' centroids (a), climate analogs (b) and the difference between the two (c). **(a)** The shifts in species' centroids from the 1950s to the 2000s for 78 focal species. The magnitude and direction of each vector represents the shift in the abundance-weighted centroid for each species over this time period; the origin of the vector represents the location of the centroid in the 1950s. (**b)** The abundance-weighted change vector for climate analogs for each species, as in (a). (**c)** The lag, or difference between the species' centroid and climate analog vectors. For each panel, the embedded rose plot shows the frequency histogram of the bearings of these shifts, with the mean bearing represented by the yellow arrow.

Figure 3. The magnitudes of the species' centroid shift vectors (Fig. 2a) and climate analog vectors (Fig. 2b). If species were able to match the magnitude of changes in their climatic conditions, we would expect points to fall along the one-to-one line shown in black. Instead, most species fall below that line (that is, lagging change in their climate analogs).

Figure 4. The magnitudes of the lags and the three process vectors: (a) colonization, (b) local extirpation and (c) changes in abundance. (a) The

magnitude of the lag is significantly related to the magnitude of the colonization vector (linear regression: $y = 107.84 - 0.26x$, $F = 4.62$, $df = 76$, $p = 0.03$, $R^2 = 0.06$). (b) There is no relationship with the magnitude of the local extirpation vector ($y = 87.56 + 0.04x$, $F = 0.19$, $df = 76$, $p = 0.66$, $R^2 = 0.002$) or (c) the change in abundance vector ($y = 102.21 - 0.27x$, $F = 3.42$, $df = 76$, $p = 0.07$, $R^2 = 0.04$).

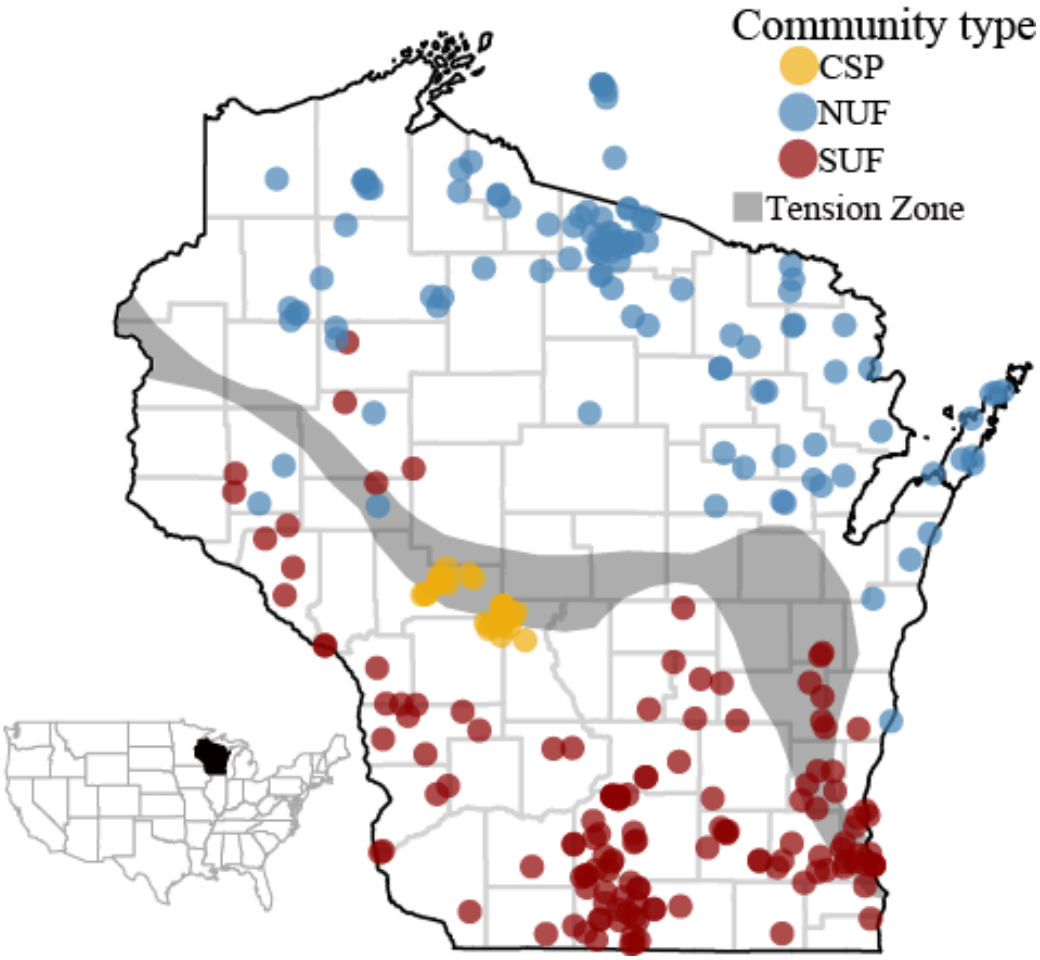


Figure 1.

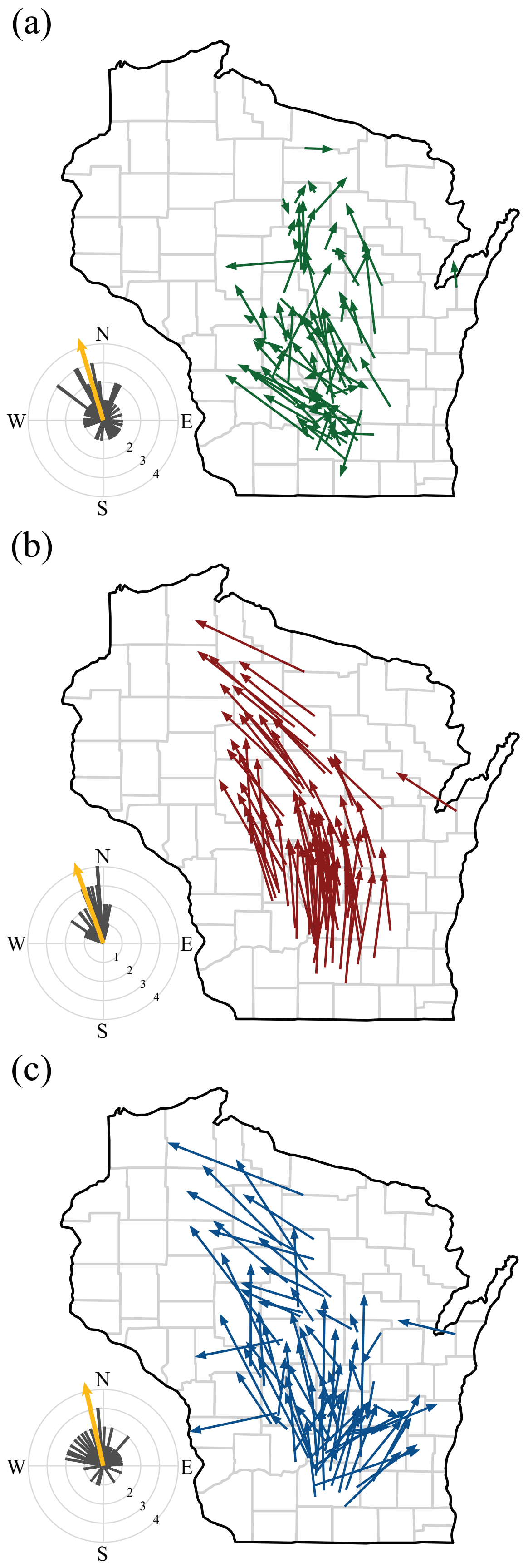


Figure 2.

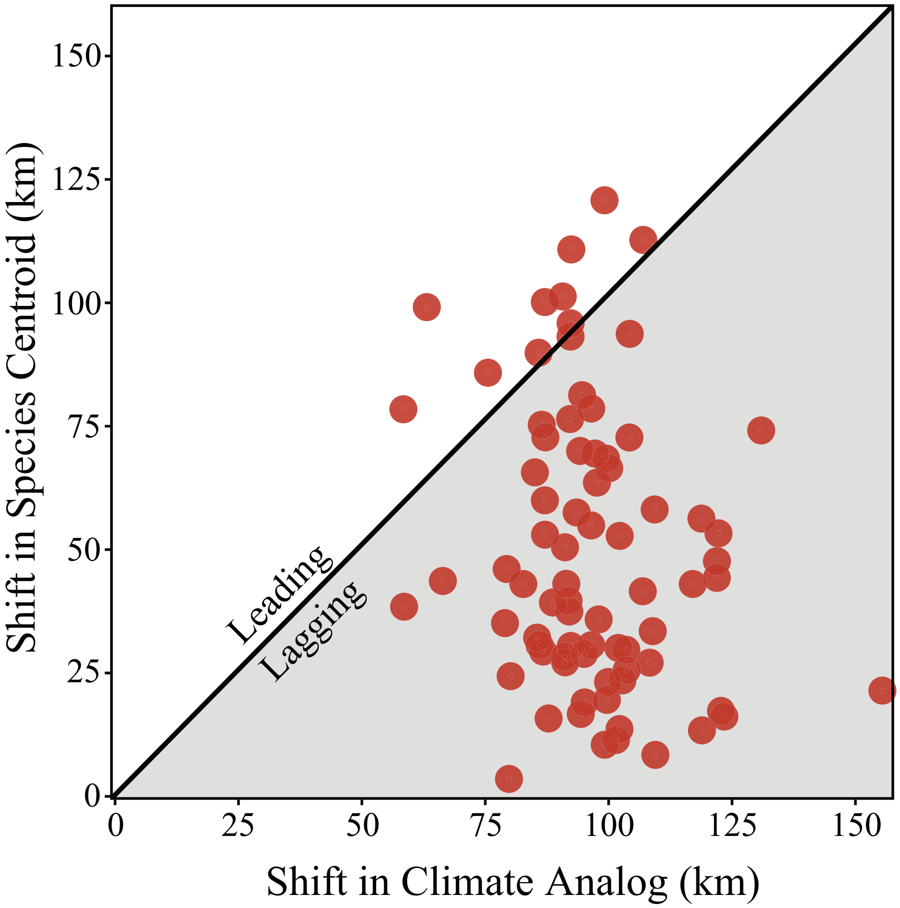

Shift in Species Centroid (km)
0
25
50
75
100
125
150
Shift in Climate Analog (km)
0
25
50
75
100
125
150
Leading
Lagging

Figure 3.

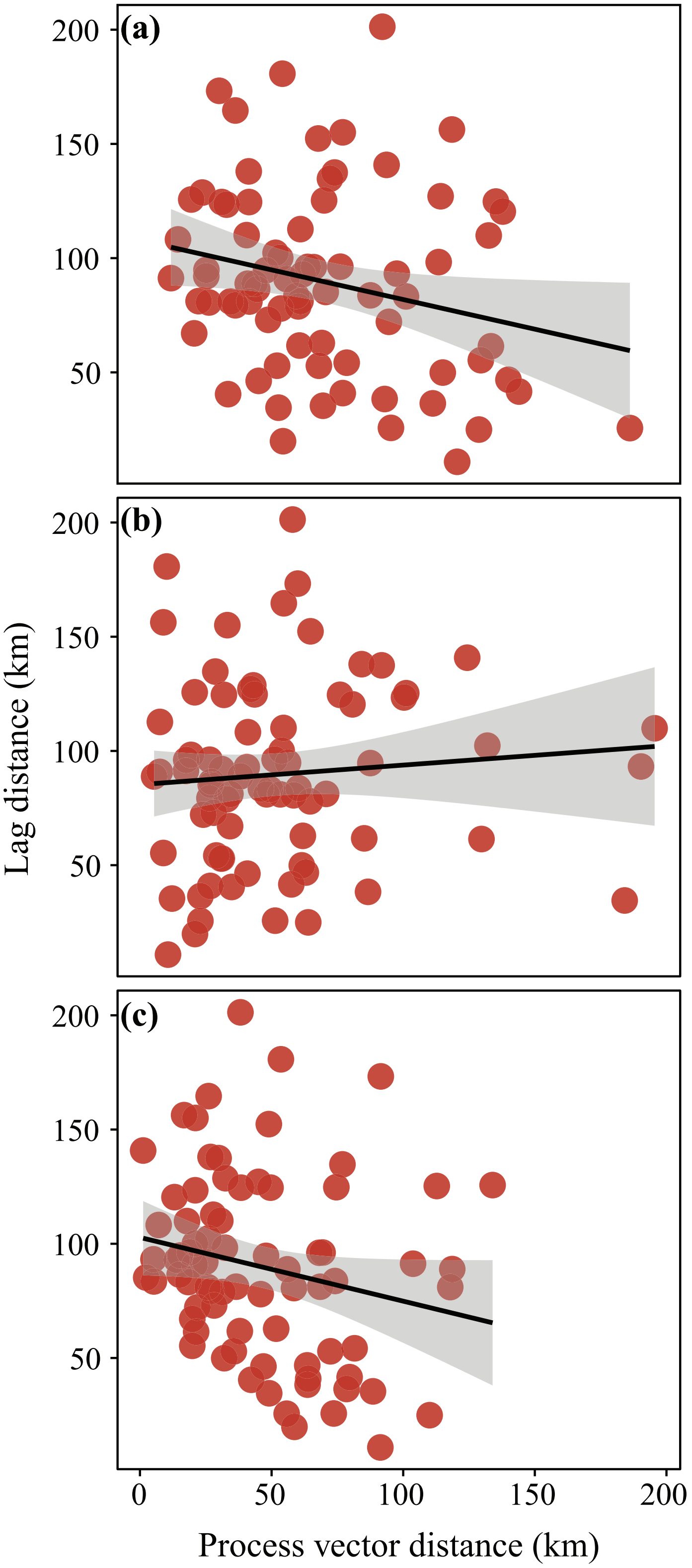

(a)
(b)
(c)
200
150
100
50
Lag distance (km)
0
50
100
150
200
Process vector distance (km)

Figure 4.

Appendix

Table S1. An excel file of the focal species, centroid metrics, dot products and traits.

Available upon request (jeremyd.ash@gmail.com).

Table S2: Regression summaries from simple linear models relating the magnitude of each species centroid shift (Fig. 2a) to genome size (c-value), habitat fidelity (coefficient of conservatism) and the suite of functional traits listed below. For dispersal mode, there was no significant difference between the mean centroid shift for animal (50.6 km), wind (46.4 km) or unassisted seed dispersal (46.0 km) (ANOVA: $F_{(2,69)} = 0.21$, $p = 0.81$).

Trait	**Intercept**	**β estimate**	**SE (β)**	***t* value**	***p* value**	**R²**	**n**
Area of occupancy	49.18	2.29	3.37	0.68	0.50	0.01	77
C-value	46.58	-1.36	3.25	-0.42	0.68	0.00	63
Coefficient of conservatism	48.52	1.50	3.39	0.44	0.66	0.00	73
Leaf carbon content (m^2 g^{-1})	48.41	-1.83	3.46	-0.53	0.60	0.00	71
Leaf circularity (no units)	48.98	-6.44	3.33	-1.94	0.06	0.05	72
Leaf dry matter content (mg g^{-1})	48.52	-0.81	3.39	-0.24	0.81	0.00	73
Leaf length (cm)	48.52	-1.13	3.39	-0.33	0.74	0.00	73
Leaf nitrogen content (m^2 g^{-1})	48.41	4.13	3.43	1.20	0.23	0.02	71
Log leaf thickness (mm)	48.52	-0.43	3.40	-0.13	0.90	0.00	73
Log leaf width (cm)	48.52	-0.66	3.40	-0.20	0.85	0.00	73
Log seed mass (g)	48.14	-3.15	3.40	-0.92	0.36	0.01	70
Log vegetative height (cm)	48.52	-0.15	3.40	-0.04	0.97	0.00	73
Specific leaf area (m^2 kg^{-1})	48.52	-2.70	3.38	-0.80	0.43	0.01	73
Stem dry matter content (mg g^{-1})	48.52	-3.02	3.38	-0.89	0.37	0.01	73

Table S3: Summary from ANCOVA model relating the magnitude of the each species lag to their dispersal mode, log seed mass and the interaction term. Only log seed mass was a significant predictor of the lags.

Term	**df**	**Sum of squares**	**Mean square**	***F* value**	***p* value**
Log seed mass	**1**	**7463.04**	**7463.04**	**5.18**	**0.03**
Dispersal mode	2	1619.04	809.52	0.56	0.57
Log seed mass*dispersal mode	2	1022.65	511.32	0.35	0.70
Residuals	63	90798.51	1441.25	-	-

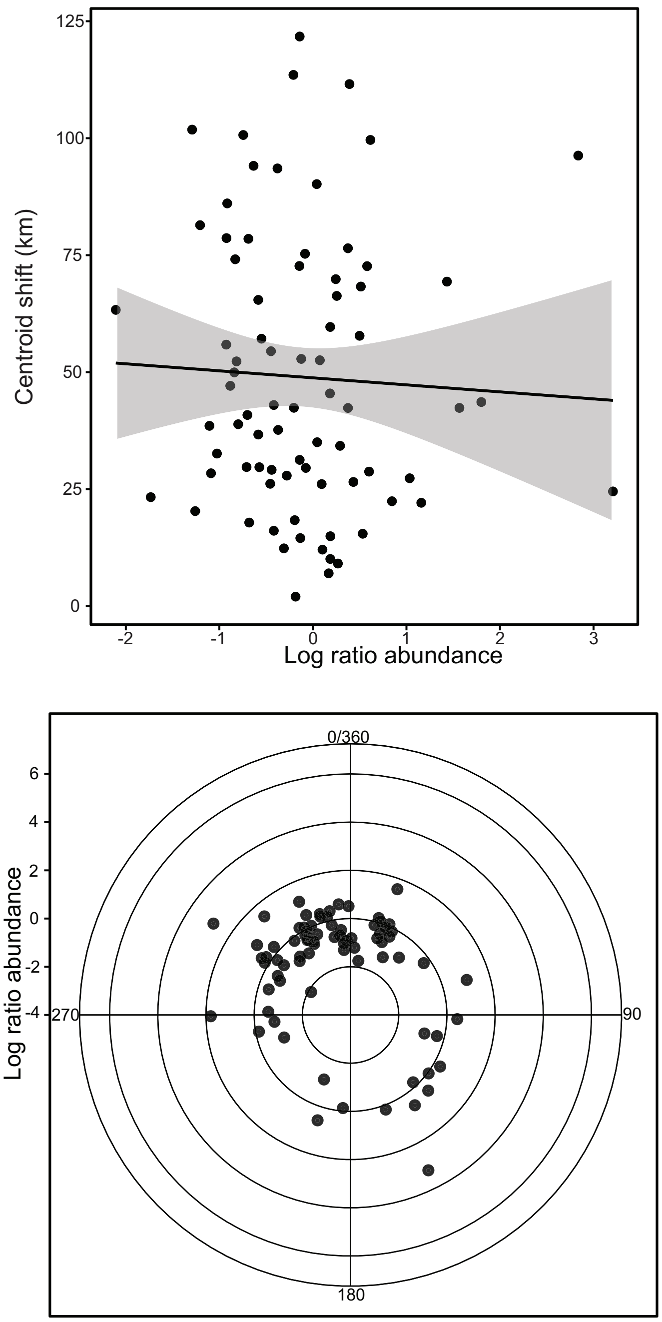


Figure S1: The proportional change in number of quadrats each species occupied (log(2000s/1950s)) and the distance (**a**) and bearing (**b**) of its centroid shift over time. **a.** The change in abundance was not a significant predictor of the species' centroid distance (linear regression, $\beta = -1.5$ [SE = 3.82], $t = -0.39$, $p = 0.70$, $R^2 = 0.002$). **b.** The change in number of sites was not a significant predictor of the species' centroid bearing (circular regression, $\beta = -0.01$ [SE = 0.08], $t = 0.17$, $p = 0.43$, $\mu = 325.80$ (SE = 7.86) and $\kappa = 1.28$ (SE = 0.21). Axes are shown on a circular scale, with the origin representing a log ratio of abundance value of -4.

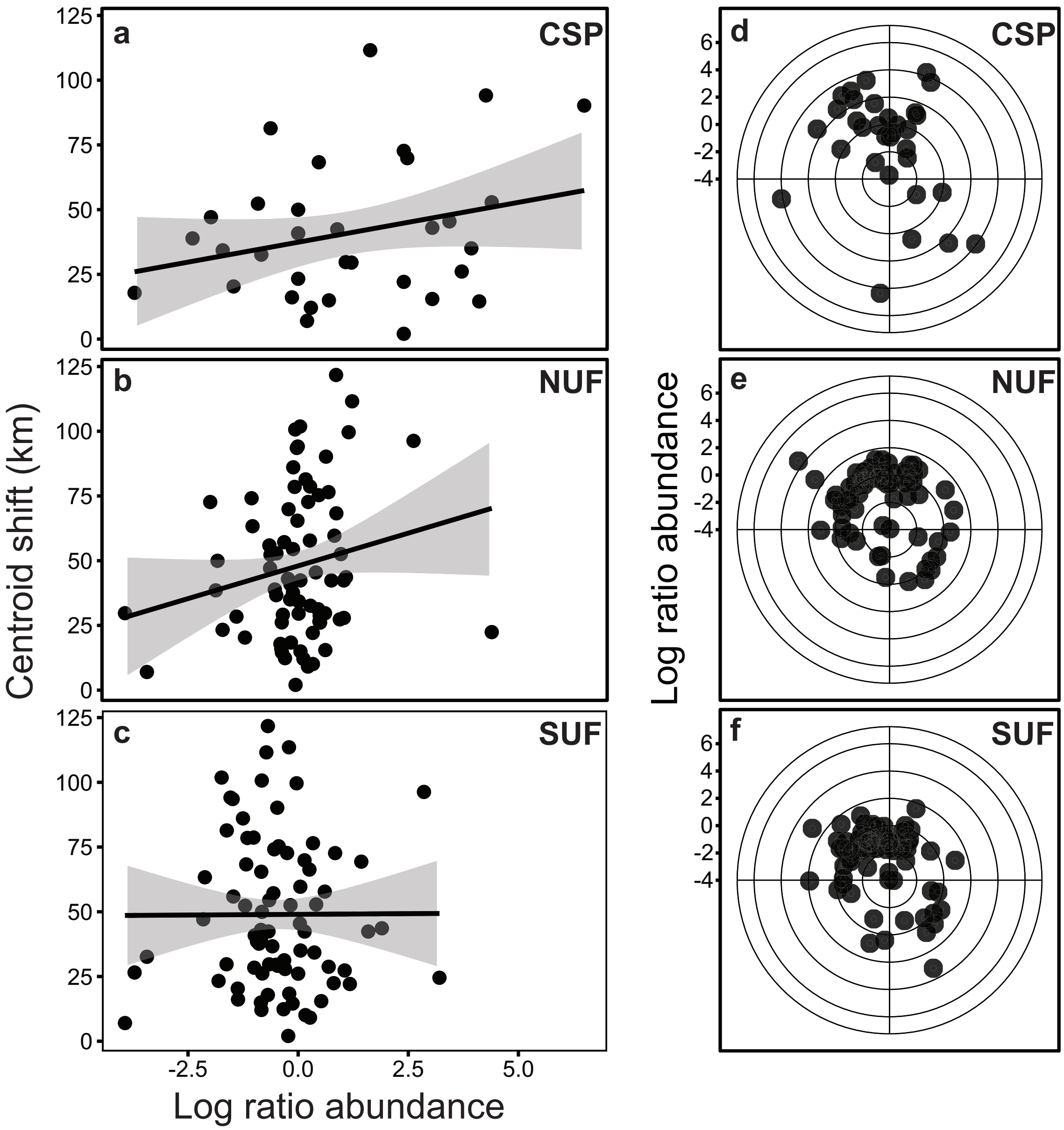


Figure S2: The proportional change in number of quadrats each species occupied (log(2000s/1950s)) in the different community types and the distance (**a - c**) and bearing (**d - f**) of its centroid shift over time. The proportional change in abundance was not a significant predictor of the species' centroid distance across all three community types (linear regression, **a**. $\beta = 3.07$ [SE = 2.02], $t = 1.52$, $p = 0.14$, $R^2 = 0.07$); **b.** $\beta = 5.06$ [SE = 2.98], $t = 1.70$, $p = 0.09$, $R^2 = 0.04$); **c.** $\beta = 0.11$ [SE = 2.82], $t = 0.04$, $p = 0.97$, $R^2 = 0.00002$). The proportional change in abundance was only a significant predictor of the species' centroid bearing for the SUF community type (circular regression, **d.** $\beta = -0.04$ [SE = 0.04], $t = 1.17$, $p = 0.12$, $\mu = 2.98$ [SE = 10.96], $\kappa = 1.46$ [SE = 0.34]); **e.** $\beta = 0.01$ [SE = 0.06], $= 0.17$, $p = 0.43$, $\mu = 330.1$ [SE = 7.92], $\kappa = 1.31$ [SE = 0.22]); **f.** $\beta = -0.09$ [SE = 0.06], $t = 1.76$, $p = 0.04$, $\mu = 309.3$ [SE = 7.70], $\kappa = 1.31$ [SE = 0.21]). The community types are the pine barrens of the central sand plains

(CSP), northern upland forest (NUF) and southern upland forests (SUF). For panels **d - f**, the axes are shown on a circular scale, with the origin representing a log ratio of abundance value of -4.

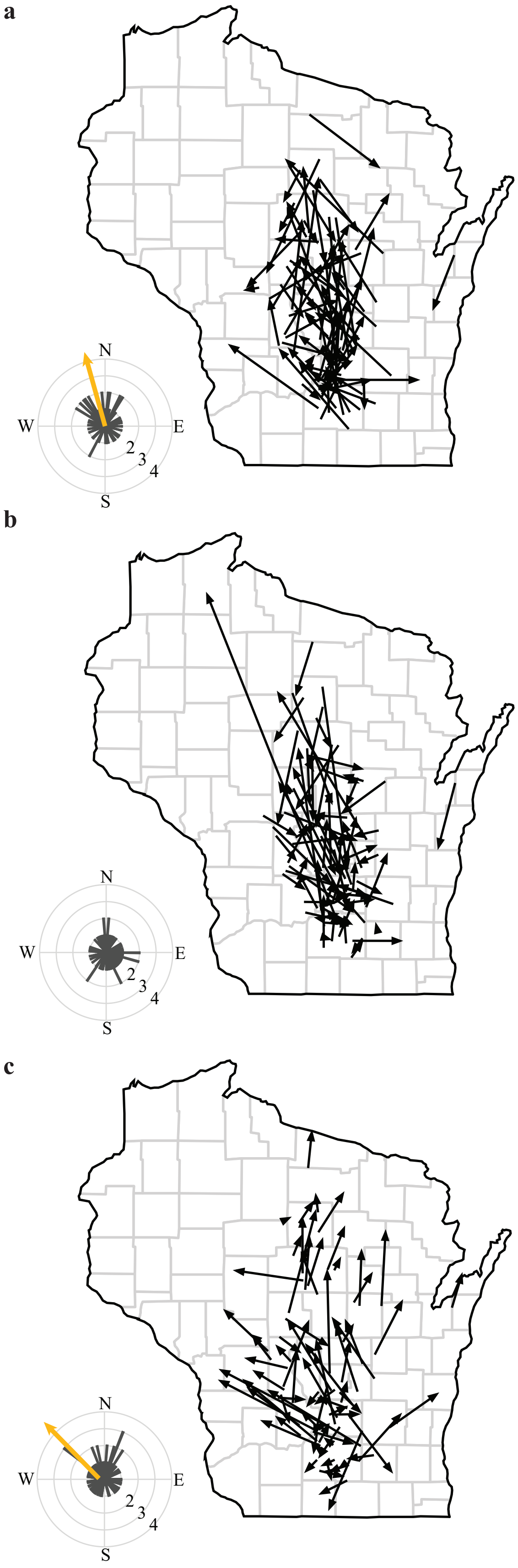
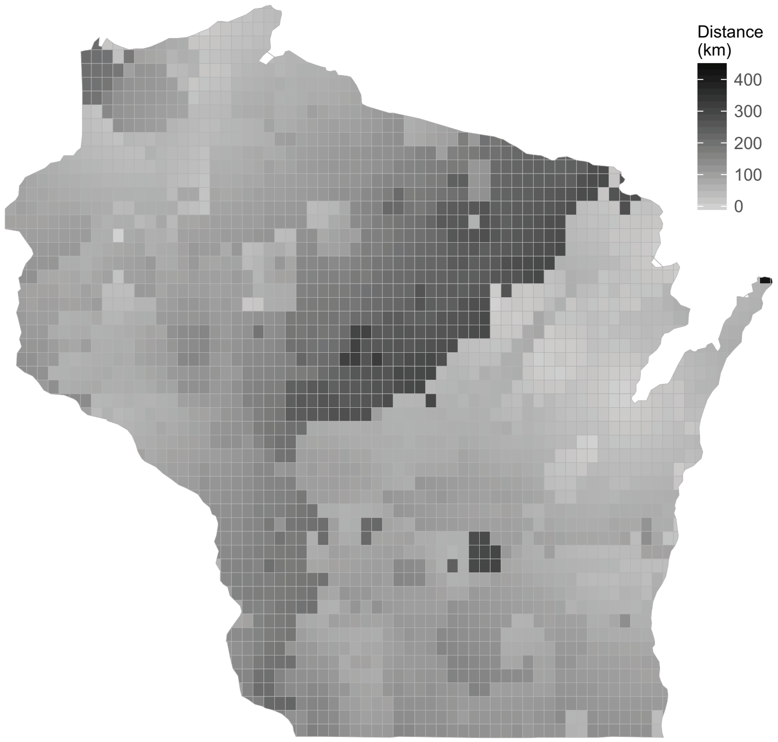


Figure S3: Vector fields showing the process vectors underlying the 78 species' centroids: **(a)** colonization **(b)** extirpation and **(c)** change in abundance. **a.** The shifts in species' centroids from the 1950s to the abundance-weighted centroid of newly colonized sites in the 2000s. **b.** The change vector to the average location of sites where species went locally extinct. The bearings of these vectors is highly varied, so no mean bearing is shown. **c.** The vector to the abundance-weighted centroid for sites where the species persisted over time. For each panel, the embedded rose plot shows the frequency histogram of the bearings of these shifts, with the mean bearing represented by the yellow arrow.

a



b

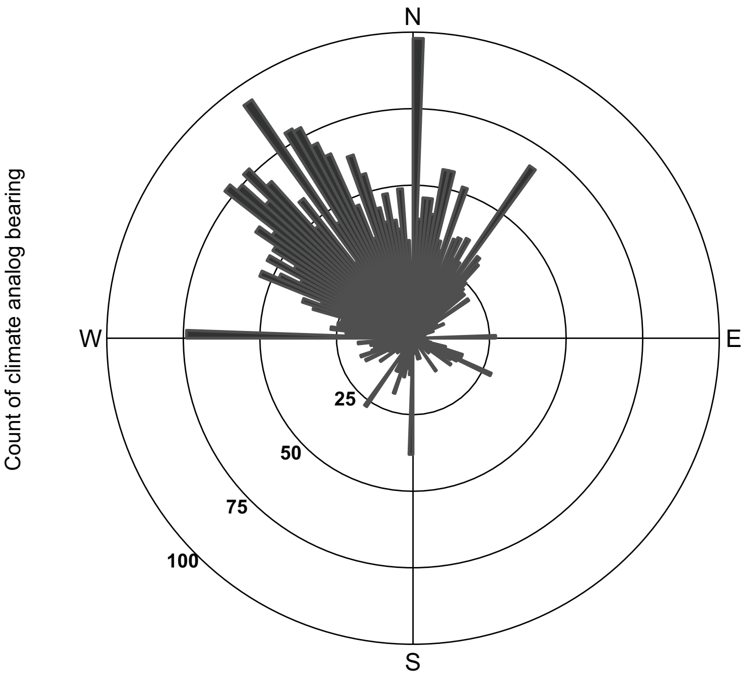


Figure S4: The distance (**a.**) and bearing (**b.**) of the multivariate climate analog shift for the whole state. These form the basis for the calculation of the species-specific climate analogs.

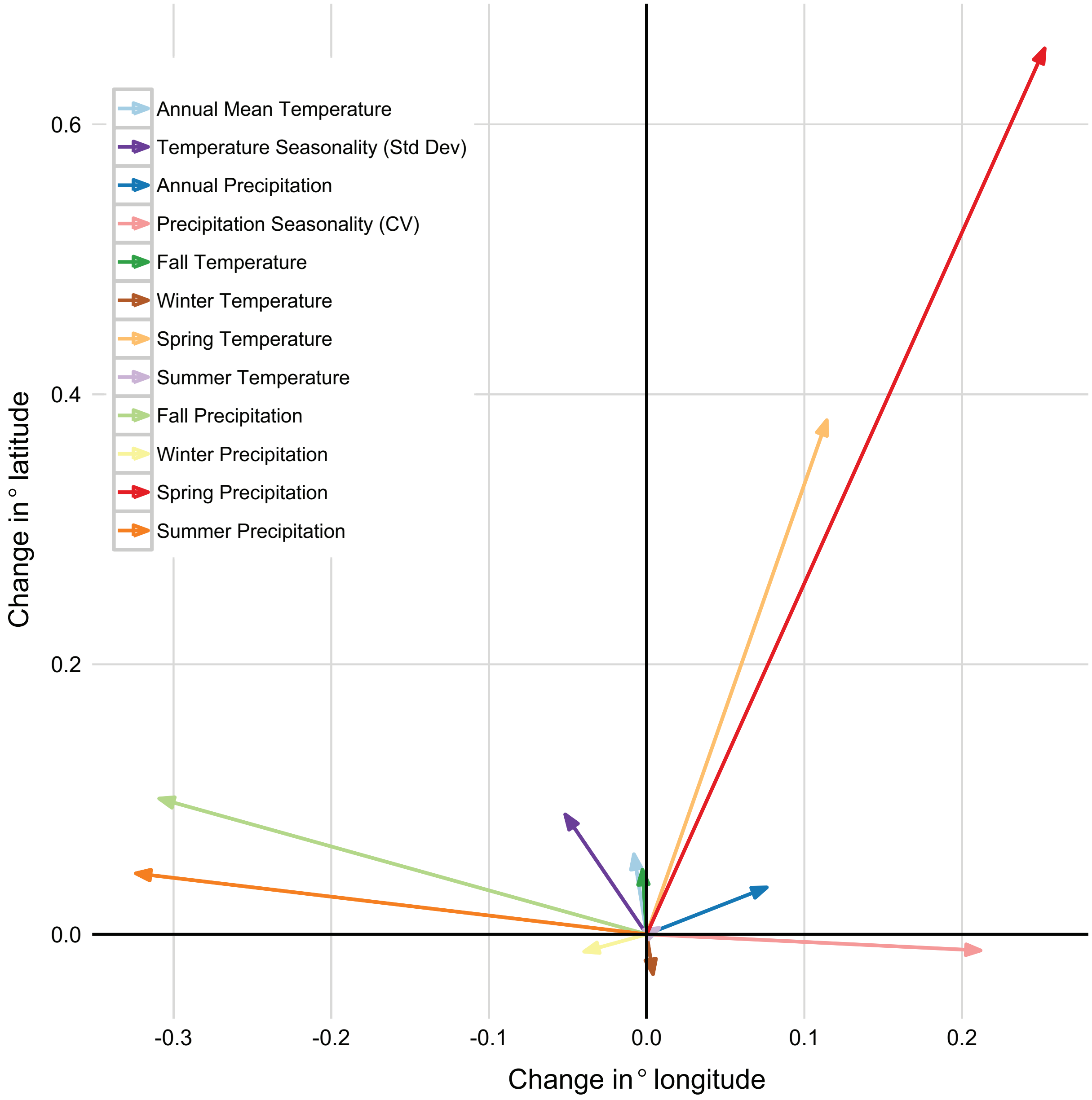


Figure S5: The mean vector for each of the species-specific univariate climate analogs included in the multivariate climate analog.

Dissertation Defense Comments

Since this chapter was *in press* at the time of the dissertation defense, I expand on committee feedback here. Specifically, I elaborate on the decisions made regarding the exclusion of species considered to be outliers. In the text, we note the decision to exclude seven species whose centroid shift was greater than three standard deviations from the overall mean. We considered this to be conservative, as the centroid shifts could have been due to taxonomic misidentification or other measurement errors. We re-ran the analyses including these species and found qualitatively similar results. We note, however, that excluding these species could also overestimate the extent of the observed lags, as these species could be better at tracking their species-specific climate analogs. Nonetheless, these species were so extreme in their responses that we leave them out of the analyses.

Chapter 2 - Do traits predict species-environment relationships among forest understory plants and how species have responded to environmental change?

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Abstract

Ecologists are keen to understand the processes that structure the abundance and distribution of species, both to explain current species' distributions and to predict how these could shift in response to dynamic environments. The ways in which species respond to environmental gradients likely depends on their particular functional traits. Thus, tracking shifts in the assemblage of species' traits through time could reveal some of the mechanisms species use to respond to dynamic environmental conditions. To test this idea, we examined the relationships among environment, traits and species' distributions to understand the determinants of species' distributions and long-term changes in the abundance of understory plants. We relied on detailed surveys and resurveys of the same Wisconsin forest plots over the last 50+ years. We used data on 18 traits and 33 site-level environmental variables to predict the distributions and change in the abundance of 153 species across a network of 284 sites. Species' distributions are strongly related to differences in the examined environmental conditions among sites at both time periods. Species also appear to respond to distinct sets of environmental variables. Traits served to accurately predict these species-environment relationships, allowing us to identify suites of traits associated with environmental sensitivity. However, neither environment nor traits served to accurately predict temporal changes in species' abundance. An understanding of how traits interact with environmental gradients to structure species' distribution patterns can be used to understand static distributions, but cannot predict changes in distributions over time.

Keywords: forest understory; climate change; species distribution model; functional traits; species-environment relationships

Introduction

Population and community ecologists have long sought to characterize the factors that determine species' distributions. These include associations between environmental conditions and species' characteristics (functional traits). Species distribution models (SDM) form one thread of this work by correlating species' occurrences with underlying environmental gradients (Franklin, 2010). These models can be effective tools for understanding recent and future shifts in species' distributions across a range of taxa (Elith & Leathwick, 2009), particularly in light of global climate change. Although many species respond to climate change by moving poleward and upward in elevation (Parmesan & Yohe, 2003), species vary greatly in their particular responses (Ibáñez *et al.*, 2013). Direct effects of climate change can also be difficult to infer when coupled with disturbance regime shifts (Nowacki & Abrams, 2014; Stevens *et al.*, 2015) or interactions with other environmental covariates (Austin & Van Niel, 2011). This variation presents us with the challenge of predicting species' responses to environmental change in terms of differences in their traits. Species' traits could prove useful not only for providing a more mechanistic understanding of how species respond to drivers of change, but also for possibly letting us generalize from individual species to more general patterns based on shared sets of traits (Buckley & Kingsolver, 2012; Brown *et al.*, 2016). Understanding how traits interact with spatial gradients to structure species' distribution patterns would also enhance our ability to predict future outcomes of environmental change (Pollock *et al.*, 2012).

Trait-based approaches have already been used to study how environmental variation constrains community assembly (Cornwell & Ackerly, 2009; Laughlin *et al.*, 2011; Frenette-Dussault *et al.*, 2012). These studies, however, use snapshot data to infer temporal dynamics and focus largely on local dynamics. Two studies exploring trait-environment relationships and how these affect long-term shifts in plant species' abundances found strong relationships in both subtropical tree communities (Li *et al.*, 2015) and alpine meadow communities (Soudzilovskaia *et al.*, 2013). Other studies of trait-based community assembly processes show that these depend strongly on spatial scale (Cavender-Bares *et al.*, 2006; Swenson & Enquist, 2009; Kraft & Ackerly, 2010; Xing *et al.*, 2014). This suggests that efforts to link traits to community responses to climate change should explicitly consider scale and spatial domain. Many traits show strong environmental relationships across broad spatial scales and gradients (Wright *et al.*, 2005a; 2005b; Moles *et al.*, 2014). How these relationships affect regional and local species' distributions and community composition is less clear.

To understand these relationships, trait-based community ecologists often use "fourth corner" approaches that use three data matrices (species by site, site by environmental variables, and species by trait) to relate species' traits to environmental gradients (McCune *et al.*, 2002; Dray & Legendre, 2008; Dray *et al.*, 2014). The resulting fourth (or missing corner) matrix informs our understanding of trait-environment relationships based on either species' incidence (presence/absence) or abundance. While this approach yields useful relational and descriptive tools, it overlooks two other questions: how are species' distributions explained by interactions between traits and environmental variables, and what set of traits and environmental variables best predict the spatiotemporal dynamics of species' distributions (Jamil *et al.*, 2013)? Jamil et al. (2012) and Pollock et al. (2012) use hierarchical models to estimate the role of traits in structuring species' distributions, including how traits and environmental conditions interact to structure species' distribution patterns. These models seek to integrate species-trait-environment relationships to make inferences beyond those provided by classical species' distribution models.

Here we ask how the distributions of forest understory plant species in Wisconsin are structured by environmental gradients and to what extent traits serve to predict species-environment relationships. To assess the stability of species-environment relationships and how well traits predict responses to environmental variation, we combine baseline data derived from the extensive surveys of J.T. Curtis and his students in the 1950s (Curtis, 1959) with re-surveys of the same sites in the 2000s (Waller *et al.*, 2012). We use these data to construct species' distribution models for each survey period, as well as a third model that seeks to predict changes in the abundance of each species between periods. By combining these three models, we can evaluate: 1) whether the predominant environmental gradients that structure species' distributions have changed over the past 50 years and 2) how site-level changes in environmental conditions have influenced spatial patterns of species' abundance. We also exploit an extensive set of life history and functional trait data to assess their effects within these models and to explore whether functionally similar species respond in a similar manner to environmental gradients.

We consider three important abiotic drivers of forest understory species' distributions: soil conditions, successional status and climatic gradients. Considerable climate change has already occurred within Wisconsin over the past half century with substantial spatial and temporal variation in each climate trend (Kucharik *et al.*, 2010; WICCI, 2011). Variation in soil chemistry and texture has been shown to be important for structuring understory communities (Hutchinson *et al.*, 1999; Small & McCarthy, 2005; Gilliam, 2014). Disturbance-driven shifts in canopy processes have had variable importance in defining compositional shifts in understory communities (Rooney *et al.*, 2004; Wiegmann & Waller, 2006; Rogers *et al.*, 2008; Johnson *et al.*, 2014; Li & Waller, 2015). Given the variable rate of change among the different biologically-important variables, we expect to find that species' distributions show period-specific responses to distinct sets of environmental variables. We previously described broad-scale geographic shifts in species' distribution patterns correlated with climate change (Ash *et al., in press*). We have also found consistent trait-environment relationships despite substantial shifts in community composition and relative abundance (Amatangelo *et al.*, 2014). The results we present here fill a gap between these studies by analyzing site-level patterns where we expect local environmental conditions to interact with trait values to affect shifts in species' abundance. We also expect that the traits serving to predict species-environment relationships within the two survey periods may not be the same, given the range of factors driving ecological change in these communities (Rooney *et al.*, 2004; Rogers *et al.*, 2008; 2009; Johnson *et al.*, 2014; Li & Waller, 2015). That is, we expect trait-environment relationships to be disrupted in the 2000s relative to the patterns found in the 1950s.

Methods

Study system

To capture a range of geographic and environmental variation, we analyze changes across 284 sites distributed among four community types in Wisconsin (**Fig. 1**): pine barrens of the central sand plains (CSP, n = 30), northern upland forests (NUF, n= 96), southern lowland forests (SLF, n = 40) and southern upland forests (SUF, n = 118). Ecological changes in these systems have been complex. Earlier work in upland forests in northern Wisconsin noted conspicuous declines in taxa susceptible to deer herbivory and increases in a few exotic species and those that avoid or tolerate deer herbivory (Rooney *et al.*, 2004; Wiegmann & Waller, 2006). The upland forests of southern Wisconsin saw more invasions by exotic species and declines in many native species, particularly under fragmented landscape conditions (Rogers *et al.*, 2009). Pine barren communities underwent succession in response to fire suppression since the 1950s (Li & Waller, 2015) and lowland forest communities have become more diverse yet more similar over time due in part to increases in habitat connectivity and more regulated hydrological regimes (Johnson *et al.*, 2014).

Details on the original sampling and resurvey methods are already published (Wiegmann & Waller, 2006; Rogers *et al.*, 2008; Johnson *et al.*, 2014; Li & Waller, 2015), but are described briefly here. In the 1950s, J.T. Curtis and colleagues engaged in a widespread sampling initiative (>1000 sites) to quantitatively characterize the vegetation of Wisconsin (Curtis, 1959). Site-selection criteria included a minimal amount of disturbance (i.e., logging) and fragmentation (i.e., sites had to be greater than 6 ha). Curtis-era sampling used 20 (rarely 40) evenly spaced quadrats along square, L-shaped or U-shaped transects, or a set of parallel transects (Waller *et al.*, 2012). In the 2000s, the UW Plant Ecology Laboratory (http://www.botany.wisc.edu/PEL/) began resurveying the forested sites, re-locating the original sites using site descriptions and maps. Resurveys in the 2000s used similar but more intensive approaches to quantify the understory communities with 42 to 120 quadrats per site. Within each quadrat, researchers recorded the presence of all vascular plant species (herbs, shrubs and trees). We estimated abundance for each species at each site from its frequency (the sum of occupied quadrats). Here, we focus on species that occurred in ten or more sites in at least one of the survey periods and for which we have complete coverage for the functional traits (see below). These filters resulted in a focal species pool of 153 species.

Environmental Variables

To characterize climate change over the study period, we used an 8 km gridded climate dataset of daily precipitation and minimum and maximum temperature covering 1950 to 2006 (Kucharik *et al.*, 2010). These data are generated using spatial interpolation across an extensive network of weather stations throughout the state. We computed ecologically meaningful seasonal and annual summary variables from these data for each of our 284 sites (**Table 1**). We chose these summary variables to reflect a broad range of both seasonal and annual aspects of climate change, as well as a set of biologically relevant climate variables (Booth *et al.*, 2013). For each variable, we calculated a mean value for the five-year interval around each of the survey periods (1950-1954 and 2000-2004) to account for inter-annual climatic variability and potential lags in species' responses to climate (De Frenne *et al.*, 2013). The BIOCLIM variables, a set of 19 biologically-meaningful climate variables, were calculated using the *dismo* package in R (Hijmans *et al.*, 2015). We determined mean temperature and precipitation for each of the seasons, as well as a set of energy-based measures. Potential evapotranspiration was calculated using the Thornthwaite equation (Thornthwaite, 1948) and approximating day-length using site latitude (Forsythe *et al.*, 1995). Annual water deficit was calculated as the difference between potential evapotranspiration and annual precipitation. We determined the number of growing degree days using 10°C as the base threshold.

To characterize site-level soil variation, we collected and combined ten randomly dispersed soil samples at each site and measured nine soil variables: pH; % organic matter; % sand, clay and silt; and concentrations of phosphorous, potassium, calcium and magnesium (in ppm). We reduced the dimensionality of the soil variables in a Principal Components Analysis and used the first two axes, which collectively explain 67% of total site variation. We inverted the values from the first axis to be positively correlated with soil cation concentration and pH. The second axis was correlated with soil texture, ranging from coarse, sandy soil (low axis scores) to finer textured soils (high axis scores). Soil measurements were only taken during the 2000s survey period, but we use these values for each survey model. We thus assume soil texture and chemistry have not changed substantially over time. To quantify canopy-level dynamics, we also included the mean basal area of overstory trees at each site to represent successional status. Curtis-era surveys relied on plotless methods to characterize the overstory, making stand-level calculations (i.e., total basal area or stem density) biased relative to the area-based methods used in the resurvey (Waller *et al.*, 2012). To reduce possible biases, we used the mean basal area as a simple measure of the overstory. All environmental variables were centered on zero and scaled by their standard deviations to facilitate comparison.

Trait Measurements

We measured a broad suite of functional traits to capture a range of life history and ecological strategies (**Table 2**). We used trait means reflecting measurements on at least 12 individuals (four individuals from each of three sites) following standardized protocols (Pérez-Harguindeguy *et al.*, 2013). We also include three other traits: each species' initial area of occurrence (a convex hull drawn around the occupied sites in the 1950s), measures of genome size for these taxa measured in Wisconsin plants, (Bai *et al.*, 2012), and each species' Coefficient of Conservatism (CC), an estimate of its habitat fidelity (Swink and Wilhelm 1994; Table 2). Values of CC range from 0 (no fidelity) to 10 (scarce species confined to specific, high-quality habitats). All continuous trait variables were centered and scaled by subtracting the mean and dividing by 2 standard deviations, following Gelman (2008) to directly compare effect sizes between binary and continuous variables.

Data Analysis

Species' Abundance

We analyzed species' distributions during each survey period, as well as their change in abundance between periods. For each survey period, we modeled species' abundance as a binomial process based on the proportion of quadrats each species occupied. To characterize changes over time, we used a logit transformation on the proportion of quadrats each species occupied (log(y/[1-y]), where y is the proportion of quadrats each species occupied at each site) to normalize the response variable (Warton & Hui, 2011). We then subtracted the logit-transformed proportions (2000s – 1950s) to generate a measure of the change in abundance for each species at each site over the study period.

Selecting Environmental Variables

Given the large number of environmental variables and issues of collinearity, we employed a systematic statistical approach to choose a subset of variables to include in each model. For the abundance change model, we subtracted the 1950s environmental values from the corresponding 2000s values. Since we only have soil measurements at one time period, we excluded these variables form the change in abundance model. We used random forest models relating the species' abundance patterns across sites to the full suite of environmental variables (**Table 1**). Random forest models are a machine learning method commonly used in regression and classification trees (Hastie *et al.*, 2009), but also with applications in species' distribution models (Prasad *et al.*, 2006). For each species x survey period and the change in abundance model, we developed a random forest model and replicated the procedure 500 times to understand which environmental variables were most important for predicting species' distributions across sites and over time (**Figs. S1 – S3**). We then compared across species to determine which environmental variables were consistently one of the top 5 most important predictors for structuring species' distribution patterns. After eliminating collinear variables (correlation > 0.6), we used the five most important variables for each of the three models. We chose this number to reduce overfitting and additional parameters resulted in convergence warnings during model optimization.

Trait Selection

As with the environmental variables, we were faced with a large number of potentially important trait variables. We therefore developed an approach to select a subset for each model. For each survey period model (with binomial error distributions) and the abundance change model (Gaussian error distribution), we developed a linear mixed model that related species' abundances (or change over time) across the network of sites to each of the trait variables while including site as a random effect. We then ranked models according to the site-level variance and selected the three traits that explained the most variance in species' abundances among the sites.

Statistical Models

Hierarchical models based on the generalized linear mixed effects modeling framework (GLMM, (Gelman & Hill, 2007) have recently been applied to address questions like those pursued here (Gelfand *et al.*, 2005; Pollock *et al.*, 2012; Jamil *et al.*, 2013). This modeling framework essentially integrates two steps into one model. First, a regression model is fit for each species relating their abundance to a set of environmental variables. Second, parameters from the first model for all species are regressed onto their trait values to explore how well traits predict the species-environment relationship. The integrative model also includes an interaction term for the trait-environment relationship and controls for site as a random effect.

Our approach mirrors the methods described in Pollock et al. (2012), who also hierarchically modeled species' distribution patterns. For each survey period model, species' abundance (the number of quadrats occupied relative to the total number of quadrats) was modeled as a response to the selected environmental variables, species' traits, and their interactions using a binomial (logit-link) generalized linear mixed model (GLMM). We also included main effects of the four community types (CSP, NUF, SLF, and SUF) and the random effect of site to account for the nested nature of our data. For the abundance-change model, we modeled the change in logit-transformed proportions as a function of species' traits, change in the environmental variables, and interactions between these in a linear mixed model assuming a Gaussian error distribution. The same community and site effects were included. Across all models, species' responses to the environmental variables were included as a random effect, meaning that the average response (intercept) and partial responses to environmental gradients (slopes) were allowed to vary across species. To test our hypothesis that trait-environment relationships would diminish over time, we applied the model specified for the 1950s data to the 2000s data and compared the coefficients between periods.

We used R (R Development Core Team, 2015) for all analyses, including the following packages: *lme4* for mixed modeling, *randomForest* for random forest modeling (Liaw & Wiener, 2002), *ncdf4*, *raster* and *dismo* for processing climate variables (Pierce, 2014; Hijmans, 2015; Hijmans *et al.*, 2015), and *ggplot2* for plotting (Wickham, 2009).

Results

Environmental variables and traits structuring species' distributions

The random forest models reveal significant associations between a few key environmental variables in each survey period and variation in species' abundance across these sites (**Fig. 2** and **Figs. S1 - 2**). In general, soils, growing season temperatures and energy-based measures (PET and GDD) appear to have strong effects on species' abundance during both survey periods. However, different climate variables emerged as most important within each period. Precipitation variables became more important during the 2000s resurvey period, while temperature-based measures appeared to be more important during the initial 1950s survey. For the change in abundance model, similar climate variables emerged as important as in the 2000s model, as well as the change in mean basal area of overstory trees (**Fig. S3**).

Our trait selection procedure revealed that leaf thickness and dry matter content consistently predicted species' abundance patterns and how these changed between periods (**Tables 3 - 4**, **Fig. S4**). Area of initial occurrence (1950s model), leaf nitrogen content (2000s model), and specific leaf area (change in abundance model) also appeared to affect variation among sites in species' abundance.

Model results from individual survey periods

On average, the mean abundance of species was similar between time periods ($\mu_{1950} = 0.042 \pm 0.965$; $\mu_{2000} = 0.036 \pm 1.492$), but abundance varied more in the 2000s, particularly in less common species (**Figs. 3-4**; intercept panel). Species varied greatly in their response to environmental gradients (**Figs. 3-4**). Species appeared to respond to distinct sets of environmental variables independently of their abundance. The estimated coefficients suggest that species respond strongly to soil chemistry (Soil PCA axis 1) in both time periods, mean temperature of the wettest quarter (BIO8) in the 1950s and summer temperature in the 2000s.

All traits appeared to mediate species-environment relationships in both survey periods, but the magnitude of these effects and how they interacted with specific environmental variables varied (**Fig. 5**). Species' area of occurrence strongly influenced their responses to climate in the 1950s (**Fig. 5a**). Widespread species declined more in areas with higher mean temperature of the wettest quarter (BIO8), but increased in abundance at sites with warmer minimum winter temperatures (BIO6). Widespread species also tended to increase with cation concentration (higher values of Soil PCA axis 1) and finer textured soils (higher values of Soil PCA Axis 2). Species with thicker leaves declined in response to higher soil cation concentration (Soil PCA Axis 1) and higher overstory tree basal area, but increased with higher minimum temperature of the coldest month (BIO6). Species with more leaf dry matter content tended to decline in response to increases in all environmental variables, except for overstory tree basal area.

For the 2000s model, species with thicker leaves declined in areas with more fall precipitation and warmer summer temperatures (**Fig. 5b**). Leaf dry matter content was important for mediating species' responses to soil gradients. Species with higher leaf dry matter content were more common in areas with sandier soils (Soil PCA Axis 2) and lower cation concentrations (Soil PCA Axis 1). Species with higher leaf nitrogen content were positively associated with soil cation concentrations and higher summer temperatures, but declined in areas with higher winter precipitation.

Do traits mediate species' abundance changes over time?

In contrast to the models developed for each survey period, few environmental variables served to predict changes in species' abundance (**Fig. S4, Table S1**). Functional traits were also weak predictors of species-environment relationships, with only one of 15 possible trait-environment interactions significant (**Fig. 5c**). Thicker-leaved species increased in areas where precipitation in the driest month increased (BIO14).

Model transferability?

Applying the 1950s model to the 2000s data shows that many of the estimated trait-environment coefficients were similar (**Fig. 6**), however six of the trait-environment interactions were no longer significant. Area of occurrence and leaf thickness appeared less predictive of species-environment relationships for the 2000s data, specifically for minimum temperature of the coldest month (BIO6) and mean temperature of the wettest quarter (BIO8). In contrast, species with more leaf dry matter content responded similarly to environmental gradients in both time periods.

Discussion

Understanding the processes that structure species' distributions and community composition remains central to the discipline of ecology (Maguire *et al.*, 2015). Knowing which factors affect the location and abundance of species adds to our understanding of contemporary ecological patterns and gives us the power to forecast future scenarios.

How species respond to changes in environment is likely mediated by life history characters and ecological strategies, but these relationships can be complex (Pollock *et al.*, 2012; Jamil *et al.*, 2013). Changing environmental conditions and landscapes alter the context that gave rise to previous patterns of distribution and abundance. This means that the factors that structured species' distributions in previous time periods need not match those affecting current distributions, or the changes in distribution that have occurred. Indeed, we observe that distinct combinations of traits, environmental factors and their interactions structure species' distributions at each time period, yet neither set of predictors influence the changes observed at these sites over time. This may reflect, in part, the fact that changes in climatic and other environmental conditions may be creating novel combinations of conditions that species have not yet experienced. This makes it even more important to understand how traits and environmental conditions interact to jointly affect plant distributions and abundances.

Environmental determinants of species' distributions

We used an extensive set of survey data of understory plant species at two time periods to examine how the distributions and abundances of these species are affected by environmental gradients and how functional traits mediate species' responses to these gradients. We found strong evidence for both. The importance of environmental variables for predicting species' distributions was similar between periods but there were also distinct differences (**Fig. 2**). Soil variation, growing season temperatures (spring and summer) and water/energy-based measures consistently acted to structure species' distributions, but precipitation-related variables emerged as more important in the 2000s model (**Fig. 2, Tables 3-4**). While temperature gradients vary more systematically across the state, precipitation also varies, both spatially and temporally, contributing strongly to the patterns we observed in these understory plants. Overstory tree basal area emerged as an important determinant of species' distribution patterns in the 1950s, but not for the 2000s model. Successional trajectories have been altered substantially across community types since the 1950s, with varying importance for understory community dynamics (Rooney *et al.*, 2004; Rogers *et al.*, 2008; Johnson *et al.*, 2014; Li & Waller, 2015). Relationships between understory communities and overstory dynamics have generally weakened over time in the southern upland forests, with landscape factors (i.e., habitat fragmentation) becoming stronger determinants (Rogers *et al.*, 2009). Results here suggest that this dynamic may extend across all community types, as overstory tree basal area was substantially less important for the 2000s species' distributions (**Figs. S1-2**). Indeed, the nature of land cover use and transformation was highly dynamic preceding the original Curtis surveys. Forests were largely cut over in northern Wisconsin from 1870 – 1920, and open savannas were becoming closed canopy forest in southern Wisconsin over a similar period of time (Rhemtulla *et al.*, 2009). Together, this suggests that local site succession was more important for shaping understory communities in the 1950s relative to the 2000s. More generally, if species-environment relationships weaken over time, it may explain the lack of predictive power when we explored the change in the abundances of species.

Despite pronounced changes in overstory and climatic conditions (Kucharik *et al.*, 2010), these did not serve to accurately predict changes in the abundances of these species at these sites (**Fig. S3**, **Table S1**). In contrast, a previous study found that shifts in species' geographic centroids over this same period are correlated with parallel spatial shifts in climatic conditions (Ash *et al. , in press*). Although species' centroids shifted in the same direction as climatic conditions, these shifts in distribution usually lagged the shifts in climate suggesting that many species may lack the ability to keep pace with current rates of climate change. These lags may reflect at least in part the action of other facets of ecological change, which in our region include high rates of herbivory by deer, limits to dispersal imposed by habitat fragmentation, nitrogen deposition, and perhaps other factors. Our results here support the conclusion that within sites, temporal species' dynamics are largely influenced by factors other than climate and overstory dynamics (**Fig. S4**). The pace at which changes in climate can drive shifts in understory communities is also likely limited because shaded, humid understories ameliorate the otherwise hotter and drier conditions that many temperate forests are experiencing (De Frenne *et al.*, 2013). Though we do not find evidence of a strong direct effect of overstory basal area, successional changes have been pronounced at many of these sites (Rogers *et al.*, 2008; Amatangelo *et al.*, 2010; Li & Waller, 2015) and may weaken climate impacts on understory species.

Patterns of species' abundance at individual survey periods reflect variation in environmental conditions among sites, but species do not all respond in the same way to these environmental variables (**Figs. 3-4**). Rather, different species respond to distinct sets of environmental variables in spatially complex and individualistic ways (**Figs. 3-4**), matching patterns observed in other studies (Ackerly *et al.*, 2010; Chen *et al.*, 2011; Grenouillet & Comte, 2014; Rapacciuolo *et al.*, 2014). If rates of environmental change continue to accelerate, our ability to predict how species will respond in the future may be diminished based on their current associations with environmental gradients. For instance, as rates of climate change accelerate in our region (WICCI, 2011) and as the spatial discordance between historical and future predicted climates increases (Ordonez *et al.*, 2014), we predict that the complexity of interactions between species' traits and changes in conditions will increase. Incorporating functional traits into the general models we presented extends our ability to infer these complex interactions.

Functional traits mediate species-environment relationships

Several key traits appear to mediate how species' abundances relate to environmental gradients in both periods (**Figs. 5a and b**). Pollock (2012) and Jamil (2013) similarly found that traits strongly mediate species-environment relationships to structure distribution patterns. This also supports earlier work showing that trait-environment relationships remained strong in the upland sites over the 50-year study period (Amatangelo *et al.*, 2014). Results here expand on this finding in that they include two additional community types and address additional questions, like how species' abundances depend on traits and environmental variables, and how traits modulate species' responses to environmental gradients. The evidence we present here shows that while species respond individualistically to environmental variables, there are also some broader trends in species' responses reflecting differences in plant traits. These help us understand more broadly what structures species' distribution patterns at both time periods.

In the 1950s model, we found that area of occurrence and leaf traits strongly affected the species-environment relationships (**Fig. 5a**). The relationships with area of occurrence are not surprising given that we expect widespread, habitat generalists to exist across wider environmental gradients relative to species with narrow distributions and/or specialized habitat requirements (Warren *et al.*, 2001). We previously found that plant species distributed more broadly track and keep up with changes in climate better than other species in this system over the same study interval (Ash *et al., in press*). Leaf traits can be strongly indicative of life history strategies in response to environmental gradients, as we observe here. Species with more leaf dry matter content were more abundant in areas with coarser, lower fertility soils and colder winter (BIO6) and summer (BIO8) temperatures. Species with more leaf dry matter content typically have longer leaf lifespans, allocate more to structural defenses and support, and display more conservative physiology and life history characteristics (Givnish, 1979; Cornelissen *et al.*, 2003). Collectively, these represent advantageous strategies in the colder climate and lower fertility soils of northern Wisconsin. Thicker-leaved species declined in areas with larger overstory trees, perhaps reflecting the shadier conditions across many of these sites (Rogers *et al.*, 2008; Johnson *et al.*, 2014; Li & Waller, 2015). Leaf thickness is also positively correlated with leaf lifespan (Pérez-Harguindeguy *et al.*, 2013) and as above with leaf dry matter content, thicker-leaved species were also more common in low fertility soils. However, unlike species with more leaf dry matter content, thicker-leaved species declined with colder winter temperatures. This highlights the complexity of species-environment relationships and perhaps the need for additional interaction terms among environmental predictors in distribution models.

The 2000s model indicated that species' traits strongly mediate responses to soil gradients and summer temperatures (**Fig. 5b**). Species with more leaf dry matter content were more common in coarse, lower fertility soils. This is the same relationship as observed for the 1950s. Species with thin, high nitrogen content leaves were more abundant in areas with higher summer temperatures. This complex of traits is often associated with higher photosynthetic rates and may also reflect a stronger association with the warmer, higher soil fertility habitats in southern Wisconsin. Indeed, the abundance of high leaf nitrogen species was positively correlated with soil fertility and lower winter precipitation, supporting their associations with southern habitats.

Summer temperatures and winter precipitation are projected to increase under future scenarios for the state, although with warming temperatures, the amount of snowfall versus rain will decline (Notaro *et al.*, 2010). The implications of this climate change for plant communities are unclear. For instance, the ecological impacts of winter climate are not well studied, particularly in temperate regions (Kreyling, 2010; Ladwig *et al.*, 2016). Nonetheless, the model results suggest that species with these trait syndromes and affinities for habitats in southern Wisconsin may be particularly responsive to future climate change. Some areas in southern Wisconsin have also experienced more habitat loss and fragmentation than northern Wisconsin, increasing risk of local extinction (Rogers *et al.*, 2009). While we did not explicitly test for interactions with habitat fragmentation, it seems likely that synergistic interactions between climate change and fragmentation could act to greatly alter the composition of these communities.

Strength of relationships over time

We found that our trait-environment model was largely unable to predict changes in species' abundances over the study period, limiting our ability to forecast species' dynamics under future environmental change (**Fig. 4c, Fig S4**). Other long-term studies have found that functional traits are strong predictors of species-climate relationships (Soudzilovskaia *et al.*, 2013; Li *et al.*, 2015), however these studies use 20+ years of annual surveys. Understory communities may respond strongly to interannual variation in climate and we are unable to capture this level of detail in our two survey periods. We did, however, find substantial consistency in the trait-environment coefficients when we applied the 1950s model to the 2000s distribution data (**Fig. 6**). This suggests that a few basic traits strongly affect how species respond to shifts in environmental conditions and may provide insight into predicting future responses. Exceptions to this were the trait relationships with minimum temperature of coldest month (BIO6) and mean temperature of the wettest quarter (BIO8; typically the summer months in Wisconsin). The majority of these trait-environment interactions lost statistical significance for the 2000s data. Seasonal temperatures have changed dramatically over the study period: winter months have experienced pronounced warming, while throughout much of the state, summer temperatures have decreased (Kucharik *et al.*, 2010). Consequently, these changes can disrupt the underlying species-environment relationships (**Fig. S5**) and decrease the predictive ability of traits. Additionally, we have previously demonstrated that many of these species substantially lag climate change in the state, likely decreasing our ability to predict species-environment relationships (Ash *et al., in press*).

Understory communities in WI display strong taxonomic and diversity changes, but little aggregate change in functional diversity (Sonnier *et al.*, 2014) despite strong trait-environment relationships (Amatangelo *et al.*, 2014) and changing environments (Rooney *et al.*, 2004; Rogers *et al.*, 2008; Kucharik *et al.*, 2010; Johnson *et al.*, 2014; Li & Waller, 2015). Our analysis shows that static distributions are structured in complex ways that depend on environmental gradients and species' traits. The environmental variables we used did not serve to reliably predict changes in species' abundances, suggesting that other factors drive site-level dynamics. As the effects of changing environmental conditions occur in the context of other drivers, it is difficult to isolate environmental effects and determine the scale at which they are affecting plant population and range dynamics. Nonetheless, ecologists urgently need predictive tools to forecast species' distributions and community patterns to provide quantitative scenarios of ecological change.

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Tables

Table 1. A list of the 34 computed environmental variables considered for each modeling effort and their abbreviations.

Variable	Explanation	Units
BIO1	Annual Mean Temperature	°C
BIO2	Mean Diurnal Range (Mean of monthly (max - min temp))	°C
BIO3	Isothermality (BIO2/BIO7) (* 100)	unitless
BIO4	Temperature Seasonality (standard deviation *100)	°C
BIO5	Max Temperature of Warmest Month	°C
BIO6	Min Temperature of Coldest Month	°C
BIO7	Temperature Annual Range (BIO5-BIO6)	°C
BIO8	Mean Temperature of Wettest Quarter	°C
BIO9	Mean Temperature of Driest Quarter	°C
BIO10	Mean Temperature of Warmest Quarter	°C
BIO11	Mean Temperature of Coldest Quarter	°C
BIO12	Annual Precipitation	mm
BIO13	Precipitation of Wettest Month	mm
BIO14	Precipitation of Driest Month	mm
BIO15	Precipitation Seasonality (Coefficient of Variation)	unitless
BIO16	Precipitation of Wettest Quarter	mm
BIO17	Precipitation of Driest Quarter	mm

BIO18	Precipitation of Warmest Quarter	mm
BIO19	Precipitation of Coldest Quarter	mm
precip_fall	Fall precipitation	mm
precip_win	Winter precipitation	mm
precip_spr	Spring precipitation	mm
precip_sum	Summer precipitation	mm
temp_fall	Mean fall temperature	°C
temp_win	Mean winter temperature	°C
temp_spr	Mean spring temperature	°C
temp_sum	Mean summer temperature	°C
water_def	Yearly water deficit (PET – BIO12)	mm/yr
gdd	Growing degree days (base temperature 10 °C)	°C
tmin_win	Mean daily minimum winter temperature	°C
pet	Potential evapotranspiration	mm/yr
Mean BA	Mean basal area of overstory trees	m^2
Soil (PCA1)	PCA axis 1 score, correlated with pH and cation content	unitless
Soil (PCA2)	PCA axis 2 score, correlated with soil texture	unitless

Table 2. A list of the 18 traits considered for each modeling effort.

Trait	**Units**	**Description**	**Ecological relevance**
Area of occurrence	km^2	Area of occupied sites in 1950s survey	Ecological specialization
Leaf circularity	unitless	0 (linear leaves) to 1 (circular leaves)	Resource acquisition/retention
Coefficient of conservatism	unitless	Habitat fidelity: 0 (low fidelity) to 10 (scarce species confined to a specific high-quality habitat)	Ecological specialization
Leaf length	mm	Maximum length of fully expanded leaf	Resource acquisition/retention
Leaf thickness	mm	Thickness of leaf tissue, avoiding veins	Stress avoidance
Leaf width	mm	Maximum width of fully expanded leaf	Resource acquisition/retention
Leaf dry matter content	$mg\ g^{-1}$	Leaf dry mass to fresh mass ratio	Resource acquisition/retention
Leaf carbon content	%	Carbon content of leaves	Resource acquisition/retention

Leaf nitrogen content	%	Nitrogen content of leaves	Resource acquisition/retention
Stem dry matter content	mg g^{-1}	Stem dry mass to fresh mass ratio	Resource acquisition/retention
Seed mass	g	Dry mass of seeds	Dispersal strategy and establishment success
Specific leaf area	m^{2} kg^{-1}	Leaf area to dry mass ratio	Resource acquisition/retention
Plant height	cm	Maximum height of vegetation	Competitive ability
Dispersal mode	Nominal	Wind, animal, unassisted, or water dispersal	Biotic interactions; dispersal strategy
Flowering season	Nominal	Aestival, autumnal or vernal flowering season	Stress and disturbance avoidance
Growth habit	Binary	Wood or non-woody growth form	Stress and disturbance avoidance
Life cycle	Binary	Annual or perennial life cycle	Stress and disturbance avoidance
Pollination mode	Binary	Abiotic or biotic pollination	Biotic interactions; pollination strategy

Table 3. Summary of model coefficients for the 1950s model. The response variable is species abundance (the number of quadrats occupied relative to the total number of quadrats) and estimates are shown on the logit scale. Abbreviations are as follows: *Environment* - BIO6: minimum temperature of coldest month; BIO8: mean temperature of wettest quarter; Mean BA: mean basal area of overstory trees; and *Traits* - LDMC: leaf dry matter content; AOO: area of occurrence; LT: leaf thickness. Significant effects ($p < 0.05$) are bolded.

	Term	**Estimate**	**Standard error**	**z value**	**P value**
	Intercept	**-4.98**	**0.19**	**-26.25**	**<0.0001**
Environment Effects	BIO6	-0.25	0.18	-1.42	0.16
	BIO8	**0.73**	**0.22**	**3.38**	**<0.01**
	Mean BA	-0.06	0.13	-0.45	0.65
	Soil (PCA1)	**-0.76**	**0.19**	**3.92**	**<0.0001**
	Soil (PCA2)	-0.20	0.17	-1.19	0.24
Trait Effects	**LDMC**	**1.73**	**0.17**	**9.89**	**<0.0001**
	AOO	-0.16	0.22	-0.74	0.46
	LT	**-0.61**	**0.30**	**-2.05**	**0.04**
Community Type	NUF	0.06	0.18	0.35	0.73
	SLF	-0.07	0.21	-0.32	0.75
	SUF	0.23	0.20	1.15	0.25
Env:trait Interactions	**BIO6:LDMC**	**-0.64**	**0.28**	**-2.26**	**0.02**
	BIO8:LDMC	**-0.87**	**0.39**	**-2.24**	**0.03**
	Mean BA:LDMC	-0.17	0.20	-0.85	0.40
	Soil (PCA1):LDMC	**-1.69**	**0.33**	**5.04**	**<0.0001**
	Soil (PCA2):LDMC	**-0.81**	**0.27**	**-3.03**	**<0.01**
	BIO6:AOO	**0.45**	**0.23**	**1.98**	**0.05**
	BIO8:AOO	**-1.37**	**0.31**	**-4.47**	**<0.0001**
	Mean BA:AOO	-0.22	0.16	-1.42	0.16
	Soil (PCA1):AOO	**0.57**	**0.26**	**-2.20**	**0.03**
	Soil (PCA2):AOO	**0.65**	**0.21**	**3.11**	**<0.01**
	BIO6:LT	**1.12**	**0.38**	**2.94**	**<0.01**
	BIO8:LT	-0.80	0.52	-1.55	0.12
	Mean BA:LT	-0.62	0.27	-2.31	0.02

Soil (PCA1):LT	**-1.44**	**0.45**	**3.18**	**<0.01**
Soil (PCA2):LT	-0.71	0.36	-1.96	0.05

Table 4. Summary of model coefficients for the 2000s model. The response variable is species abundance (the number of quadrats occupied relative to the total number of quadrats) and estimates are shown on the logit scale. Trait abbreviations are as follows: LDMC: leaf dry matter content; LNC: leaf nitrogen content; LT: leaf thickness. Significant effects ($p < 0.05$) are bolded.

	Term	**Estimate**	**Standard error**	**z value**	**P value**
	Intercept	**-6.23**	**0.23**	**-27.4**	**<0.0001**
Environment Effects	Fall precip	-0.17	0.14	-1.25	0.21
	Soil (PCA1)	**-1.01**	**0.22**	**4.61**	**<0.0001**
	Soil (PCA2)	-0.27	0.16	-1.65	0.1
	Summer temp	-0.1	0.32	-0.3	0.76
	Winter precip	**-1.12**	**0.18**	**-6.26**	**<0.0001**
Trait Effects	**LDMC**	**-1.55**	**0.38**	**-4.1**	**<0.0001**
	LNC	-0.37	0.33	-1.13	0.26
	LT	**-2.77**	**0.48**	**-5.78**	**<0.0001**
Community Type	NUF	0.21	0.2	1.03	0.3
	SLF	0.09	0.22	0.43	0.67
	SUF	0.26	0.2	1.25	0.21
Env:trait Interactions	Fall precip:LDMC	-0.09	0.2	-0.44	0.66
	Soil (PCA1):LDMC	**-1.85**	**0.43**	**4.35**	**<0.0001**
	Soil (PCA2):LDMC	**-0.64**	**0.27**	**-2.34**	**0.02**
	Summer temp:LDMC	-1.08	0.59	-1.82	0.07
	Winter precip:LDMC	-0.56	0.33	-1.7	0.09
	Fall precip:LNC	0.19	0.18	1.1	0.27
	Soil (PCA1):LNC	**1.09**	**0.37**	**-2.95**	**<0.01**
	Soil (PCA2):LNC	0.45	0.24	1.87	0.06
	Summer temp:LNC	**1.95**	**0.51**	**3.83**	**<0.0001**
	Winter precip:LNC	**-0.91**	**0.29**	**-3.11**	**<0.01**
	Fall precip:LT	**-0.57**	**0.27**	**-2.09**	**0.04**
	Soil (PCA1):LT	-0.63	0.55	1.16	0.24
	Soil (PCA2):LT	0.19	0.37	0.52	0.6
	Summer temp:LT	**-1.84**	**0.78**	**-2.37**	**0.02**
	Winter precip:LT	-0.68	0.43	-1.58	0.11

Figure Captions

Figure 1. Map of the network of survey and resurvey sites, color coded by community type (CSP: pine barrens of central sand plains; NUF: northern upland forests; SLF: southern lowland forests; SUF: southern upland forests).

Figure 2. How the relative importance of the environmental variables for predicting species' distributions compare between the two time periods (with a one-to-one line for comparison). Values are derived from random forest models at each time period and represent the percent of species that the particular variable was one of the top five predictor variables explaining species' distributions. Points are color-coded by the broad category of climate variables. The energy variables are potential evapotranspiration, growing degree days and annual water deficit. Soil PCA axes and mean overstory basal area (Mean BA) are separately labeled.

Figure 3. The estimated species' abundance intercepts and species' environmental response intercepts for the 1950s model. The *Intercept* panel shows how far species depart from the mean abundance, with species arranged in order of that departure. The remaining panels show how far species depart from the expected response for each of the five environmental variables significant during that period (ranked according to the order in the *Intercept* panel). The gray bars are 95% confidence intervals and yellow points indicate species for which that interval does not overlap zero. Note the high level of variation among species' responses and how this appears unrelated to species' abundance.

Figure 4. The estimated species' abundance intercepts and species' environmental response intercepts for the 2000s model. The *Intercept* panel shows how far species depart from the mean abundance, with species arranged in order of that departure. The remaining panels show how far species depart from the expected response for each of the five environmental variables significant during that period (ranked according to the order in the *Intercept* panel). The gray bars are 95% confidence intervals and yellow points indicate species for which that interval does not overlap zero. As in **Fig. 3**, there is a high level of variation in species' responses. However, in contrast to the 1950s model, the less abundant species show considerable variation (wider confidence intervals) in their responses to environmental variation.

Figure 5. Estimated trait coefficients showing the degree to which each of the three traits predict species' responses to the significant environmental variables for the 1950s (a), 2000s (b), and change in abundance models (c). The gray bars are 95% confidence intervals with yellow points again indicating where the interval does not include zero.

Figure 6. The estimated trait coefficients when applying the 1950s model structure (circles) to the 2000s species' distribution data (diamonds). The gray bars are 95% confidence intervals and yellow points indicate when the interval does not overlap zero. Note the similarity in estimates from both time periods, particularly for leaf dry matter content. While many of the estimates are similar, area of occurrence and leaf thickness were less predictive of species-environment relationships in the 2000s data.

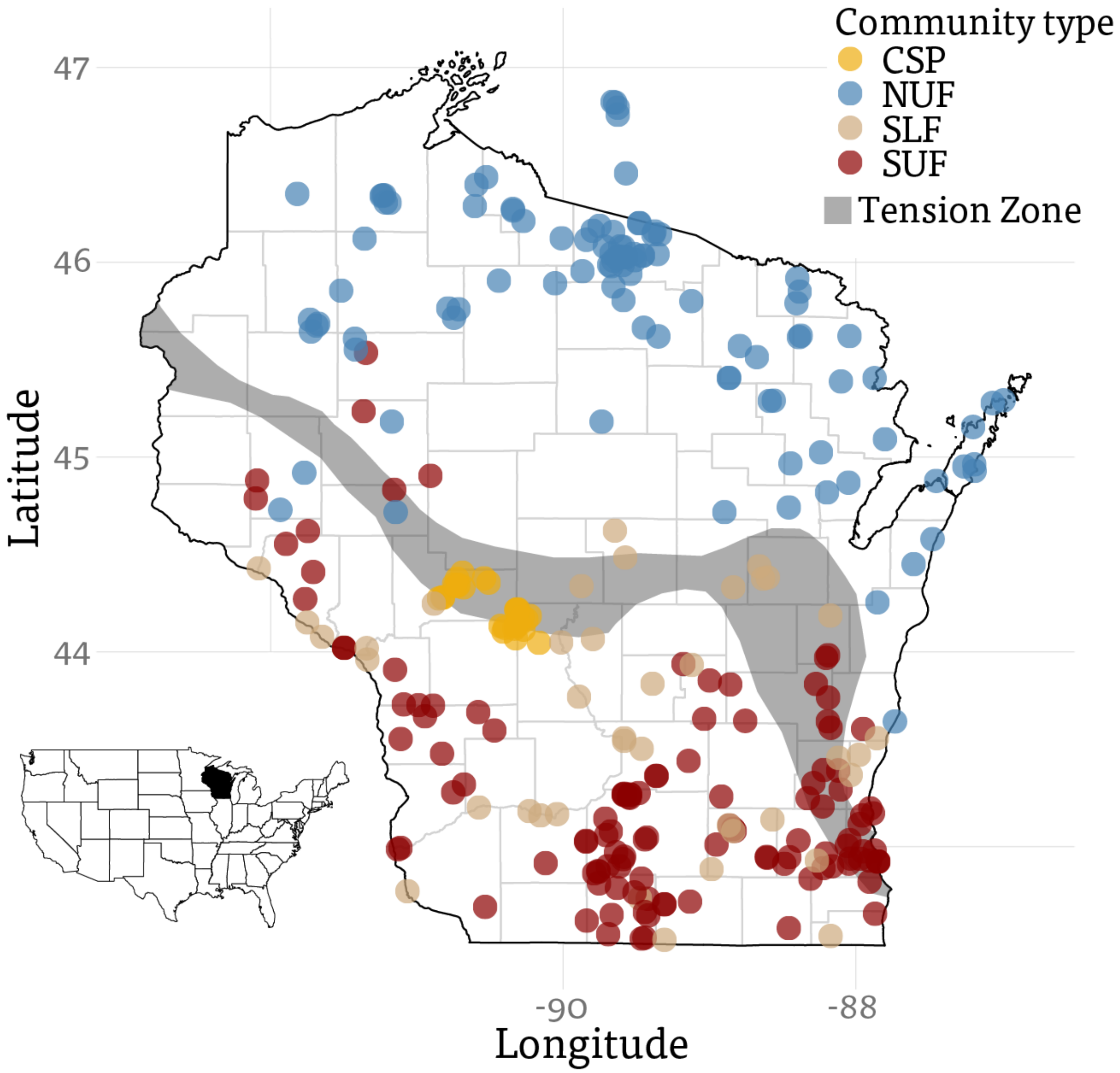
Community type
CSP
NUF
SLF
SUF
Tension Zone
47
46
45
44
Latitude
-90
-88
Longitude

Figure 1.

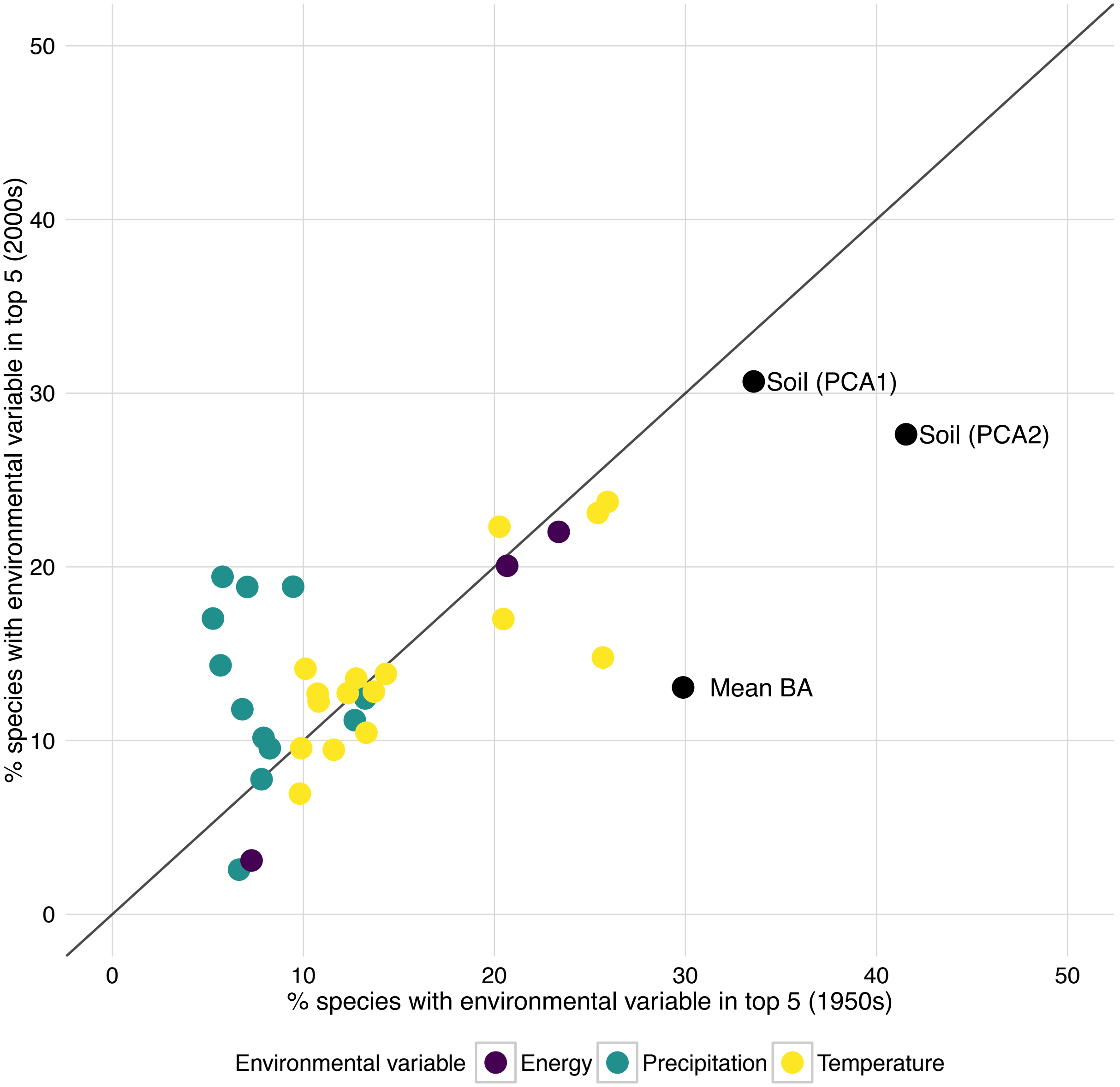
% species with environmental variable in top 5 (2000s)
% species with environmental variable in top 5 (1950s)
0
10
20
30
40
50
0
10
20
30
40
50
Soil (PCA1)
Soil (PCA2)
Mean BA
Environmental variable
Energy
Precipitation
Temperature

Figure 2.

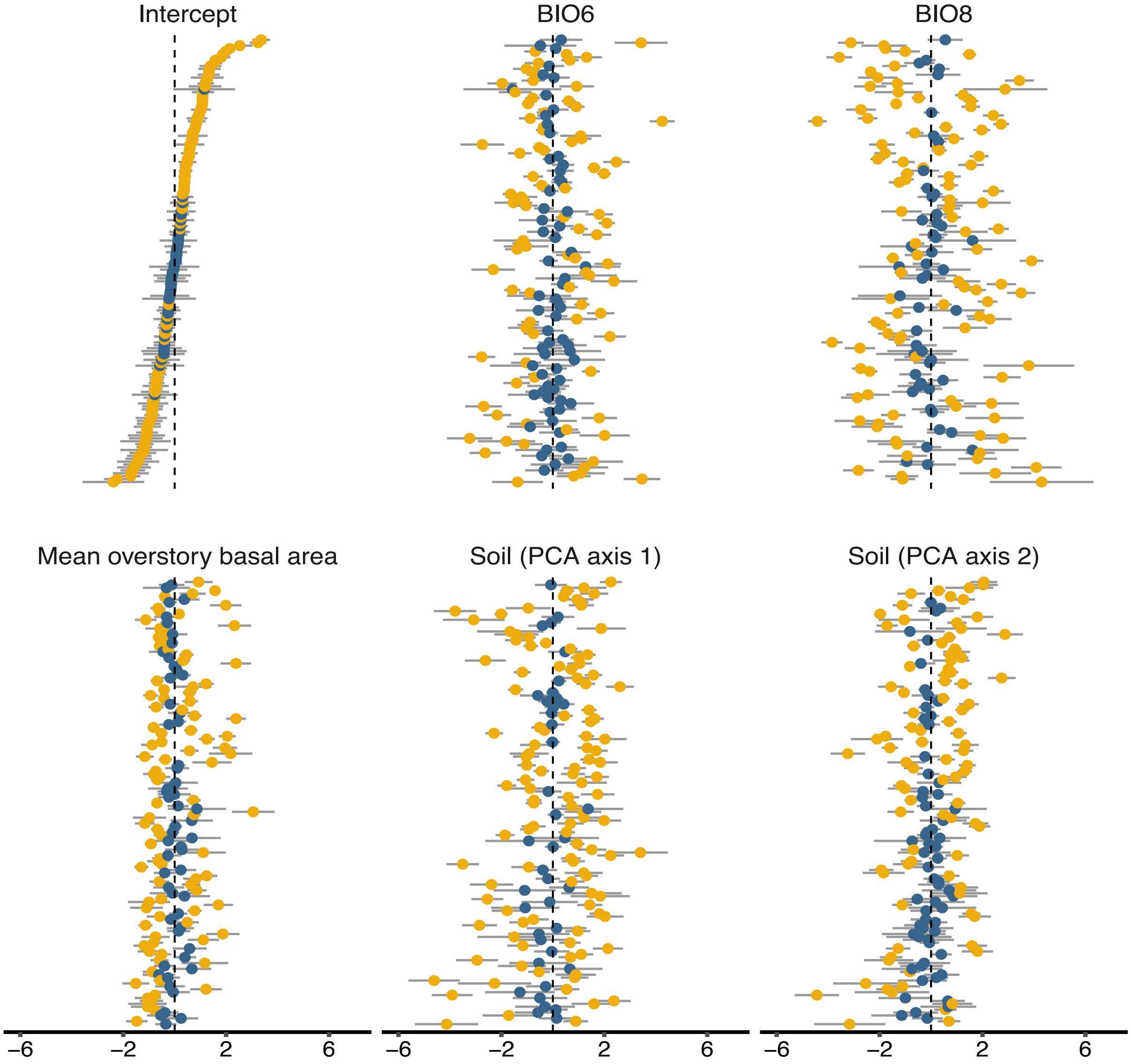
Intercept
BIO6
BIO8
Mean overstory basal area
Soil (PCA axis 1)
Soil (PCA axis 2)
–6
–2
2
6
–6
–2
2
6
–6
–2
2
6

Figure 3.

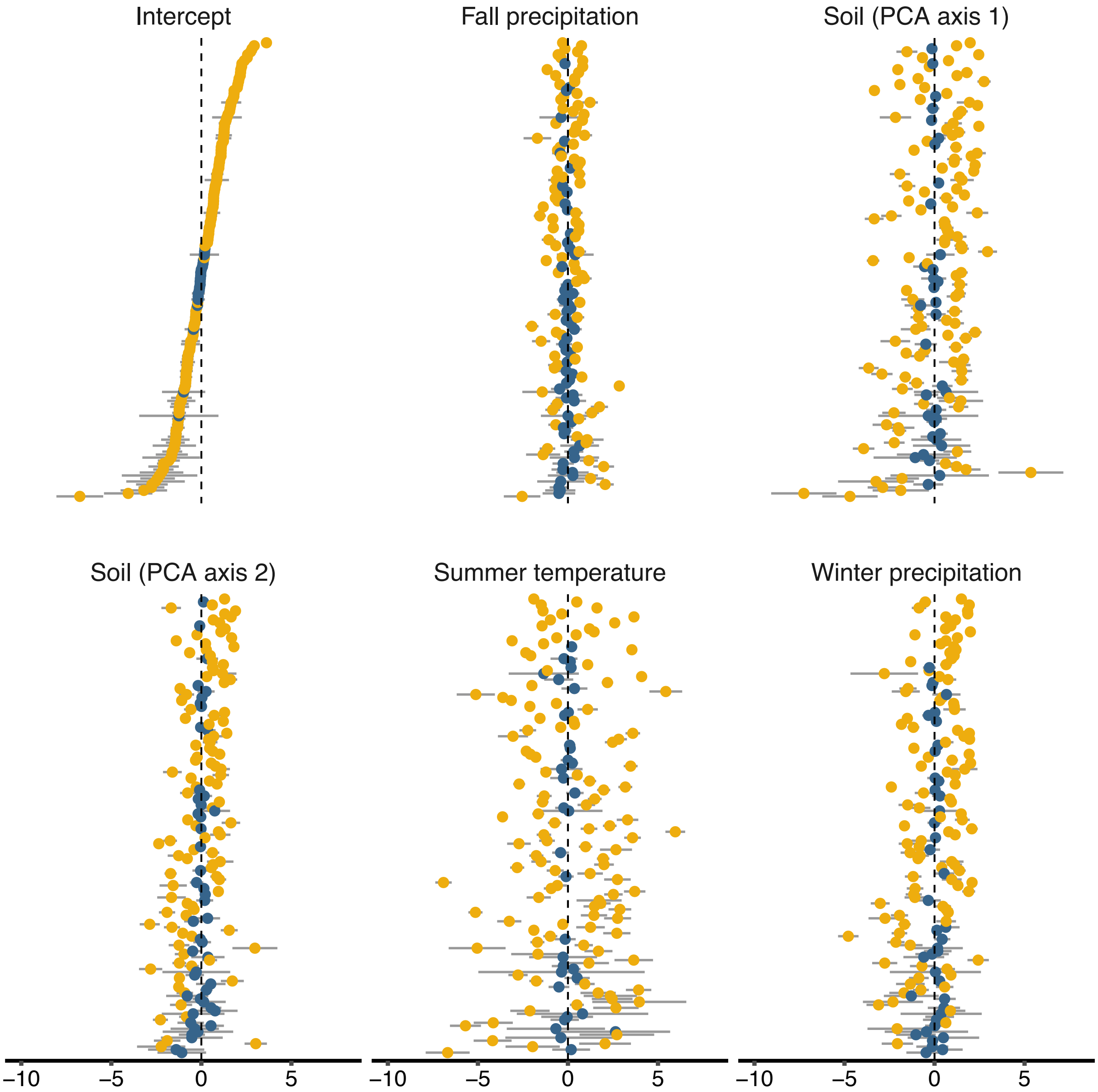
Intercept
Fall precipitation
Soil (PCA axis 1)
Soil (PCA axis 2)
Summer temperature
Winter precipitation
–10
–5
0
5
–10
–5
0
5
–10
–5
0
5

Figure 4.

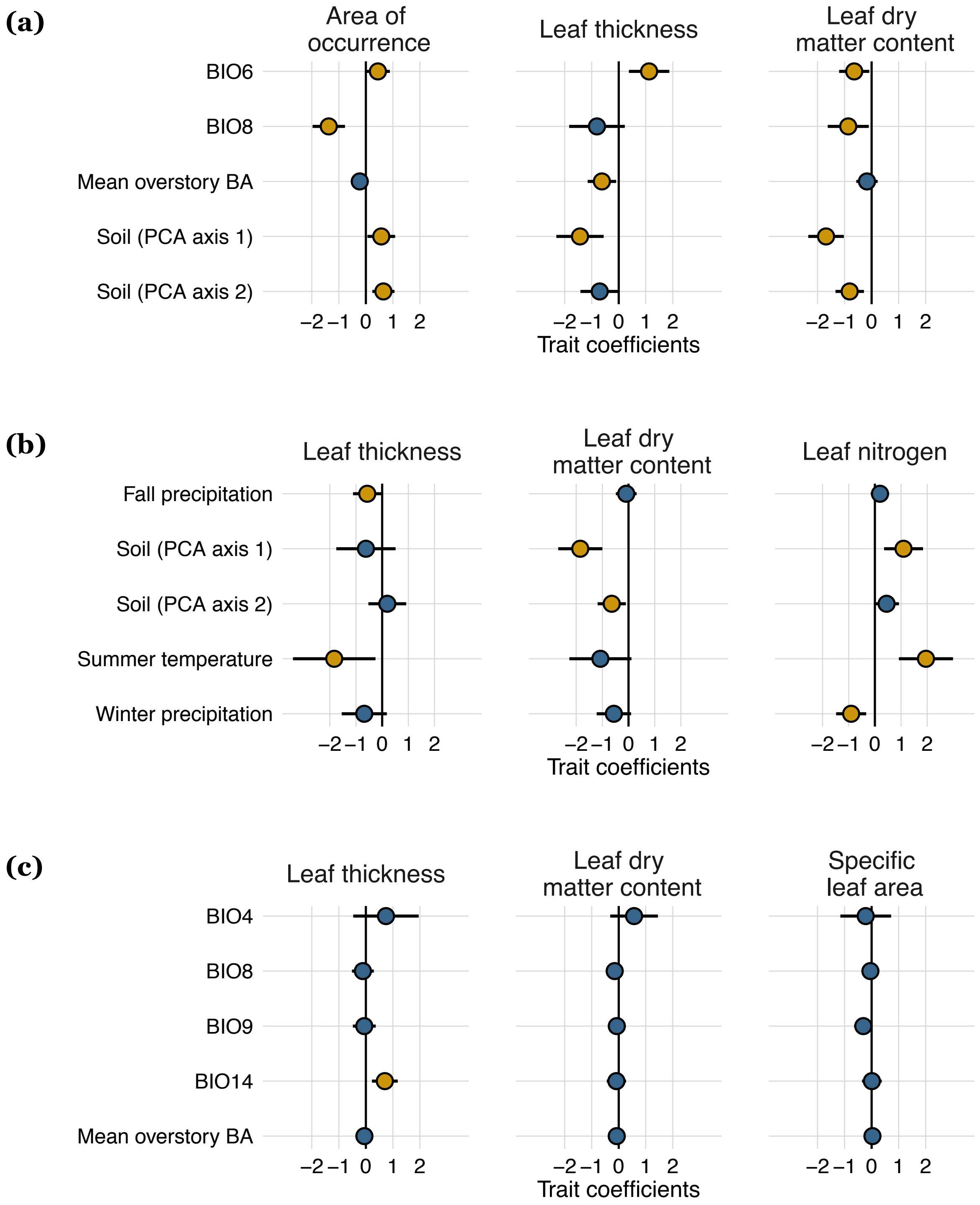
(a)
Area of occurrence
Leaf thickness
Leaf dry matter content
BIO6
BIO8
Mean overstory BA
Soil (PCA axis 1)
Soil (PCA axis 2)
−2 −1 0 1 2
Trait coefficients
(b)
Leaf thickness
Leaf dry matter content
Leaf nitrogen
Fall precipitation
Soil (PCA axis 1)
Soil (PCA axis 2)
Summer temperature
Winter precipitation
−2 −1 0 1 2
Trait coefficients
(c)
Leaf thickness
Leaf dry matter content
Specific leaf area
BIO4
BIO8
BIO9
BIO14
Mean overstory BA
−2 −1 0 1 2
Trait coefficients

Figure 5.


Area of occurrence
Leaf thickness
Leaf dry matter content
BIO6
BIO8
Mean overstory BA
Soil (PCA axis 1)
Soil (PCA axis 2)
−2 −1 0 1 2
−2 −1 0 1 2
−2 −1 0 1 2
Trait coefficients

Figure 6.

Appendix

Table S1. Summary of model coefficients for the change in abundance model. Estimates whose confidence interval does not overlap zero are in bold. Environmental abbreviations are shown in Table 1 and traits are as follows: LDMC: leaf dry matter content; SLA: specific leaf area; LT: leaf thickness.

	Term	**Estimate**	**Standard error**	**t value**
	Intercept	0.22	0.16	1.42
Environment Effects	BIO4	0.09	0.28	0.32
	BIO8	-0.06	0.09	-0.73
	BIO9	-0.11	0.09	-1.24
	BIO14	**0.29**	**0.10**	**2.98**
	Mean BA	-0.09	0.06	-1.45
Trait Effects	**LT**	**-0.60**	**0.28**	**-2.10**
	LDMC	-0.24	0.22	-1.08
	SLA	0.24	0.23	1.03
Community Type	**NUF**	**-0.49**	**0.18**	**-2.75**
	SLF	**-0.81**	**0.17**	**-4.87**
	SUF	**-0.76**	**0.16**	**-4.89**
Env:trait Interactions	BIO4:LT	0.74	0.62	1.20
	BIO8:LT	-0.11	0.21	-0.53
	BIO9:LT	-0.06	0.22	-0.27
	BIO14:LT	**0.70**	**0.24**	**2.88**
	Mean BA:LT	-0.05	0.14	-0.37
	BIO4:LDMC	0.57	0.45	1.26
	BIO8:LDMC	-0.15	0.15	-1.01
	BIO9:LDMC	-0.07	0.16	-0.45
	BIO14:LDMC	-0.09	0.18	-0.47
	Mean BA:LDMC	-0.07	0.11	-0.68
	BIO4:SLA	-0.22	0.48	-0.46
	BIO8:SLA	-0.04	0.15	-0.29
	BIO9:SLA	-0.31	0.17	-1.77
	BIO14:SLA	0.01	0.19	0.06
	Mean BA:SLA	0.03	0.11	0.28

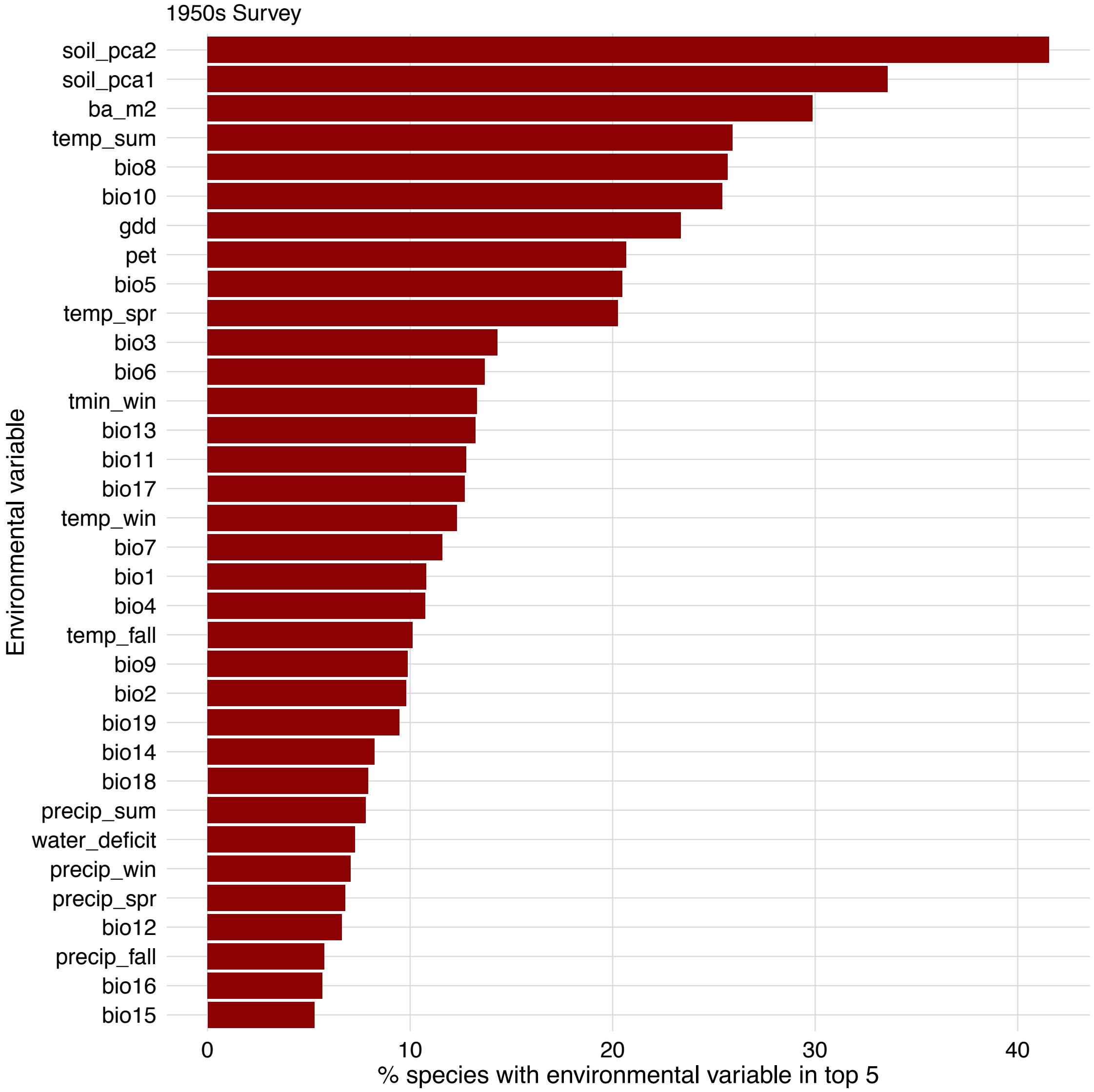

Figure S1. The relative importance of all 34 environmental variables for explaining the distribution of species in the 1950s survey based on random forest models. Random forest models were generated for each species and environmental variables are ranked according to the percentage of models where the variable was one of the top five most important variables.

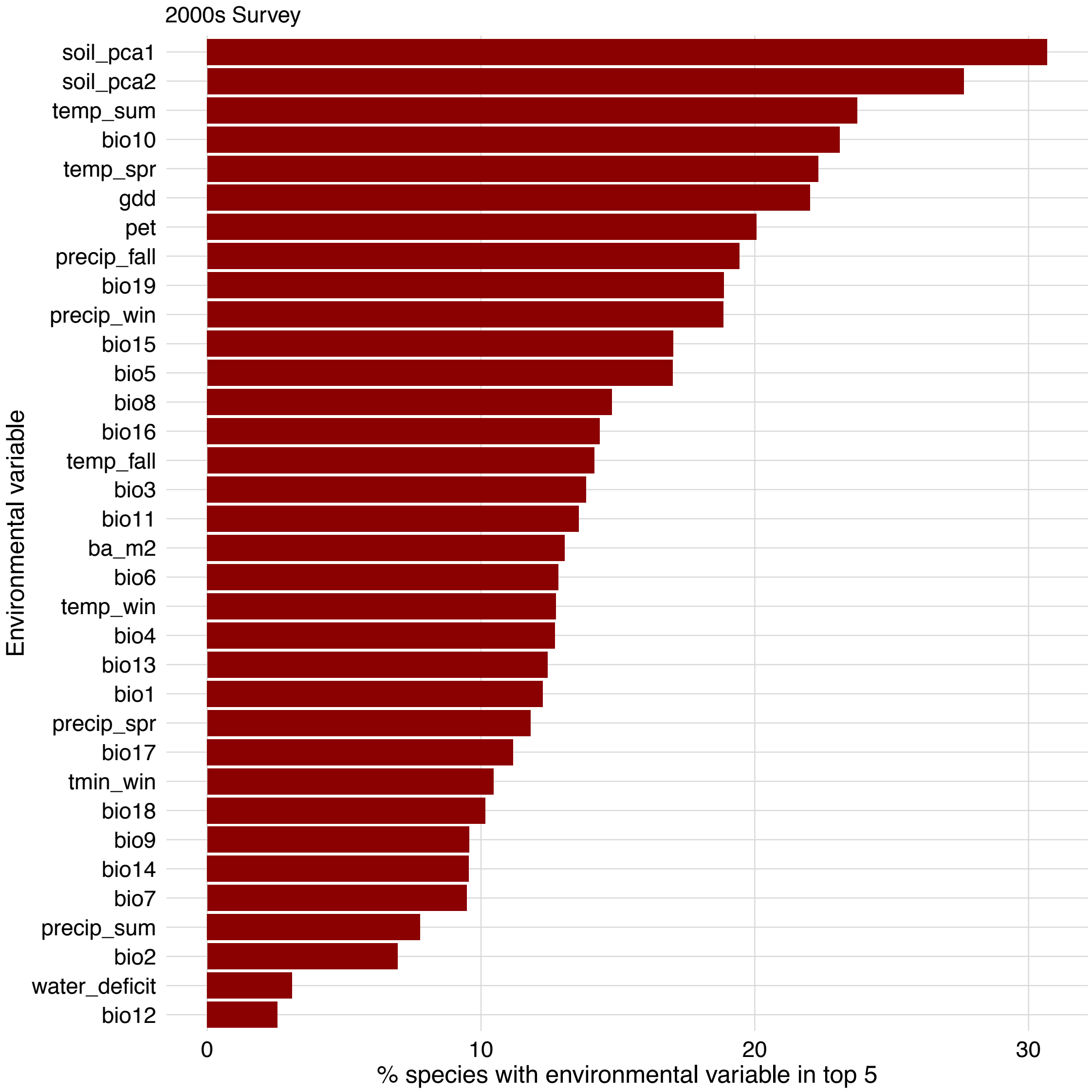

Figure S2. The relative importance of all 34 environmental variables for explaining the distribution of species in the 2000s survey based on random forest models. Random forest models were generated for each species and environment variables are ranked according to the percentage of models where the variable was one of the top five most important variables.

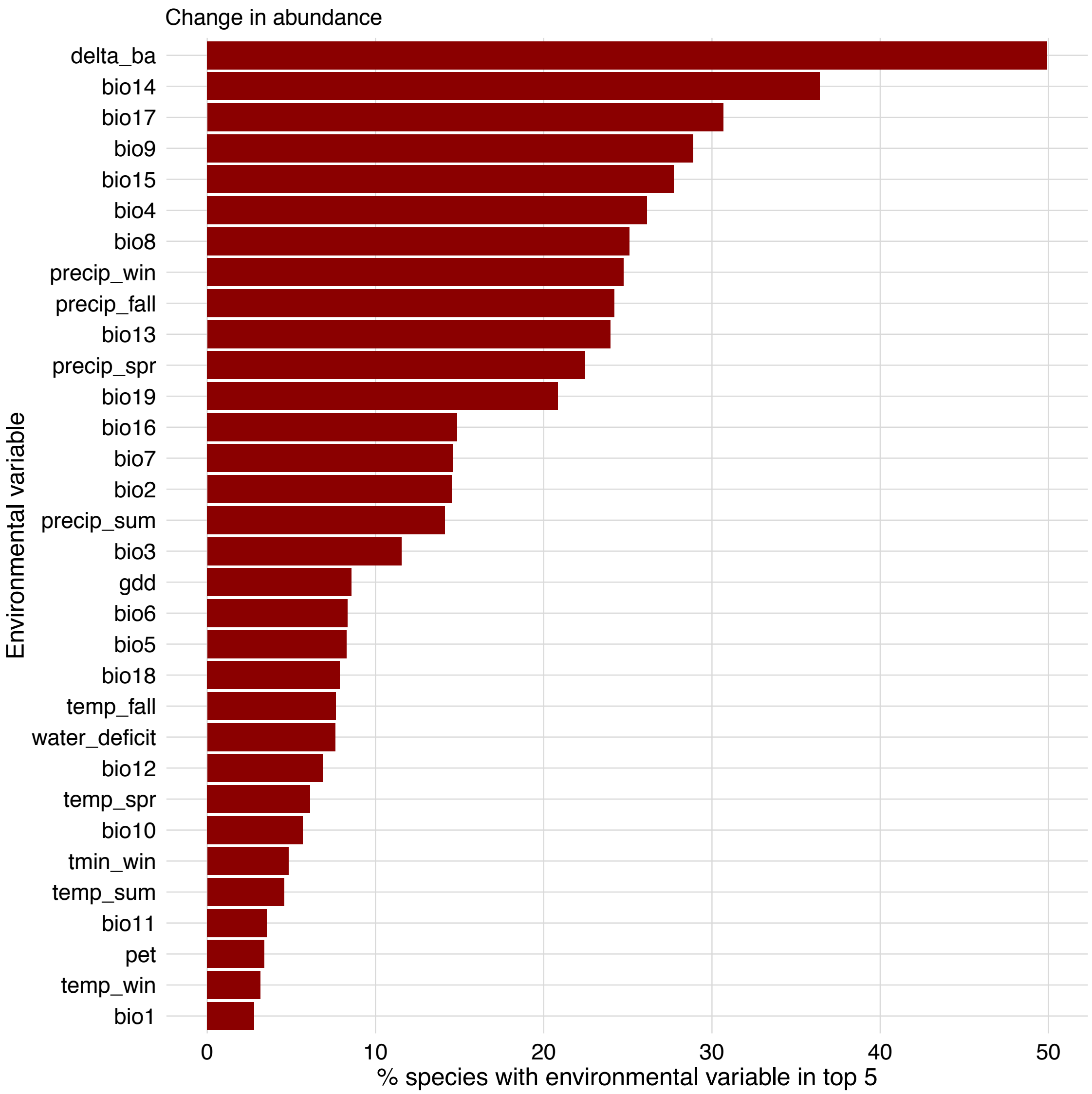

Figure S3. The relative importance of all 34 environmental variables for explaining the change in abundance for each species based on random forest models. Random forest models were generated for each species and environmental variables are ranked according to the percentage of models where the variable was one of the top five most important variables.

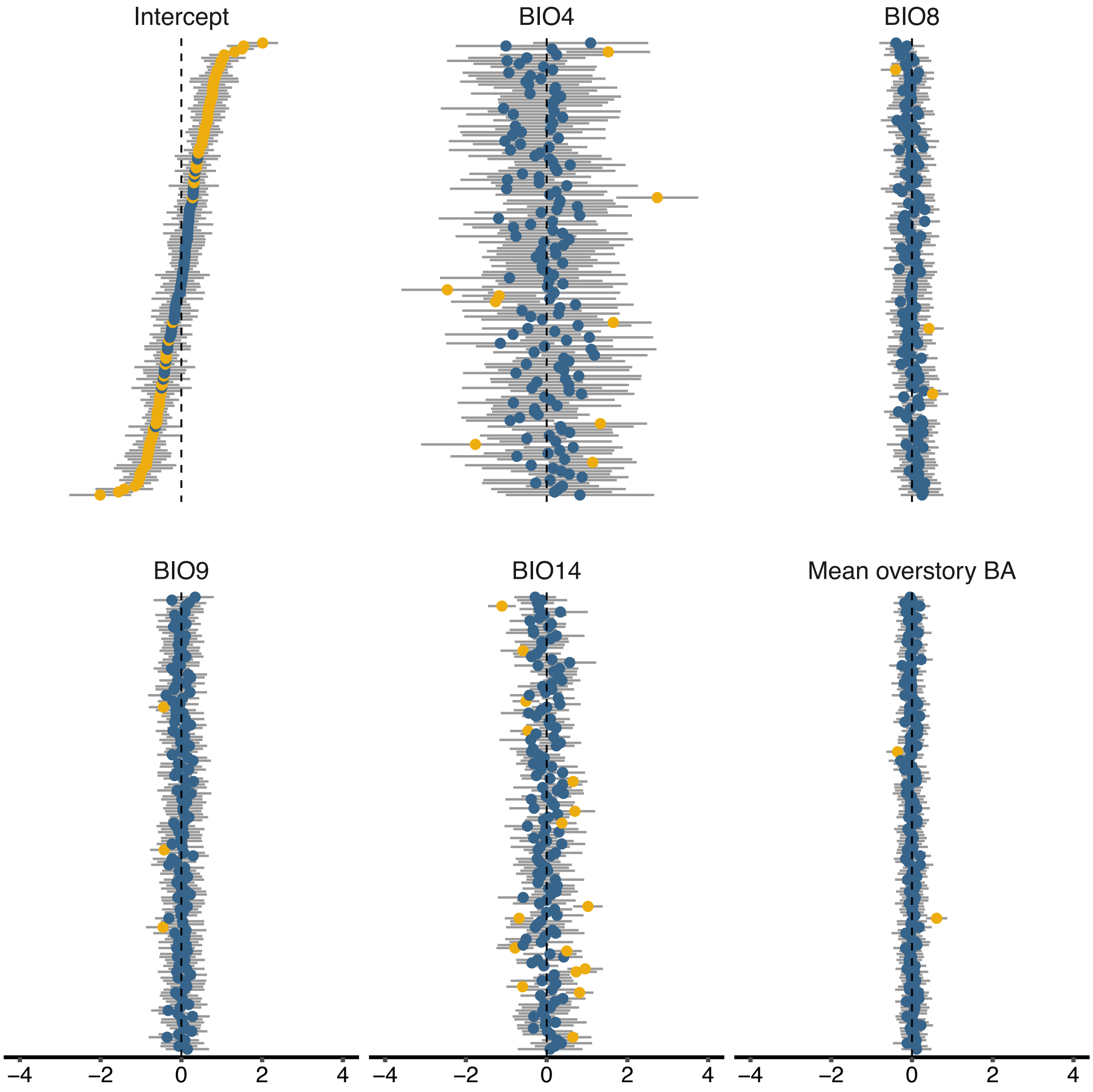

Figure S4. The estimated species intercepts and species-environment response intercepts for the change in abundance model. The *Intercept* panel shows how far species depart from the mean change in abundance. The remaining panels show how far species depart from the expected response to each of the 5 environmental variables. The gray bars are 95% confidence intervals and yellow points indicate when the interval does not overlap zero.

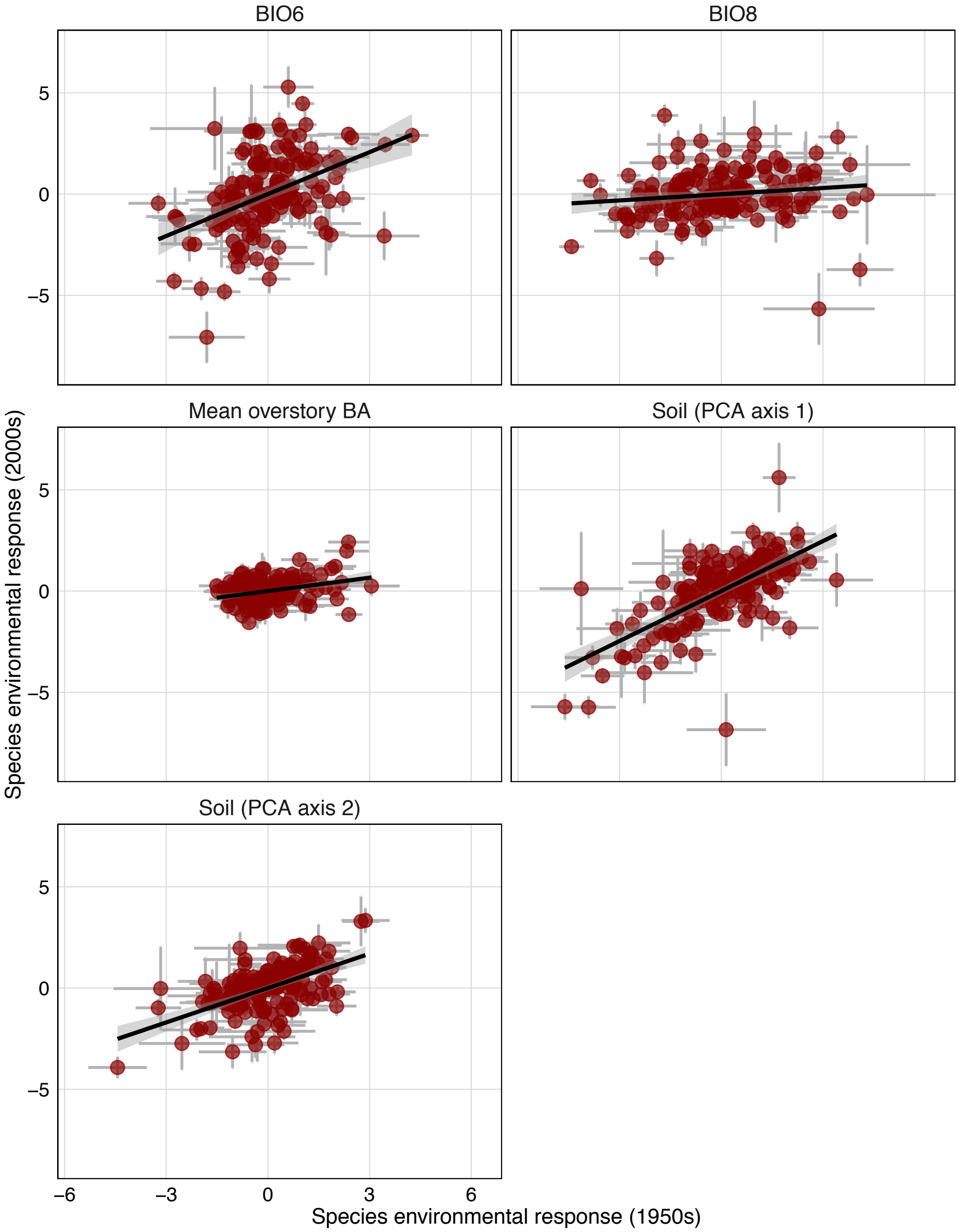

Figure S5. The relationship between the estimated species-environment response intercepts for the 1950s model (as in Fig. 3a) and when the 1950s model structure is applied to the 2000s data. Relationships are shown for each for the environmental predictor variables. The gray bars are 95% confidence intervals. Note the increased variation for the BIO6 and BIO8 relationships. These two variables have experienced larger changes over time, relative to other climate change trends.

Chapter 3 - Environmental filtering outweighs species' interactions in structuring spatial variation in understory plant communities

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Abstract

Species' distributions and community composition reflect a complex interplay between biotic and abiotic factors. Integrative models allow us to test the relative importance of environmental filtering and biotic interactions. Here we implement a multivariate probit regression model to 1) test whether the co-occurrence of forest understory plant species is driven by environmental filtering or species' interactions, 2) explore whether these patterns differ across time and 3) assess whether the functional similarity between species serves to predict species' interactions. We use detailed forest survey data from the 1950s and the early 2000s to parameterize models for 151 species across a network of 284 sites. We calculate pairwise functional dissimilarity using 16 life history and functional traits. Across both survey periods, environmental filtering predicted more of the spatial variation in community composition (11%) than the model including species' interactions (an additional 4%). Species-level patterns varied greatly, but species' interactions were still less important than environmental factors. Environmental conditions explained a consistent proportion of the species-level patterns over time, however the identity of the environmental variables changed considerably. Additionally, we did not detect any systematic shift in the relative importance of species' interactions for structuring species' distributions over time. Functional similarity was not a strong predictor of these estimated species' interactions. Collectively, these results support the idea that environmental filtering acts as the dominant mechanism structuring the assembly of these communities. These individualistic responses to environmental variation challenge our ability to forecast shifts in species' distributions under future climate change scenarios.

Keywords: joint species distribution model; forest understory; biotic interactions; environmental filtering; functional similarity

Introduction

The diverse processes that shape plant community assembly continue to generate lively speculation and debate. Ecological theory and empirical evidence suggest that biotic interactions (HilleRisLambers *et al.*, 2012) and environmental filtering (Kraft *et al.*, 2014) act as key factors to drive species' distributions and community composition. Both of these processes affect co-occurrence patterns as detected in pairwise species association tests (Gotelli & McCabe, 2002; Veech, 2014) and broader meta-community patterns (Leibold & Mikkelson, 2002; Almeida-Neto *et al.*, 2008; Presley *et al.*, 2010). Our ability to disentangle the relative importance of these processes is challenged as ecological changes expand and accelerate. Global climate change and shifts in species' distributions are reshuffling communities, creating novel environmental conditions and species' associations (Williams & Jackson, 2007; Sheldon *et al.*, 2011; Urban *et al.*, 2012; Alexander *et al.*, 2015). Modeling these dynamics requires us to understand the species-environment relationships that underlie species' distributions and occurrences.

Species distribution modeling (SDM) is a key tool for understanding how species respond to environmental variation, but has limited scope and predictive power (Ibanez *et al.*, 2006). As we apply these models to understand species sensitivity to climate change (Araujo & Peterson, 2012), we should remain aware of how such models abstract species from the biotic processes that also shape their distribution. Efforts to include species' interactions have primarily involved overlaying independently fit models to assess their collective responses to environmental gradients. While there has been a shift towards multi-species forecasting, such models are often still developed for individual species and then combined in an ad hoc fashion (Mokany & Ferrier, 2011). Newer integrative approaches incorporate analytical tools from community ecology (i.e., co-occurrence patterns) into multi-species distribution models to more fully depict the conditions under which distribution patterns might change (Kissling *et al.*, 2012). Our goal in applying these methods is to develop predictive models that can capture both abiotic and biotic influences on species' distributions. Although co-occurrence patterns have a contentious history in ecology (see Gotelli & McCabe, 2002 for a summary), they can provide a surrogate for biotic interactions by identifying non-random species' associations. Additionally, we can compare estimates of species' interactions to functional similarity to gain a more mechanistic understanding of how species' interactions contribute to co-occurrence patterns and responses to environmental gradients (Pollock *et al.*, 2014).

A promising set of analytical tools for assessing both environmental responses and species' interactions has emerged in the form of joint species distribution models (Ovaskainen *et al.*, 2010; Clark *et al.*, 2014; Pollock *et al.*, 2014; Warton *et al.*, 2015). A JSDM advances the inferential ability of single species models in two important ways: by modeling environmental filtering at the community level and by incorporating statistical correlations among species (Ovaskainen *et al.*, 2016). The response variable (the co-occurrence matrix) can then be decomposed into the components described by shared environmental responses and the residual co-occurrence patterns (Pollock *et al.*, 2014). These tools fit our urgent current need to understand how ecological changes will affect the relative importance of environmental filtering and biotic interactions, allowing us to make more accurate predictions (Blois *et al.*, 2013; HilleRisLambers *et al.*, 2013). Historical datasets have yielded important insights into species' range shifts in response to climate change (Tingley & Beissinger, 2009) and can afford similar insights into assessing the relative importance of biotic interactions and environmental filtering.

Here we develop independent JSDMs for Wisconsin forest understory plant communities at each of two time periods. Our goal is to assess the relative importance of biotic interactions and environmental filtering and how these have changed over the last half century. To build these models, we use data from both the baseline surveys conducted by J.T. Curtis and his students in the 1950s (Curtis, 1959) and re-surveys of the same sites in the 2000s (Waller *et al.*, 2012). We investigate the forces affecting pairwise species' associations by decomposing co-occurrence patterns into shared environmental responses and species' interactions. Because species' distributions and community structure emerge from fine-scale processes, we model co-occurrence at the biologically relevant scale of 1m^2 quadrats. However, we draw inferences for species' distributions and the meta-community at the landscape scale based on our data from an extensive network of 284 sites. We also seek to understand the biological characteristics that underlie these species' responses to variable environmental conditions and interactions with other species. We therefore use 16 life history and functional traits to estimate the distances between species in trait space and use these to assess whether functional differences account for how species co-vary in these species' distribution models. In sum, our objectives are to:

1) examine patterns of species' co-occurrence to determine the relative contributions of environmental filtering and species' interactions to community assembly;
2) compare the relative importance of these processes between the two survey periods; and
3) assess the relationship between how species co-vary in the distribution models and their functional similarity.

Methods

Vegetation Data

Our baseline data derive from the surveys of Wisconsin forest communities conducted by J.T. Curtis and his students between 1942-1956 (Curtis, 1959). Their goals were to understand the distributions of plant species among habitats, characterize the composition of Wisconsin plant communities, and test the continuum hypothesis that species respond individually to gradients in environmental conditions. Follow-up re-surveys in the 2000s add value to this rich baseline by allowing us to evaluate the ecological changes that occurred over this 50-year interval (Waller *et al.*, 2012). Here, we focus on 284 sites from four types of forests: 30 sites in the central sand plain pine barrens (CSP), 96 northern upland forest sites (NUF), 40 southern lowland forest sites (SLF), and 118 southern upland forest sites (SUF – **Fig. 1**).

Curtis and colleagues sampled the understory using twenty 1m x 1m quadrats evenly spaced along a U-shaped transect. Within each quadrat, they recorded all herb, shrub and tree seedling species present. The 2000s resurveys relocated these sites and applied similar protocols, but sampled these sites more intensively using 42-120 quadrats per site (Waller *et al.*, 2012). For this study, we evenly sub-sampled 20 quadrats from the 2000s data for each site to standardize sampling effort. For each survey period, we combined the quadrat by species matrices for each site into a single matrix with entries reflecting the presence (1) or absence (0) of each species in each quadrat and site. We restrict our analyses to the 151 species present in at least ten sites at one of the survey periods. We also ran the analyses described below using presence-absence at the site level, given the high turnover occurring at the quadrat scale. The results were qualitatively similar, so we report on the higher resolution, quadrat scale.

Environment Data

To characterize climate change over the study period, we used an 8 km gridded climate dataset of daily precipitation and minimum and maximum temperature covering 1950 to 2006 (Kucharik *et al.*, 2010). These data are generated using spatial interpolation across an extensive network of weather stations throughout the state. We computed ecologically meaningful seasonal and annual summary variables from these data for all 284 sites (**Table 1**). We chose these summary variables to reflect a broad range of both seasonal and annual aspects of climate change, as well as a set of biologically relevant climate variables (Booth *et al.*, 2013). For each variable, we calculated a mean value for the five-year interval around the survey periods (1950-1954 and 2000-2004) to account for inter-annual climatic variability and potential lags in species' responses to climate (De Frenne *et al.*, 2013). The BIOCLIM variables, a set of 19 biologically-meaningful climate variables, were calculated using the *dismo* package in R (Hijmans *et al.*, 2015). We determined mean temperature and precipitation for each of the seasons, as well as a set of energy-based measures. Potential evapotranspiration was calculated using the Thornthwaite equation (Thornthwaite, 1948), approximating day-length using site latitude (Forsythe *et al.*, 1995). Annual water deficit was calculated as the difference between potential evapotranspiration and annual precipitation. We determined the number of growing degree days using 10°C as the base threshold.

Our models also included soil texture and chemistry and the size of overstory trees. We collected and combined ten randomly dispersed soil samples at each site and measured nine soil variables: pH; % organic matter; % sand, clay and silt; and concentrations of phosphorous, potassium, calcium and magnesium (in ppm). To reduce dimensionality of these soil variables, we extracted the first two axes from a Principal Components Analysis. These together explain 67% of the total variation in soil conditions among sites. The first axis primarily reflects variation in soil cations and pH, while the second reflects soil texture. We measured these soil variables only in the 2000s and assume that they did not change appreciably since the 1950s. We also include the mean basal area of overstory trees at each site to represent successional status. Succession has structured changes in many of these understory communities (Wiegmann & Waller, 2006; Rogers *et al.*, 2008; Johnson *et al.*, 2014; Li & Waller, 2015). We standardized these environmental variables to obtain a mean of zero and standard deviation of one to facilitate comparisons.

Functional Trait Data

We measured a broad suite of functional traits to capture a range of life history and ecological strategies (**Table 2**). We use trait means reflecting measurements on at least 12 individuals (four individuals from each of three sites) following standardized protocols (Pérez-Harguindeguy *et al.*, 2013). We also standardized all the continuous trait variables.

Environmental Variable Selection

We first built separate models of the distribution of each species in each survey period. These probit regression models used maximum likelihood and a forward stepwise procedure to identify and select the variables best associated with these distributions. Our initial null model included a main effect of community type to account for the nested structure of the data. In each successive step, we added environmental variables until we identified a set of predictors that minimized the model's Akaike Information Criterion. We then retained these predictors for each of the full JSDMs.

Joint Species Distribution Model

We also developed two separate JSDMs for each survey period following Golding et al. (2015). Briefly, we built Bayesian multivariate probit regression models to predict species' distributions and community composition from the environmental variables. These models sought to predict the full co-occurrence matrix of all focal species across all sites. We modeled species' distributions (presence/absence) using independent binomial regressions on the environmental variables. We included species' correlations in the model using a symmetric matrix of the correlations in regression errors between distributions of all pairs of species (Pollock *et al.*, 2014). Because we first modeled the environmental determinants of species' distributions, these positive and negative correlation coefficients are assumed to reflect positive and negative biotic interactions between species.

The JSDM we use here resembles the model of Ovaskainen et al. (2010), but uses a latent variable formulation of the probit link function instead of a logit link function (Pollock *et al.*, 2014). Latent variable models are a flexible class of models which introduce unobserved ("latent") predictors into the model (Warton *et al.*, 2015). In our case, the latent variable is used as a link function to relate our continuous predictors to the binary outcomes of species presence/absence. Correlations among the species-level latent variables indicate non-random species' associations. The model is developed below, following Golding et al. (2015):

$$y_{ij} = 1(z_{ij} > 0)$$

$$z_{ij} = \mu_{ij} + e_{ij}$$

$$\mu_{ij} = \mathbf{X}_j \beta_j$$

$$\mathrm{e}_i \sim N(\mathbf{0}, \mathbf{R}),$$

where y_{ij} is a binomial variable indicating the presence (1) or absence (0) of species j (j = 1,…,n) at site i (i = 1,…,m) and z is a normally distributed latent variable. The latent variable is the indicator or link function whose value is 1 when $z > 0$ and 0 otherwise. For species j, $\mathbf{X}_j$ is an n by k_j matrix and β_j is a vector of k_j regression coefficients. The error term is defined by an m-dimensional standard multivariate normal distribution $N(\mathbf{0},\mathbf{R})$ with mean vector $\mathbf{0}$ and symmetric, positive definite correlation matrix **R.** The extent to which the distribution of species j is predicted by the environment is defined by k_j, the number of environmental covariates used in the model. The elements of **R** describe whether species co-occur more or less often than would be expected by their environmental determinants alone and thus are used as a proxy for the underlying species' correlations across sites. The correlation matrix is calculated by re-scaling the variance/covariance matrix of the multivariate normal distribution by dividing the terms by the corresponding standard deviations and setting an inverse Wishart prior (Chib & Greenberg, 1998).

As in Ovaskainen et al. (2010), we developed four models to explore the importance of different mechanisms of community variation: a null or completely random assembly model, a community only model, an environment only model, and a full model containing both environmental predictors and species' interactions. All models include intercept terms and a variable for community type. We included the environment variables identified in the stepwise selection procedure in the environment and full models. For the null and environment models, the correlation matrix was set to the identity matrix to allow for independence among the model errors for each species.

In the community and full model, the species' correlation matrix was parameterized as described above.

We then compared the environment, community and full models to the null model using a deviance partitioning method (Golding, 2015). The null model assumes all species have equal occurrence probability across all sites, conditional on community type. Deviations from this assumption are considered to be the observed species' distribution patterns and quantified as the residual deviance of the null model. The residual deviance patterns for the other models are similarly quantified and compared to the remaining null deviance to determine the proportion of species distributions explained by each model. We additionally compared models using Deviance Information Criterion (DIC). Similar in concept to other information criterion, lower DIC model values are considered to be a better model fit, with differences greater than five indicating a substantial improvement in explanatory ability. For each model, we used 11,000 iterations, discarding a burn-in of 1000 and thinning the posterior chains by a factor of ten. We used vague normal priors for the model parameters ($\mu = 0$, $\sigma = 10$). All models were fit using BayesComm (Golding & Harris, 2015) in R version 3.3.0.

As discussed in Clark et al. (2014), this is not an outright test of species' interactions. Rather, the output from the JSDM quantifies the co-occurrence patterns found in the observational dataset and provides an estimate of the importance of species' correlations, after accounting for shared environmental responses. This assumes that we have fully characterized the important environmental variables and that the residual correlation is not due to other unmeasured factors. We acknowledge that we are unable to meet these assumptions, but instead try to relate our measures of species' interactions to available life history information and functional traits. We used the Gower distance in multivariate trait space between each pair of species to measure functional dissimilarity (relative to mean pairwise dissimilarity). The Gower distance is a flexible metric that can integrate both continuous and categorical data (Podani, 1999). We then related the pairwise species' correlations to these functional dissimilarities using linear regression. Because the distribution of species' correlation coefficients was strongly bimodal (omitting correlation coefficients near 0 judged to be non-significant), we analyzed negative and positive species' correlations separately.

Results

Environmental variables and species' interactions (measured by pairwise species' correlations) together explain a modest, but consistent proportion of the total variation in species' spatial distributions in these understory communities in both the 1950s and 2000s. The environmental variables together explained ~11% of the community variation in both survey periods. Across species, the environmental variable selection process yielded similar results between time periods (**Fig. 2**). For both time periods, soil variation and overstory tree basal area were the variables most consistently selected for explaining species' distributions (**Fig. 2**). Including species' interactions in the full model increased the explained deviance for community variation by ~4% in both survey periods. Species-level patterns varied more (**Fig. 3**). Patterns in the 1950s and 2000s were generally similar, except that including species' interactions in the 2000s model decreased (rather than increased) the explained deviance for several individual species. In both survey periods, the full models provided the best fit, as measured by DIC (**Table 3**). Thus, both environmental factors and species' interactions continue to affect the distribution of species in these communities to roughly the same degree that they did in the 1950s.

Species varied considerably in the extent to which environmental variables account for their distributions (**Fig. 4a**) and the extent to which species' interactions served to increase the explanatory power of these models (**Fig. 4b**). The explanatory power of the environment-only models varied greatly, but was correlated between periods (**Fig. 4a**). However, the identity of the environmental variables for each species-level model differed considerably over time. The average overlap in environmental variables across time was only 14%, suggesting species responded to distinct environmental gradients at each time period. The explanatory power of species' interactions in these species-level models (as estimated from the correlations) was not correlated (**Fig. 4b**). This suggests that the factors affecting how species interact (or perhaps the consequences of interactions among species) changed between the 1950s and 2000s. There was a positive relationship between the explanatory power for the environment models and additional power from including species' interactions in the 1950s (**Fig. S1**). In other words, species whose distributions were well defined by the environment were also explained better by including species' interactions. No such relationship existed for the 2000s data (**Fig. S2**).

Species that are functionally similar generally show more positive correlations in co-occurrence (**Fig. 5**). That is, the correlations between species' distributions declined as their functional dissimilarity increased, but these relationships were weak. Overall, we observed more positive than negative correlations between species (**Table 4**). The number of significant negative correlations declined greatly from the 1950s to the 2000s, but not the number of positive correlations, further skewing these ratios.

Relative to the community only model, the full model showed fewer significant species' correlations.

Discussion

Many abiotic and biotic factors affect where species occur and how they co-occur with other species. Our understanding of how these forces play out in plant communities, however, remains incomplete. We sought to understand how differences in soil conditions, successional state, shifting climatic conditions, and interactions among species affect the sorting of plant species into forest understory communities distributed across Wisconsin at two distinct periods. In particular, we applied a sophisticated set of species' distribution models, as these can provide insights into how such factors affect community structure and dynamics (Elith & Leathwick, 2009). Most previous species' distribution models have relied on correlations with environmental variables while ignoring biotic effects. We know, however, that interactions among species influence distribution patterns and community assembly, particularly under climate change (Adler *et al.*, 2009; 2011; Liancourt *et al.*, 2013). Although experiments allow us to quantify the effects of species' interactions most exactly, it is clearly impractical to manipulate dozens to hundreds of species and community composition across hundreds of sites. Instead, we combined a wealth of species' occurrence and co-occurrence data with joint species distribution models to infer how environmental filtering and estimated species' interactions affect species' distributions and community assembly as recently pursued by others (Ovaskainen *et al.*, 2010; Clark *et al.*, 2014; Pollock *et al.*, 2014; Warton *et al.*, 2015; Maguire *et al.*, 2016).

Our first objective was to assess the relative contributions of environmental filtering and species' interactions in the assembly of these forest plant communities. Variation in soil conditions, successional status, and climatic conditions all affected understory species' distributions and community composition, and did so in a consistent manner in both the 1950s and 2000s (**Fig. 2**). These environmental variables explained a significant and consistent (but modest) proportion of the community-wide distribution patterns. The species-level patterns varied more and environmental predictors served to predict up to 67% of the variation in some species' distributions (**Fig. 3**). Including species' interactions along with the environmental factors increased the explanatory power of the community models further. These increases were statistically significant, but modest (~4%). Species-level patterns were again varied, but less so than the responses to environmental variables.

Species' distributions and community composition often reflect species' environmental tolerances (Kraft *et al.*, 2014). Other studies of understory communities also found environmental conditions to dominate spatial variation in community composition (Rogers *et al.*, 2008; Burton *et al.*, 2011; Johnson *et al.*, 2014; Sabatini *et al.*, 2014; Li & Waller, 2015). Although species' interactions influenced species' distributions and community assembly less than environmental filtering in this study, they added appreciably and significantly to model fit, as found by others (Clark *et al.*, 2014; Pollock *et al.*, 2014; Warton *et al.*, 2015; Maguire *et al.*, 2016). In a wide ranging analysis of terrestrial vertebrate co-occurrence patterns, Araujo et al. (2011) found a few species to be highly connected to others, but most species responded independently and individualistically to climate change. We also found evidence of strongly individualistic responses to environmental gradients, as noted by others working on species distribution modeling (Pearson & Dawson, 2003; Araujo *et al.*, 2011).

The survey and resurvey data used to construct the models presented here reflect remarkably intensive and extensive sampling of 151 species distributed over four community types and 284 sites. These samples were separated by an interval of 50 years, allowing us to assess potential changes in the importance of environmental factors and species' interactions in driving species' distributions and community assembly. In addition, we used detailed data on the environmental conditions present at each site (soils, climates, and successional state) and 16 functional traits for each of the 151 species. These sizes of these samples give us high power to address our objectives and confidence that the results we report accurately reflect the conditions and ecological processes acting in these communities.

Nevertheless, relying on presence-absence data may have diminished the estimated importance of species' interactions in our models. Another study found that biotic interactions defined abundance patterns better than presence-absence patterns (Boulangeat *et al.*, 2012). Nonetheless, simultaneously modeling species' interactions and environmental responses yielded the best model fit at both time periods (**Table 3**). As noted by others (Clark *et al.*, 2014; Pollock *et al.*, 2014; Golding, 2015; Royan *et al.*, 2015), we found that models that did not include shared responses to environmental gradients inflated estimates of non-random species correlations. Additionally, Maguire et al. (2016) found that community-level models were generally more accurate than individual species distribution models when predicting distributions under rapidly-changing and novel climatic conditions. Thus, joint species distribution models appear to capture more predictive power and biological realism over single species distribution models.

We also compared the importance of environmental factors and species' interactions between the two survey periods (our second objective). The absolute and relative power of these two categories of predictors had a steady influence on community composition in both the 1950s and 2000s. Their mean effects on the distributions of individual species also remained steady. However, these means hid considerable variation in the extent to which environmental factors and species' interactions affected the distributions of individual species (**Fig. 3**). The power of environmental factors for affecting these single species' distributions was correlated between the two periods (**Fig. 4a**). However, the identity of the environmental factors in the species-level models was remarkably different over time (on average, the overlap in variables was only 14%). Thus, the overall importance of abiotic factors driving species' distributions remained relatively constant, however the predominant environmental gradients have shifted considerably for individual species. Additionally, the power with which species' interactions affected individual species' distributions showed no correlation over time (**Fig. 4b**). This result suggests that the ways in which biotic factors affect species' distributions have changed or that different biotic factors dominated within each period. Collectively, it appears that the landscape of biotic interactions and environmental filtering differs substantially over time. Species' distributions appear to be uniquely structured by distinct combinations of abiotic and biotic factors at each time period.

Lacking measurements of soil characteristics from the 1950s, we assumed that soil texture and chemistry remained constant, as presumably do species' responses to these. Species presumably also respond similarly to climatic conditions and light levels now as they did 50 years ago. Climate and light conditions within forests, however, have shifted during this period (Rooney *et al.*, 2004; Rogers *et al.*, 2008; Kucharik *et al.*, 2010; WICCI, 2011; Johnson *et al.*, 2014; Li & Waller, 2015). Extensive fire suppression in the Central Sand Plains (Li & Waller, 2015) and Southern Upland Forests (Rogers *et al.*, 2008) have allowed succession to proceed, shifting canopy composition in ways that have also influenced these understory communities. Shady forest understory microclimates may be buffered against heat and drought, too (De Frenne *et al.*, 2013). In sum, although many abiotic factors affect species distributions across these communities and the identity of these factors are changing, their overall contribution to species' distributions has not changed appreciably.

Our third objective was to understand how functional similarity among species related to the sign and magnitude of their estimated interactions. Species with similar functional traits tended to be more positively correlated with one another (**Fig. 5**), suggesting that environmental filtering outweighs competitive interactions in structuring species' distributions. This was indeed the case for both the positive and negative correlations (**Fig. 5)**, but these relationships were weak. We conclude that these functional traits play only limited roles in directing biotic interactions among species as estimated by these correlations. These interactions, in turn, play only a limited role in structuring these communities.

We consistently found more positive than negative correlations among species' co-occurrences in these models (**Table 4**). We are not sure how to interpret this. Positive correlations could reflect either mutualistic interactions or the fact that the species share the same microsites, potentially leading to strong competition (Clark *et al.*, 2014). Negative correlations could reflect either competition or a limited overlap in occupied sites. These various processes may help account for the high variation seen in both these correlations and their covariation with functional dissimilarity. Functionally similar species did tend to co-occur, again suggesting that environmental filtering outweighs competitive interactions. The deviance partitioning also showed environmental factors to be more important in explaining species' distribution patterns than species' interactions. We also observed declines in negative correlations between the 1950s and 2000s (**Table 4**). If environmental filtering into differentiated microenvironments became less important and/or specialized rare species declined in abundance, we might expect to see such a trend. In analyzing co-occurrence patterns in the NUF occupying a continuous forest matrix, Li and Waller (2016) found strong environmental filtering in both periods. In the SUF and CSP community types, in contrast, biotic interactions and dispersal limitation played larger roles and dispersal limitation became more import in the 2000s. This leads us to hypothesize that declines in specialized species and/or higher dispersal limitation in the 2000s may have reduced the number of negative species' correlations.

What promise do joint species distribution models hold for predicting the effects of future changes in climate (or other environmental conditions)? Even combined together, environmental conditions and species' interactions accounted for only a modest fraction of the total variation in community composition and similarly low, but highly variable fractions of the variation in distributions of individual species. Nonetheless, analyzing species' co-occurrence patterns alone did not suffice to identify non-random species' associations, as these are strongly influenced by shared environmental responses. Environmental responses differed among species and across time, with species' distributions structured by distinct suites of environmental factors at each time period. We also saw that species' interactions as captured by the correlations showed no continuity between the 1950s and 2000s. This may reflect the fact that several environmental factors are changing at once, producing novel combinations of environmental conditions and species' associations. Collectively, these results suggest it will be difficult to build and parameterize joint species distribution models accurate enough to reliably forecast shifts in community composition under future environmental change scenarios. However, results here and elsewhere (Ovaskainen *et al.*, 2010; Clark *et al.*, 2014; Pollock *et al.*, 2014; Royan *et al.*, 2015; Maguire *et al.*, 2016) suggest that joint species distribution models offer a distinct improvement over single species distribution models. Expanding applications and developments for this new class of distribution modeling (Ovaskainen *et al.*, 2016) will hopefully continue to improve their explanatory power and yield realistic, predictive tools.

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Table 1. The computed environmental variables considered for inclusion in the models and their abbreviations.

Variable	**Explanation**	**Units**
BIO1	Annual Mean Temperature	°C
BIO2	Mean Diurnal Range (Mean of monthly (max - min temp))	°C
BIO3	Isothermality (BIO2/BIO7) (* 100)	unitless
BIO4	Temperature Seasonality (standard deviation *100)	°C
BIO5	Max Temperature of Warmest Month	°C
BIO6	Min Temperature of Coldest Month	°C
BIO7	Temperature Annual Range (BIO5-BIO6)	°C
BIO8	Mean Temperature of Wettest Quarter	°C
BIO9	Mean Temperature of Driest Quarter	°C
BIO10	Mean Temperature of Warmest Quarter	°C
BIO11	Mean Temperature of Coldest Quarter	°C
BIO12	Annual Precipitation	mm
BIO13	Precipitation of Wettest Month	mm
BIO14	Precipitation of Driest Month	mm
BIO15	Precipitation Seasonality (Coefficient of Variation)	unitless
BIO16	Precipitation of Wettest Quarter	mm
BIO17	Precipitation of Driest Quarter	mm
BIO18	Precipitation of Warmest Quarter	mm

BIO19	Precipitation of Coldest Quarter	mm
precip_fall	Fall precipitation	mm
precip_win	Winter precipitation	mm
precip_spr	Spring precipitation	mm
precip_sum	Summer precipitation	mm
temp_fall	Mean fall temperature	°C
temp_win	Mean winter temperature	°C
temp_spr	Mean spring temperature	°C
temp_sum	Mean summer temperature	°C
water_def	Yearly water deficit (PET – BIO12)	mm/yr
gdd	Growing degree days (base temperature 10 °C)	°C
tmin_win	Mean daily minimum winter temperature	°C
pet	Potential evapotranspiration	mm/yr
Mean BA	Mean basal area of overstory trees	m^2
Soil (PCA1)	PCA axis 1 score, correlated with pH and cation content	unitless
Soil (PCA2)	PCA axis 2 score, correlated with soil texture	unitless

Table 2. The 16 functional traits used to calculate trait similiarities / differences among all pairs of species.

Trait	**Unit**	**Description**	**Ecological relevance**
Dispersal mode	categorical	Animal, wind, or unassisted seed dispersal	Dispersal strategy
Growth habit	binary	Woody or non-woody	Stress and disturbance avoidance
Invasive status	binary	Invasive or native	Competitive ability
Leaf circularity	unitless	0 (linear leaves) to 1 (circular leaves)	Resource acquisition/retention
Leaf length	mm	Maximum length of fully expanded leaf	Resource acquisition/retention
Leaf thickness	mm	Thickness of leaf tissue, avoiding veins	Stress avoidance
Leaf width	mm	Maximum width of fully expanded leaf	Resource acquisition/retention
Leaf dry matter content	mg g^{-1}	Leaf dry mass to fresh mass ratio	Resource acquisition/retention
Leaf carbon content	%	Carbon content of leaves	Resource acquisition/retention

Leaf nitrogen content	%	Nitrogen content of leaves	Resource acquisition/retention
Life cycle	binary	Annual or perennial	Stress and disturbance avoidance
Pollination mode	binary	Abiotic or biotic	Reproductive success
Stem dry matter content	mg g^{-1}	Stem dry mass to fresh mass ratio	Resource acquisition/retention
Seed mass	g	Dry mass of seeds	Dispersal strategy and establishment success
Specific leaf area	m^{2} kg^{-1}	Leaf area to dry mass ratio	Resource acquisition/retention
Plant height	cm	Maximum height of vegetation	Competitive ability

Table 3. The DIC values for each of the four models estimated in each survey period. The full model includes species interactions' and environmental factors. Lower values indicate better fit. Note large declines in DIC at each step, indicating that including both environmental filtering and species' interactions contribute significantly to improving the model.

Model	**1950s**	**2000s**
Null	194458	168670
Community	184104	160510
Environment	171470	147027
Full	**159459**	**137843**

Table 4. A comparison of the proportion of negative and positive species' correlations in the community and full model for each survey period. We also note the raw number of non-zero correlations (in parentheses). The community model estimates species' correlations alone, while the full model estimates species' correlations after accounting for shared environmental responses. Species' correlations are used as estimates of positive and negative species' interactions. The proportions do not change substantially over time, however the number of correlations declines in the 2000's full model

	Community Model		**Full Model**	
	Negative	*Positive*	*Negative*	*Positive*
1950s	44% (2315)	56% (2913)	39% (1600)	61% (2524)
2000s	36% (1561)	64% (2811)	28% (894)	72% (2339)

Figure Captions

Figure 1. Map of the survey and resurvey sites, color coded by community type. Abbreviations: CSP – pine barrens of the central sand plains; NUF – northern upland forests; SLF – southern lowland forests; and SUF – southern upland forests.

Figure 2. Comparing the relative importance of the environmental variables for predicting species' distributions between the two time periods (with a one-to-one line for comparison). Values are derived from stepwise regression procedures at each time period and represent the percent of species-level models that included the particular variable. Points are color-coded by the category of climate variables. The energy variables are potential evapotranspiration, growing degree days and annual water deficit. Soil chemistry (Soil-PCA1), soil texture (Soil-PCA2) and mean basal area of overstory trees (Mean BA) are all labeled

Figure 3. Proportions of the variance in species spatial distributions explained by the environment-only model in each survey period plus the additional deviance explained by including species' interactions (as estimated via the correlations in their residuals).

Figure 4. a) The proportions of variance in species' spatial distributions explained by environmental factors in the 1950s covaried significantly with the corresponding proportions in the 2000s ($R^2 = 0.14$). b) The additional explanatory power provided by the species' interactions (correlations) is uncorrelated between the two periods. Both figures contain a one-to-one line for comparison.

Figure 5. The relationship between pairwise species' correlations (used to estimate species' interactions) and their functional dissimilarity. Relationships are shown for each time period and divided between positive and negative correlations. All relationships are significantly negative.

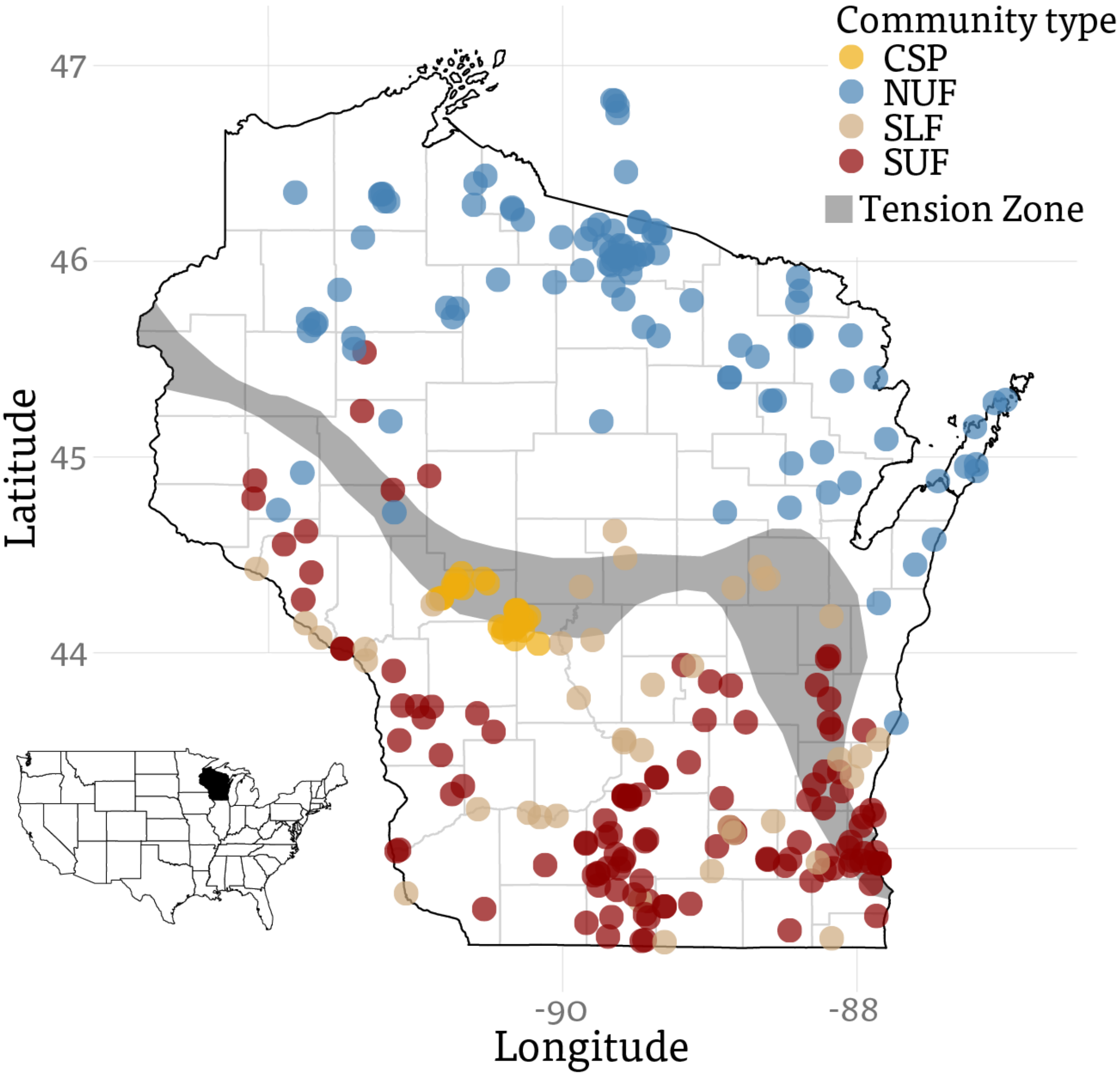
Community type
CSP
NUF
SLF
SUF
Tension Zone
47
46
45
44
Latitude
-90
-88
Longitude

Figure 1.

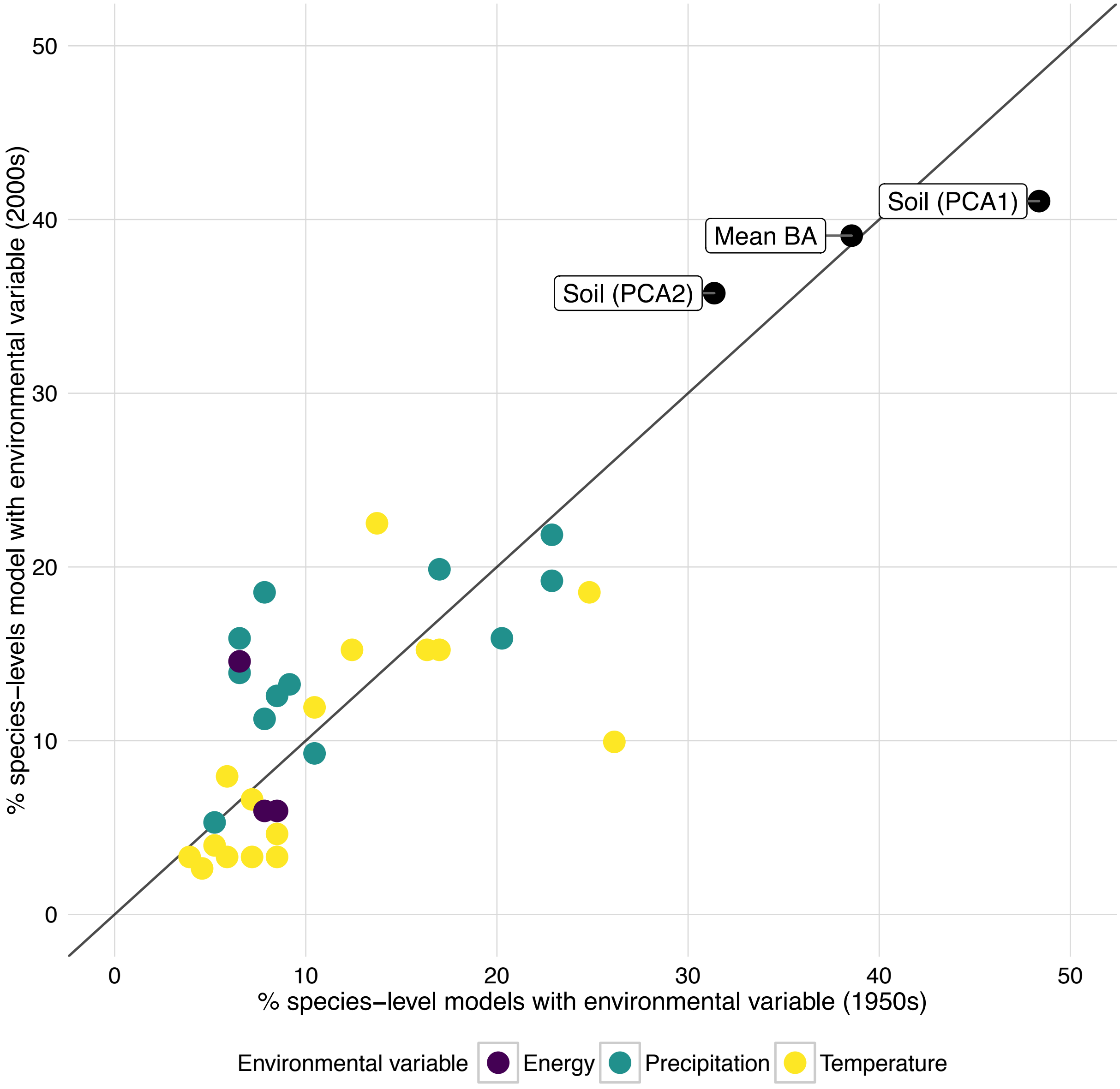
% species–levels model with environmental variable (2000s)
% species–level models with environmental variable (1950s)
0
10
20
30
40
50
0
10
20
30
40
50
Soil (PCA1)
Mean BA
Soil (PCA2)
Environmental variable
Energy
Precipitation
Temperature

Figure 2.

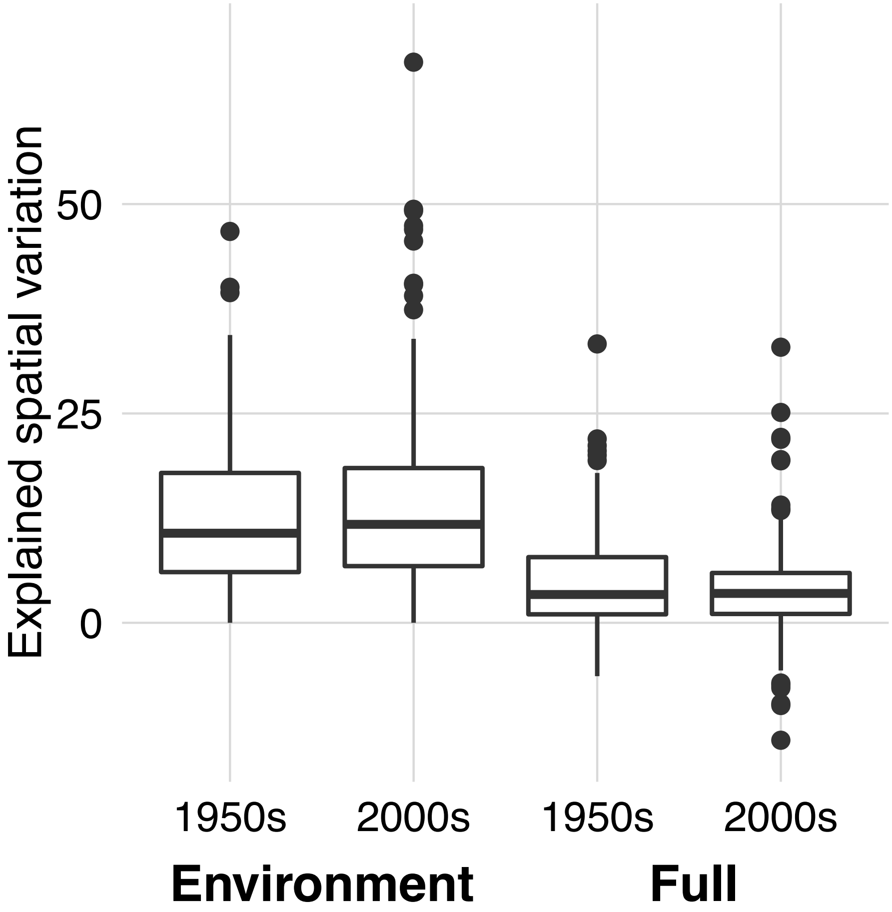
Explained spatial variation
50
25
0
1950s
2000s
1950s
2000s
Environment
Full

Figure 3.

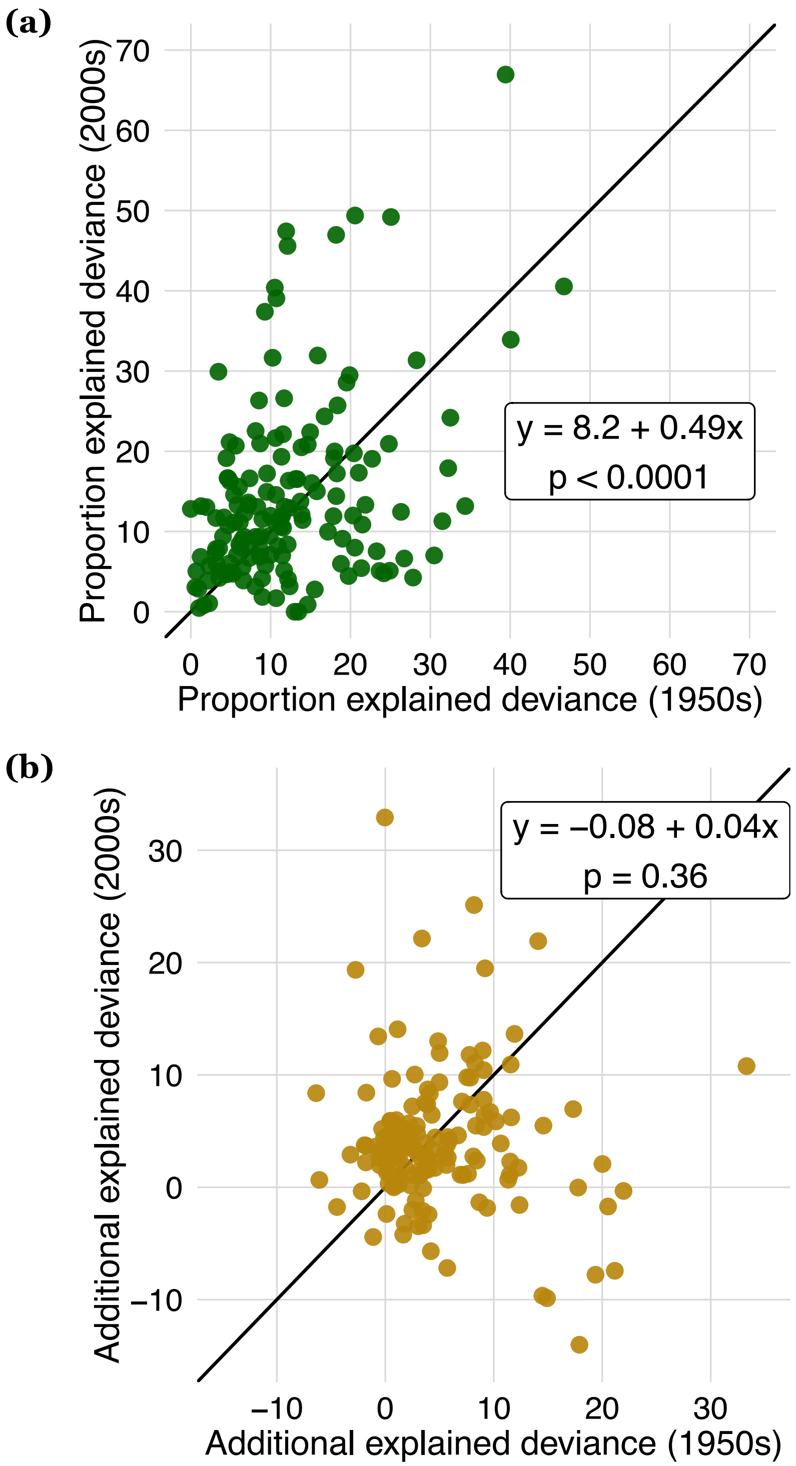
(a)
Proportion explained deviance (2000s)
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Proportion explained deviance (1950s)
y = 8.2 + 0.49x
p < 0.0001
(b)
Additional explained deviance (2000s)
30
20
10
0
−10
−10
0
10
20
30
Additional explained deviance (1950s)
y = −0.08 + 0.04x
p = 0.36

Figure 4.

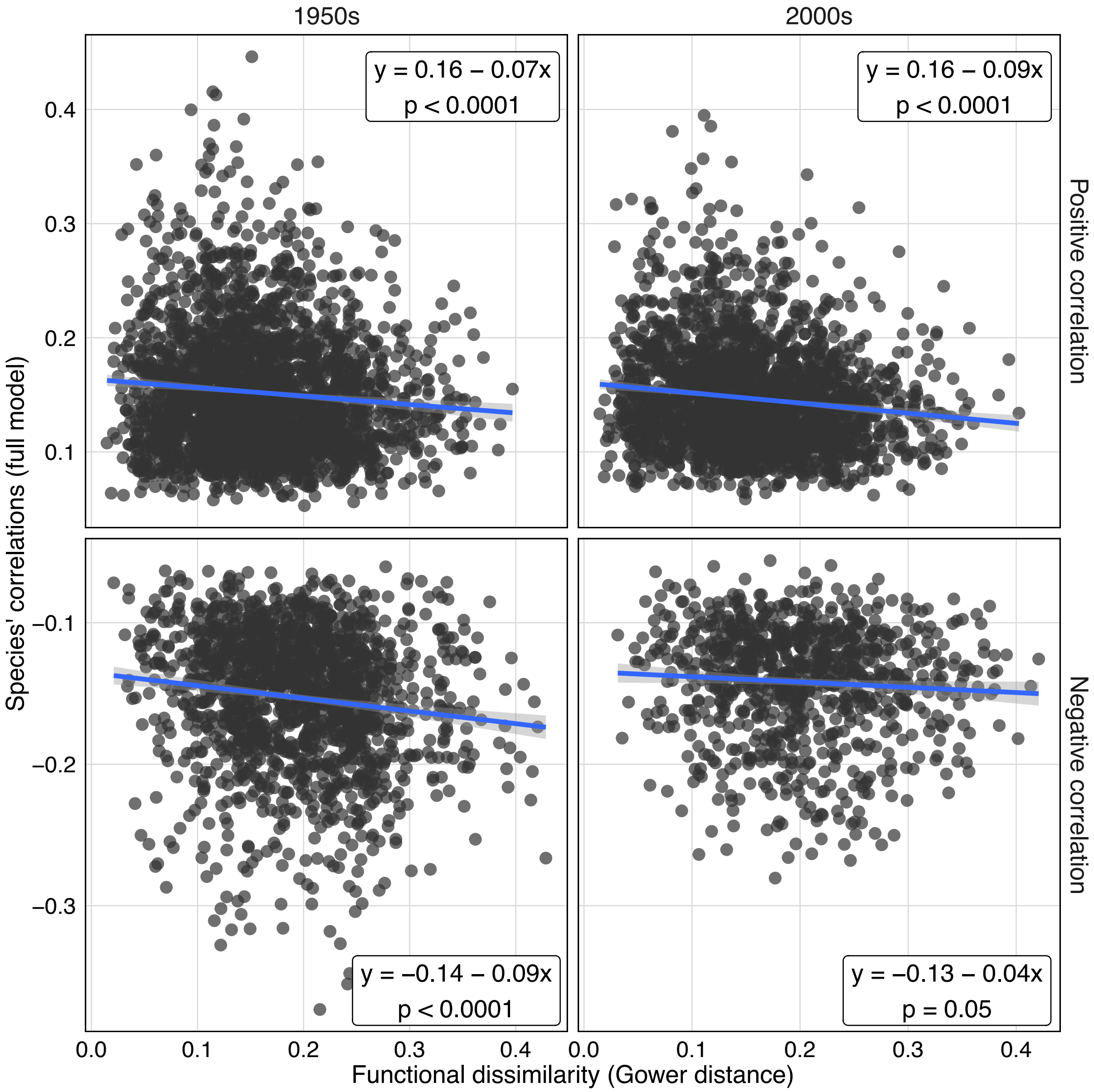
1950s
2000s
y = 0.16 – 0.07x
p < 0.0001
y = 0.16 – 0.09x
p < 0.0001
y = −0.14 – 0.09x
p < 0.0001
y = −0.13 – 0.04x
p = 0.05
Positive correlation
Negative correlation
Species' correlations (full model)
Functional dissimilarity (Gower distance)
0.4
0.3
0.2
0.1
−0.1
−0.2
−0.3
0.0
0.1
0.2
0.3
0.4

Figure 5.

Appendix

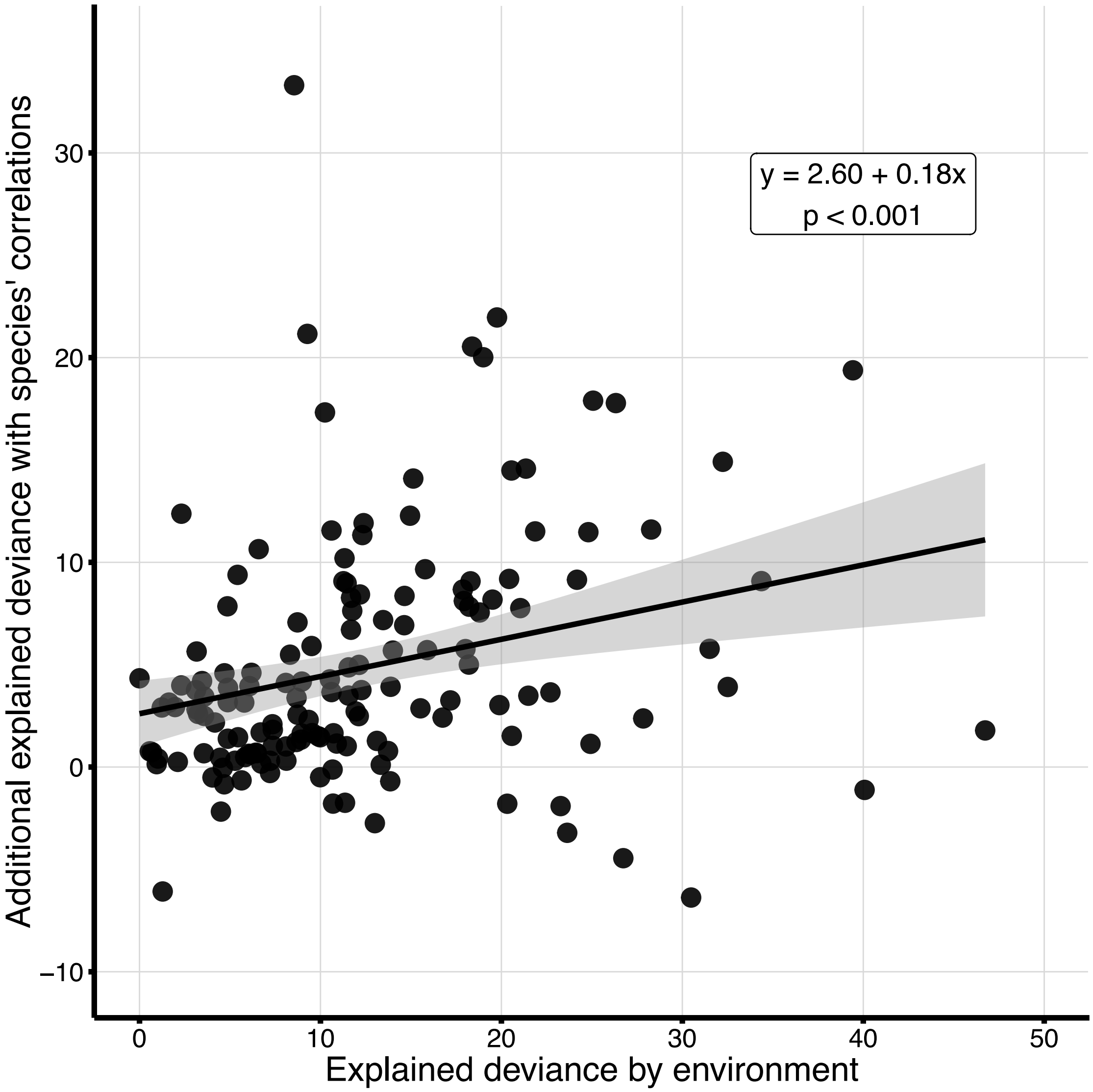

Figure S1. The relationship between deviance explained by the environment-only model (x-axis) and the additional power from including species' correlations (y-axis) for the 1950s data. We found a statistically significant relationship, although the relationship is weak ($R^2 = 0.07$).

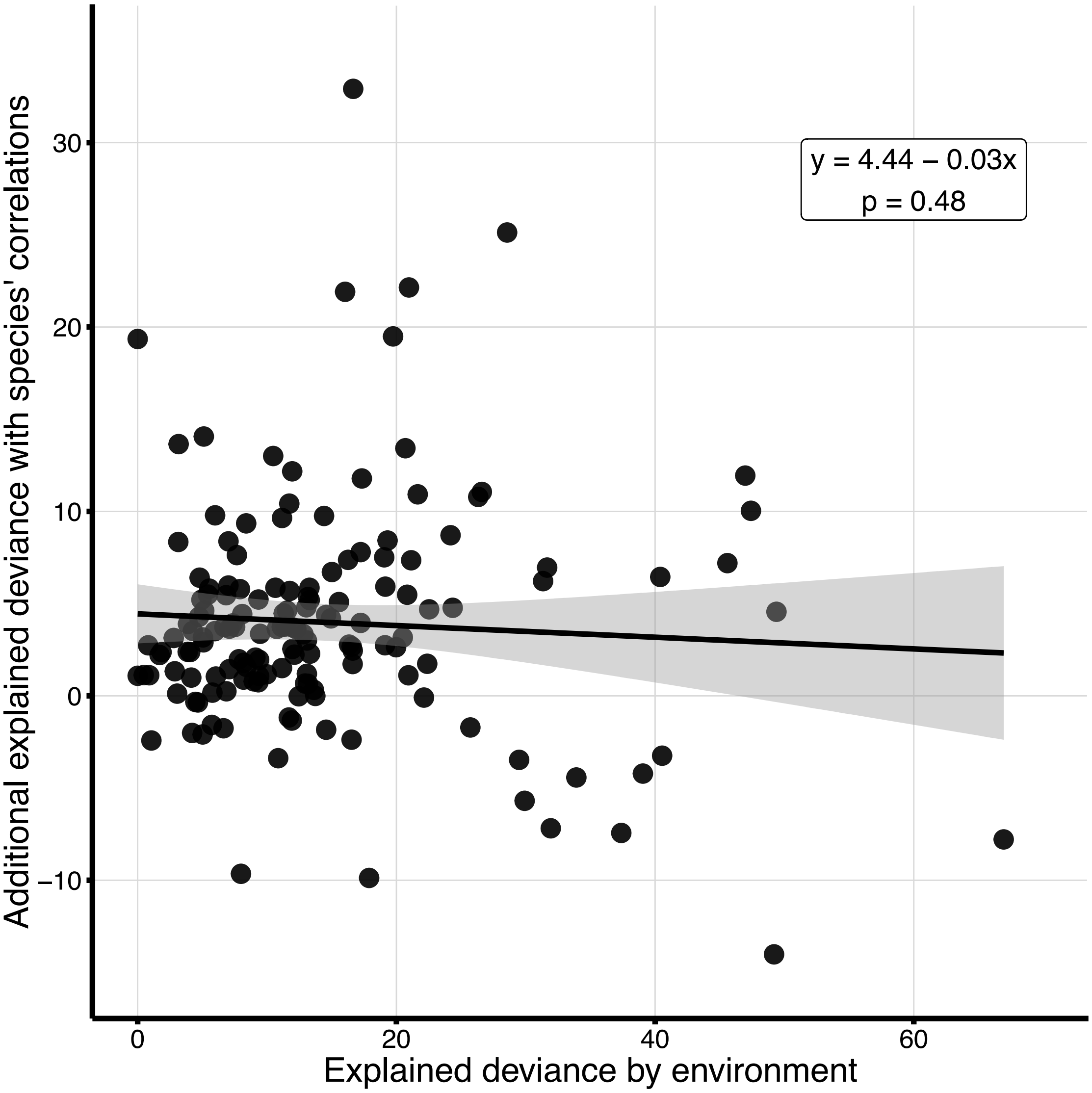

Figure S2. The relationship between deviance explained by the environment-only model (x-axis) and the additional power from including species' correlations (y-axis) for the 2000s data. We did not find a statistically significant relationship.