

**SPECIES- TO COMMUNITY-LEVEL RESPONSES TO CLIMATE
CHANGE IN EASTERN U.S. FORESTS**

by

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This dissertation is dedicated to my parents, Steve and Jan, and my wife, Kailey. To my mom, who passed away during my last semester at Purdue, thank you for all your love over the last 27 years, I miss you immensely. To my dad, thank you for instilling in me a passion for the outdoors from a very young age that led me to pursue a career studying the natural world. To my wife, thank you for supporting me every step of the way, I could not have done it without you.

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FORWARD

I am a quantitative ecologist, and I study ecology at macroscales. In some of my work with collaborators at Purdue University and across the globe, I showed that climate change is the most rapidly growing research area in ecology (McCallen et al., 2019), and that macrosystems biology is at the leading edge of ecological research (LaRue et al., *In press*). Therefore, my research aims to elucidate macroscale forest responses to climate change, which has impacted forests globally.

Besides climate change, forests are facing many other threats including invasion by non-native plants and pests, land use change, fire regime shifts, and management and timber harvest. I have worked on some of these topics, such as investigating patterns of non-native species richness along elevational gradients (Guo et al., 2018) and the mesophication hypothesis that eastern U.S. forests are transitioning from fire-tolerant to shade-tolerant species (Knott et al., 2019). Additionally, I worked on a project quantifying species-level tree migrations in response to climate change (Fei et al., 2017), which provided motivation for studying the effects of climate change on community-level dynamics.

In this dissertation, I present two main studies which focus on (1) species-level phenological responses and (2) community-level spatial and compositional responses to climate change (Knott et al., 2020). The purpose of these studies was to identify and quantify forest responses to climate change across organizational scales (population to community levels). These projects revealed (1) consistent spring phenological shifts in response to climate warming but a lack of autumn phenological responses, and (2) spatial shifts in forest communities that are not keeping pace with climate change. The results of these projects have implications for the sustainability of forest ecosystems and will hopefully inform management decisions in the face of continuing climate change. This dissertation is a culmination of many years of work and the support from many others, and I hope you enjoy reading my dissertation.

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ABSTRACT

Climate change has dramatically altered the ecological landscape of the eastern U.S., leading to shifts in phenological events and redistribution of tree species. However, shifts in phenology and species distributions have implications for the productivity of different populations and the communities these species are a part of. Here, I utilized two studies to quantify the effects of climate change on forests of the eastern U.S. First, I used phenology observations at a common garden of 28 populations of northern red oak (*Quercus rubra*) across seven years to assess shifts in phenology in response to warming, identify population differences in sensitivity to warming, and correlate sensitivity to the productivity of the populations. Second, I utilized data from the USDA Forest Service's Forest Inventory and Analysis Program to identify forest communities of the eastern U.S., assess shifts in their species compositions and spatial distributions, and determine which climate-related variables are most associated with changes at the community level. In the first study, I found that populations were shifting their spring phenology in response to warming, with the greatest sensitivity in populations from warmer, wetter climates. However, these populations with higher sensitivity did not have the highest productivity; rather, populations closer to the common garden with intermediate levels of sensitivity had the highest productivity. In the second study, I found that there were 12 regional forest communities of the eastern U.S., which varied in the amount their species composition shifted over the last three decades. Additionally, all 12 communities shifted their spatial distributions, but their shifts were not correlated with the distance and direction that climate change predicted them to shift. Finally, areas with the highest changes across all 12 communities were associated with warmer, wetter, lower temperature-variable climates generally in the southeastern U.S. Taken together, these studies provide insight into the ways in which forests are responding to climate change and have implications for the management and sustainability of forests in a continuously changing global environment.

CHAPTER 1. INTRODUCTION

Climate change has impacted the ecological landscape of the eastern U.S. (Parmesan, 2006; Parmesan & Yohe, 2003). Climate has shifted rapidly in the eastern U.S. over the last three decades, with shifts in temperature ranging from -0.5 to $+1.5^{\circ}\text{C}$ and shifts in total annual precipitation ranging from ± 150 mm (Fei et al., 2017). Although climate change has become the fastest growing area of research in ecology (McCallen et al., 2019), there still remain many unknown impacts of climate change on ecological systems.

Shifts in temperature and precipitation can shape the dynamics of populations, species, and communities, and alter many ecological systems and processes, such as phenology, migration, productivity, and biodiversity (Corlett & Westcott, 2013; Kharouba et al., 2018; Parmesan & Yohe, 2003; Piao et al., 2019; Richardson et al., 2010). A general paradigm to describe responses to climate change is “move or adapt.” Species need to either adapt to novel environments or migrate to areas that are more suitable (Corlett & Westcott, 2013; Fei et al., 2017; Kokko et al., 2017; Parmesan & Yohe, 2003; Woodall et al., 2009). For most species—especially sessile species such as plants—these mechanisms can take a long time. Adaptation requires genotypes suitable for novel conditions either preexisting within the population or entering the population through gene flow and mutation (Kokko et al., 2017), and migration requires dispersal to new locations (Fei et al., 2017; Woodall et al., 2009; Zhu et al., 2012). As such, adaptation and migration require multiple generations to respond to climate change, which is typically much slower than the rate of climate change (Corlett & Westcott, 2013). In this dissertation I studied two aspects of the “move or adapt” paradigm: shifts in phenology—the timing of reoccurring biological events—as a short-term response to climate change when moving or adapting are not possible (i.e. within a generation) and shifts in the spatial distribution and species composition of regional forest communities as a result of species-level migrations.

Species often use their phenology as a buffer to changing conditions. When environmental conditions shift from year to year, species can adjust their phenology—the timing of certain events such as leaf out in the spring and leaf senescence in the autumn—to align with novel conditions (Cleland et al., 2007; Piao et al., 2019). Many studies have shown that spring phenology is advanced and autumn phenology is delayed in warmer years (Cleland et al., 2007; Fu et al., 2015; Morin et al., 2010; Piao et al., 2019). There is some evidence that phenological responses lead to

an extended growing season and increased productivity (Richardson et al., 2010), but these shifts can also have negative impacts such as increasing the competitive advantage of invasive species, mismatch in the timing of species interactions, and increased risk to frost damage when early spring warming is followed by frost events (Fridley, 2012; Kharouba et al., 2018; Piao et al., 2019; Zohner et al., 2020). However, it is still mostly unknown if shifts in phenology are species- or population-specific and if shifts in phenology are always translated in to productivity.

Species that are unable to adapt to new conditions at their current location may be able to move to new locations that better align with their current climate adaptations. Several studies have shown that species are shifting their ranges to higher elevations and poleward to track with climate change (Fei et al., 2017; Parmesan, 2006; Woodall et al., 2009). However, it has been hypothesized that these migrations may alter species interactions, consequently impacting human well-being, ecosystem functioning, and climate feedbacks (Corlett & Westcott, 2013; Pecl et al., 2017).

Studies on climate-driven migration usually focus at the population and/or species level, but rarely the community level. However, as species shift their distributions in response to climate change, it is likely that communities are being impacted as well. Historically, migration of tree species after the last glaciation led to large-scale patterns of forest communities (Davis, 1983), such as those described E. Lucy Braun's publication *The Deciduous Forests of Eastern North America* (Braun, 1950) which is still widely used today (Dyer, 2006). Others such as Ricklefs (1987) have argued that regional climatic drivers are more important for understanding long-term, large-scale community change. Therefore, as result of species migrations in response to climate change, regional communities are likely to experience shifts in species interactions and/or shifts geographic distributions. For instance, as communities shift through geographic and climatic space, a component species may either track with the community as a whole, lag behind and become disconnected from its historic community, or migrate more quickly and outpace other species. This can lead to species becoming associated with other pre-existing communities as well as species generating novel communities.

At the macroscale, shifts in forest communities have generally not been studied because of data availability and computational intensity. Early studies, such as the foundational work by Clements (1916) and Gleason (1926) or the aforementioned work by Braun (1950) and Davis (1983), used small sample sizes and anecdotal evidence to identify communities and address how they change over time. Recently, large scale databases such as the USDA Forest Service's Forest Inventory and Analysis Program (FIA) have allowed researchers to apply new modeling

approaches to identify forest communities in big data (Costanza et al., 2017, 2018; Dyer, 2006; Valle et al., 2014); however, these approaches have not directly tested for community responses to climate change.

In this dissertation, I utilized two studies to understand climate change impacts on eastern U.S. forests. First, I assessed how phenology varies across populations in a common garden of northern red oak (*Quercus rubra*). Specifically, I aimed to (1) quantify how rapidly populations shift their phenology in response to warmer spring and autumn temperature, (2) identify historic adaptations to climate that lead to increased sensitivity to warming, and (3) assess whether increased sensitivity leads to increased productivity. Second, I identified forest communities in the eastern U.S. using Latent Dirichlet Allocation (LDA) and Forest Inventory and Analysis (FIA) data. I then used the communities identified by LDA to assess (1) how species composition within the communities has changed over time, (2) how the centroid of each community has shifted geographically, and (3) how these changes are related to climate change both within and across communities. These studies will provide both evidence of ways that forests are impacted by climate change and insight into the sustainability of forests for management and other stakeholders.

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CHAPTER 2. DIFFERENTIAL PERFORMANCE OF TREE POPULATIONS IN RESPONSE TO CLIMATE CHANGE

2.1 Abstract

Climate change can dramatically alter species performance and survival unless species can quickly respond to novel environments. Shifts in phenology in response to climate change have been widely observed, but it is unclear if these shifts are population-specific and can be translated into actual changes in fitness/growth. Here, we tested population-level sensitivity to climate change using phenological data from a 58-year-old common garden of 28 distinct range-wide populations of northern red oak. Spring phenology consistently advanced in response to warmer temperatures, but fall phenology remained static. Populations originating from warmer and wetter locales were more sensitive to spring warming, but greater sensitivity did not result in faster growth, as intermediate levels of sensitivity correlated to the highest productivity. Our results indicate that although trees are able to shift their phenology in response to climate change, productivity is often limited by local adaptations, which highlights the potential impacts on the sustainability of forest ecosystems as species distributions continue to shift in response to climate change.

2.2 Introduction

Climate change can dramatically impact species performance and survival, and it is unclear how populations or species as a whole can adapt to rapidly changing climate. Mechanisms to respond to climate change, such as adaptation to novel environments and migration to more suitable habitat, require long periods of time (1–3). Adaptation assumes that genotypes that are more suitable for novel conditions either exist within a population or are entering the population through gene flow or mutation and increase via selection over many generations (1, 3, 4). As such, adaptations for species with long generation times—especially for long-lived tree species—can take centuries to millennia. Migration of species requires dispersal to new locations, and dispersal events are often paired with population declines or extirpations at the trailing edge of the species' range where conditions have become unsuitable (5, 6). Migration is also limited by time to maturation but has been observed at decadal time scales (2, 5–7). Given that projected rates of climate change exceed the rates of adaptation and migration (1, 3), species' success must rely on more rapid adaptive responses to climate change at daily to annual time scales.

Many tree species can shift their phenology—the timing of recurring biological events such as bud burst, leaf out, and leaf senescence—to act as short-term (daily to seasonal time scale) responses to climate change (8–10). Advances in spring bud burst and leaf out and delays in autumn leaf senescence in response to warmer conditions have been observed across many tree species; these responses extend their growing season and can increase productivity (8–12). Evidence of accumulation of chilling requirements (cold temperature accumulation) and/or photoperiod requirements (day- and night-length cues) to trigger phenological events (13–16) suggests the possibility of muted or reversed responses to climate warming if these requirements are no longer met. Multiple ecosystem processes, such as plant-insect synchrony, nutrient and water cycling, and climate-productivity feedbacks, are closely linked to phenological transitions, so shifts in phenology in response to climate change can have important implications for the sustainability of forest ecosystems and the services they provide (8–10, 17). Assessing phenological sensitivity to changing environmental conditions provides an opportunity to assess which populations or species are most capable of extending their growing season to keep up with continued climate warming.

Common garden studies (provenance tests), which transplant trees from a wide variety of historic climate conditions to a new location, act as pseudo-climate change experiments (space-for-time substitutions) (18–20). Populations from widespread species are genetically different from one another due to adaptations to local climate and are expected to have different responses to climate change (4), thus leading to differential thermal accumulation and/or photoperiod requirements across the species' range (13, 19–21). Therefore, when transplanted to a common garden, populations of the same species may differ in the rate of response to warming conditions (gene-by-environment interaction, G x E). By monitoring common gardens over multiple years, interannual shifts in environmental conditions can elucidate which populations are most sensitive to climate change and which ones are most likely to be hindered by continued warming. Common garden studies provide a wide range of pseudo-climate change conditions and cover a large spatial extent, which alleviate some of the limitations of remote sensing and experimental warming studies due to natural climate fluctuations and spatial distribution of populations, respectively.

Here, we utilized a 58-year-old common garden of northern red oak (*Quercus rubra*), a widespread North American tree species, to (i) quantify phenological responses to climate change, (ii) identify which populations are most capable of taking advantage of changing climate, and (iii)

test if phenological sensitivity to climate change is reflected in productivity. Specifically, we hypothesized that (i) in warmer years, spring bud burst and leaf out are advanced and autumn senescence is delayed, but that (ii) populations from colder climates, that are experiencing the highest levels of climate change at the common garden, have lower phenological sensitivity to climate change than warmer populations. We also hypothesized that (iii) populations that are more sensitive to climate change would be more capable of extending their growing season, resulting in higher productivity. Our results will examine the range of phenological responses within northern red oak to identify which populations are most sensitive to climate change and whether phenological sensitivity has measurable effects on productivity.

2.3 Results and Discussion

2.3.1 Phenology shift in response to changing climate

Populations of northern red oak took advantage of warmer spring temperatures by breaking buds and leafing out earlier. The date of bud burst (the first date when 50% of the buds had swollen) and leaf out (first date when 90% of leaves unfolded) at the common garden varied from year to year (**Fig 2.1**), with climate warming (shifts in growing degree days, GDD) explaining 56% and 36% of variability in bud burst and leaf out, respectively ($P < 0.001$ for both bud burst and leaf out). At the population level, both spring bud burst and leaf out were consistently advanced in warmer years as indicated by significant negative relationships between shifts in GDD and shifts in bud burst and leaf out (hereafter, “sensitivity values”) (**Table S2.1, Figs 2.2 and S2.1**). In general, bud burst showed greater sensitivity to changing spring temperatures than leaf out, with mean sensitivity values of -0.49 days GDD^{-1} (range: -0.65 to -0.35 days GDD^{-1}) for bud burst compared to -0.11 days GDD^{-1} (range: -0.14 to -0.07 days GDD^{-1}) for leaf out (**Table S2.1**). Within populations, the day of year (DOY) of bud burst shifted from 33.2 days earlier in response to warmer spring temperatures to 27.1 days later in response to colder spring temperatures than the mean DOY of bud burst, whereas the DOY of leaf out shifted from 10.7 days earlier to 14.6 days later than the population mean DOY of leaf out (**Table S2.1**).

Despite consistent spring responses to warming, leaf senescence showed little response to changing autumn climate. Autumn sensitivity to shifts in chilling degree days (CDD) were non-significant except for one population which had a small significant delay in senescence in warmer

years (slope = -0.04 days CDD⁻¹, **Table S2.1, Figs 2.2 and S2.1**). Although senescence did vary across years (**Fig 2.1**), shifts in senescence were not consistently related to shifts in temperature. Non-significant senescence sensitivity to interannual temperature variability indicates that populations are limited in their ability to take advantage of warmer autumn weather. Since a mixture of delays and advances in senescence in response to warming have been observed for other species (22–25), it was not surprising to find little evidence of autumn responses to warming; however, it was concerning that even when conditions were favorable populations did not extend their growing season into autumn. A lack of temperature sensitivity of senescence often indicates a stronger photoperiod cue (20, 26, 27), and photoperiod effects in combination with other stressors such as drought and frost before and during autumn can override the effects of warming (25, 28).

2.3.2 Factors influencing phenology sensitivity

Historic adaptations to temperature gradients were most associated with leaf out sensitivity, whereas adaptations to temperature-precipitation interactions were more associated bud burst sensitivity (**Figs 2.3 and S2.2, Table S2.2**). We extracted the value of 19 bioclimatic (BIOCLIM) variables from the WorldClim database (29) at each population's seed source as proxies for historical adaptation, and we tested these as explanatory variables of population differences in bud burst and leaf out sensitivities using linear regression. Bud burst sensitivity was best predicted by seed source temperature-precipitation interactions (**Fig 2.3A**), with populations from areas with cooler wet seasons having lower bud burst sensitivity (BIOCLIM 8, mean temperature of the wettest quarter, MeanTWetQ; background gradient in **Fig 2.2A**; $P < 0.001$, $R^2 = 0.35$, AIC weight = 0.737). Leaf out was more temperature-driven (**Fig 2.3B**), with populations from warmer areas having higher leaf out sensitivity to climate change (BIOCLIM 10, mean temperature of the warmest quarter, MeanTWarmQ; background color in **Fig 2.2B**; $P = 0.003$, $R^2 = 0.29$, AIC weight = 0.289). Both bud burst and leaf out sensitivities had significant yet weaker associations with precipitation gradients (**Fig 2.3**). We also calculated average springtime accumulated GDD at the seed sources using Daymet daily temperature data (30) and found that average springtime accumulated GDD was a poor predictor of bud burst sensitivity but a significant negative predictor of leaf out sensitivity, consistent with temperature-related BIOCLIM variables (**Fig 2.4, Table S2.2**). Although more phenologically-relevant, average springtime GDD was only marginally better than BIOCLIM predictors (AIC weight = 0.352 and 0.289 for Daymet GDD and the best

BIOCLIM predictor, MeanTWarmQ, respectively). Populations with high leaf out sensitivity (large negative values) tended to have longer growing seasons (**Fig 2.5B**), but bud burst sensitivity had no measurable connection with growing season length (**Fig 2.5A**). Additionally, annual shifts in leaf out and senescence were weakly negatively correlated ($r = -0.15$), indicating northern red oak does not have a fixed longevity of its leaves.

Our results indicated that populations from colder, drier climates were limited in their spring sensitivity to climate change. These populations are facing two-fold challenges: (1) they are unable to rapidly respond to climate change due to their chilling requirements being compromised which leads to delayed dormancy release, and (2) they are experiencing climate change at rates faster than other areas within the species' range (2). Given that climate is expected to continue to warm over the next century (31), it is likely that these cold-adapted populations will face additional limitations in their responses to warming spring conditions.

2.3.3 Phenology sensitivity vs. productivity

Populations with more sensitive leaf out dates and longer growing seasons did not show increased productivity. We used allometric equations to estimate total aboveground biomass of populations as a proxy for productivity (32). Estimates were based on diameter at breast height (DBH) measurements taken after the study period. Annual accumulated aboveground biomass (hereafter, “biomass”) was calculated by dividing total aboveground biomass by the number of years since establishment of the common garden (**Table S2.3**). Biomass showed no relationship with bud burst sensitivity ($R^2 = 0.04$, $P = 0.297$, **Fig 2.5C**) and a concave down (hump-shaped) relationship with leaf out sensitivity (Adj. $R^2 = 0.22$, $P = 0.02$, **Fig 2.5D**). Growth estimates based on periodic annual increment of basal area (PAI) (change in basal area over the study period) showed the same trend as biomass (correlation between PAI and biomass = 0.95, $P < 0.001$, **Fig S2.3**). Maximum productivity was observed for populations with leaf out sensitivity values similar to estimated local sensitivity (designated by vertical lines in **Fig 2.5**).

Sensitivity to climate change does not lead to increased growth of the trees. We found that both low and high sensitivity populations showed lower productivity than populations with moderate sensitivity to climate change, which reflects local climate. Populations from colder climates with low leaf out sensitivity are generally more conservative due to their high chilling requirements and tend to leaf out later in the season (**Fig S2.4**), guaranteeing leaf out under more

climatically safe conditions. Conversely, populations from warmer climates with high leaf out sensitivity tended to shift their phenology more rapidly in response to warming conditions, but their lack of increased productivity suggests that other constraints (such as damage from subsequent frost events, reduced growth rate during the early spring, and/or increased respiration in warmer years) prevented these populations from taking full advantage of an extended growth period (9, 11, 12, 33). Local populations were predicted to have moderate levels of sensitivity which correlates to the highest levels of productivity, generally supporting the hypothesis that populations are best adapted to local conditions (4, 20). This suggests that, despite populations from warmer, wetter climates being most able to react to spring warming, populations ultimately grow best nearest to their area of origin. This has implications for species migration (both natural migration and human-mediated management strategies such as assisted migration); as populations disperse to new areas they are likely to be poorly adapted to those areas even if environmental conditions are favorable, and they may have reduced productivity relative to their historic range.

There are a few caveats to our study that must be considered. First, our study encompasses seven years of data collection. While these seven years included a wide range of environmental conditions and phenological shifts, there are possibly even more dramatic shifts expected under future climate change. Within populations, bud burst and leaf out were linearly related to climate warming (**Fig S2.1**), however, if chilling requirements were no longer met at high levels of warming, it would be possible for gains in the spring season to be slowed or reversed. Second, although northern red oak is an ecologically and economically important North American tree species, there are other species that comprise North American forests that are also responding to climate change. Other species may help offset the consequences of shifts in northern red oak phenology such as productivity, mast production, canopy closure, and structure (likewise, northern red oak may also offset shifts in other species), leading to balancing effects of community complexity (34, 35). Finally, there exist many proxies of species fitness besides productivity. Additional measures such as recruitment and dispersal may be closely linked to the potential sustainability of trees species; however, we found little-to-no recruitment of northern red oak in the understory, which is consistent with regional patterns of oak species decline over recent decades (5, 36, 37).

2.4 Conclusions

Taken together, our results provide evidence of potential impacts on the sustainability of oak forests under climate change. Our study revealed that populations are able to shift their spring phenology in response to climate change, but autumn responses are lacking, and the ability to more rapidly shift spring phenology in response to warmer temperatures was not linked to higher productivity. Recent studies have shown that oak species have been declining over recent decades, resulting in significant northward migration of northern red oak (2, 36, 37). Paired with the expected reduced productivity of relocated populations, continued species migration will likely have impacts on the productivity and sustainability of this economically and ecologically valuable species.

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2.5 Figures and Tables

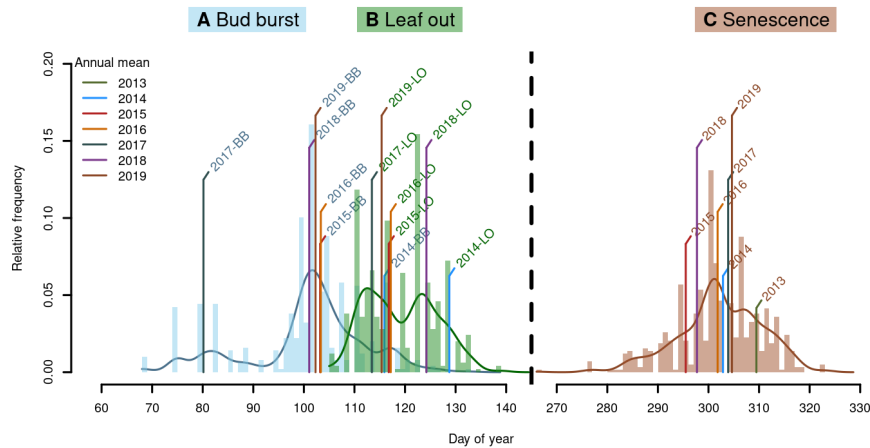


Fig. 2.1. Timing of (A) bud burst, (B) leaf out, and (C) senescence. Histogram indicates distribution of phenological events for all plots across all years, with histogram and density line color reflecting stage (blue = bud burst, green = leaf out, brown = senescence). Vertical lines indicate annual mean for each event, with colors specifying individual years and labels “BB” and “LO” representing bud burst and leaf out, respectively due to the overlap in these two events. Note that sampling began in autumn 2013 as indicated by the additional vertical line for 2013 in (C) that is not present in (A) or (B). Vertical dashed line indicates break in X axis between spring and autumn seasons.

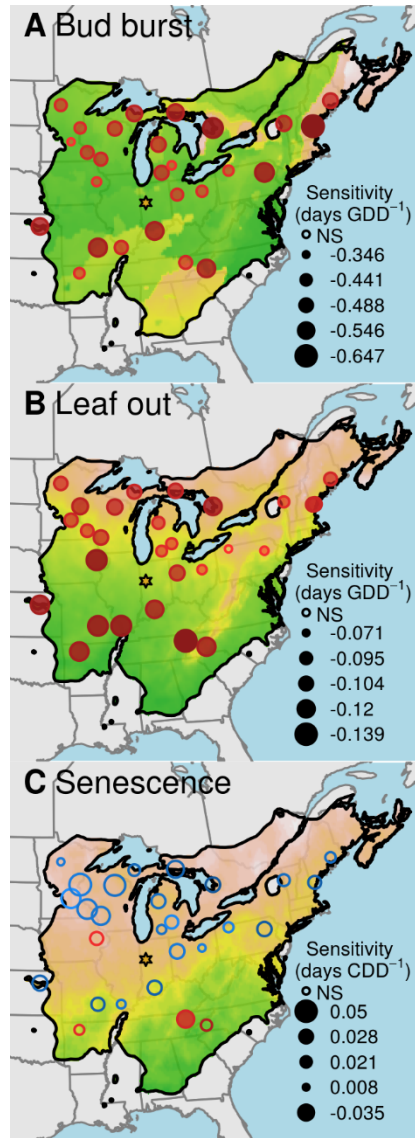


Fig. 2.2. Maps of phenological sensitivity to climate change. Shifts in day of year (DOY) of phenological events at the common garden (gold star) were modeled as a function of shifts in growing degree days (GDD) for (A) bud burst and (B) leaf out, and shifts in chilling degree days (CDD) for (C) senescence. Background gradient represents the strongest bioclimatic predictor of sensitivity (green colors are higher values; see **Fig 2.3** for relationships): (A) BIOCLIM 8, mean temperature of wettest quarter (MeanTWetQ); (B) BIOCLIM 10, mean temperature of warmest quarter (MeanTWarmQ); (C) BIOCLIM 3, isothermality (Isotherm). Larger circles indicate more sensitivity to climate change (larger slope coefficients). Red circles indicate negative relationship (spring advancement/autumn delay in response to warming); blue circles indicate positive relationship (autumn advancement in response to warming); open circles are non-significant. See **Table S2.1** for climate sensitivity values.

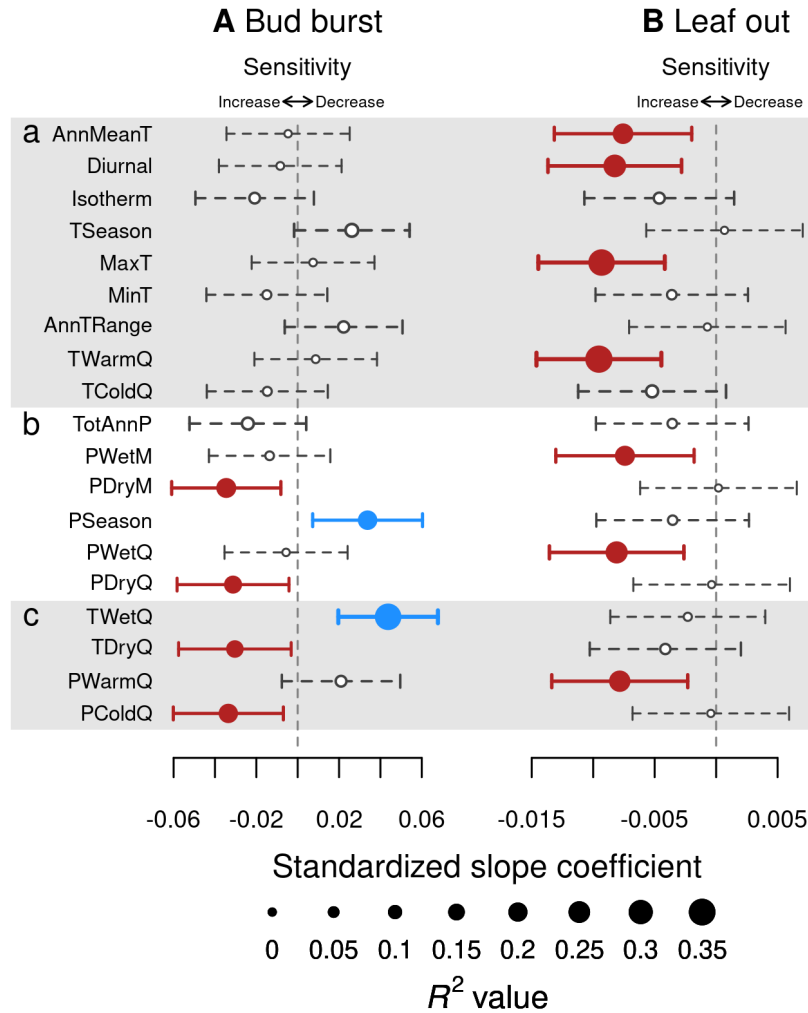


Fig. 2.3. Historical climate impacts on phenological sensitivity to climate change. The sensitivity of bud burst and leaf out to shifts in growing degree days were modeled as a function of seed source climate conditions using Worldclim BIOCLIM variables. BIOCLIM variables were standardized by subtracting the value at the common garden and dividing by the standard deviation. Circles indicate coefficient values, and color indicates direction of relationship: red = negative, blue = positive, and black = non-significant. Negative coefficient values are interpreted as an increase in the BIOCLIM variable leads to an increase in sensitivity (more negative sensitivity value); conversely, positive coefficient values are interpreted as an increase in the BIOCLIM variable leads to a decrease in sensitivity (less negative sensitivity value). Circle sizes are proportional to R^2 values. Error bars represent 95% confidence intervals; those that overlap the dashed vertical line at zero are non-significant ($P > 0.05$). Variables are grouped by category (designated by gray shading), from top to bottom: (a) temperature, (b) precipitation, and (c) temperature-precipitation interactions. See **Fig S2.2** for scatterplots of these relationships and **Table S2.2** for a description of the BIOCLIM variables.

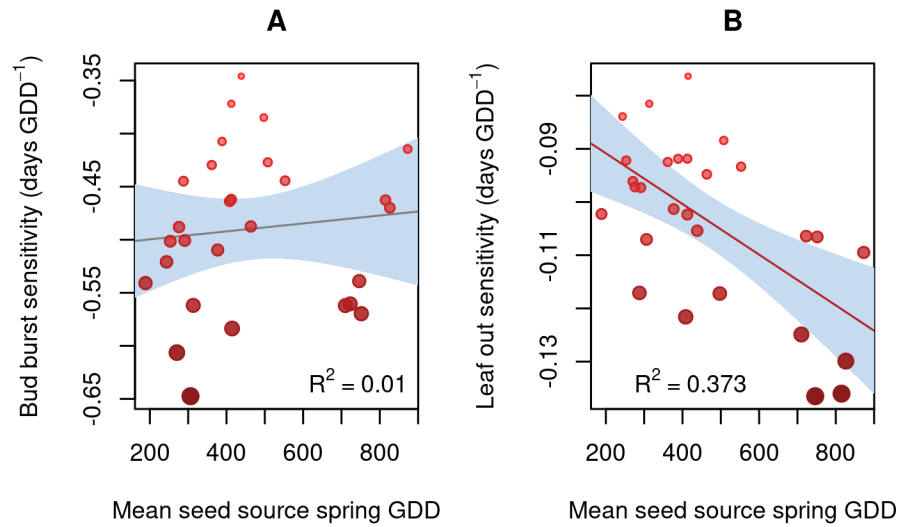


Fig. 2.4. Seed source growing degree days as a predictor of phenological sensitivity. Daymet temperature data were used to create 30-year average springtime accumulated growing degree days for each of the seed sources. Red line in (B) indicates significant negative relationship between seed source GDD and leaf out sensitivity; warmer seed sources tend to have more sensitivity to warmer spring temperature. Black line in (A) indicates non-significant relationship. Dot size and hue represent phenological sensitivity and reflect symbology of **Fig 2.2**.

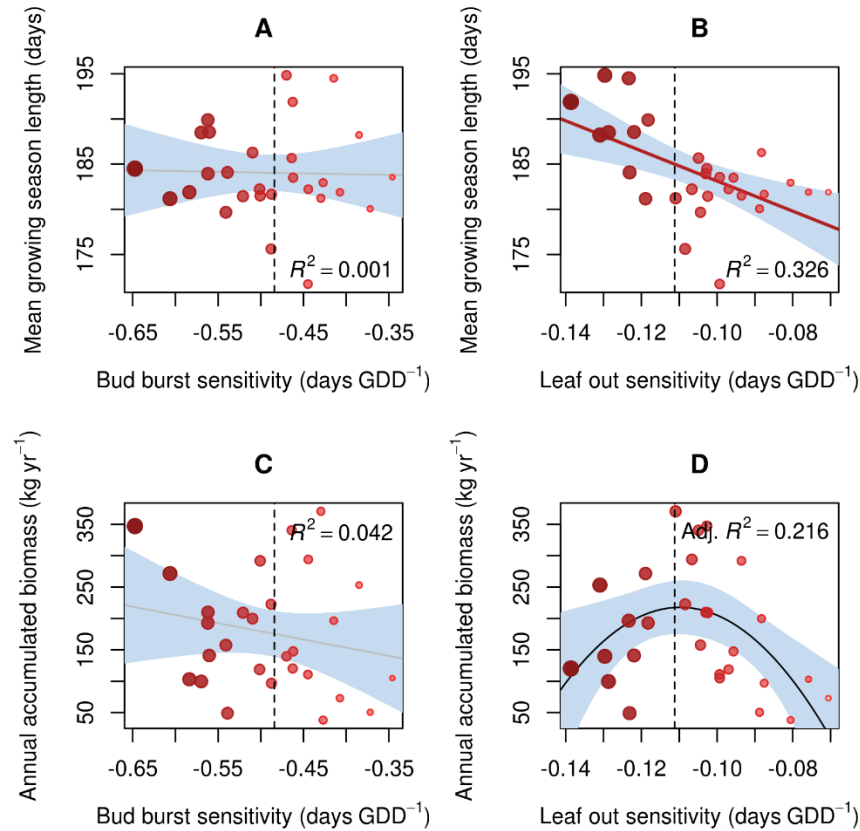


Fig. 2.5. Effects of spring phenology sensitivity on growing season length and productivity. Mean growing season length for the 28 populations was modeled as a function of (A) bud burst sensitivity and (B) leaf out sensitivity to climate change. Estimated annual accumulated biomass, a proxy for productivity, was modeled as a function of (C) bud burst sensitivity and (D) leaf out sensitivity. Red line (B) indicates significant negative relationship and black line (D) indicates significant concave down quadratic relationship at $P < 0.05$; gray lines (A and C) indicate non-significant relationships. Blue areas represent 95% confidence intervals. Vertical dashed lines indicate predicted sensitivity of local populations based on spatial patterns of bud burst and leaf out sensitivity. Circle size and hue represents leaf out sensitivity values and significance of sensitivity (darker hue = more significant), respectively, and reflects symbology of **Fig 2.2 A and B**.

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2.7 Supplementary Information

2.7.1 Materials and Methods

Phenology test site

In the early 1960s, a common garden (hereafter, “test site”) of northern red oak (*Quercus rubra*) was established at Martell Forest near West Lafayette, IN (40.438°N, -87.038°W). The original study aimed to quantify the effects of transplanting northern red oak trees on growth and survival (38, 39). The test site contained populations of northern red oak from 32 locations across most of the native range in eastern North America, but currently 28 populations with large enough sample sizes remain (**Fig S2.5**). Seed source locations ranged from 35.6°N to 47.3°N and -96.5°W to -68.5°W. Each population was replicated in three blocks for a total of 96 plots. Each plot originally contained 16 trees, but due to mortality the median number of remaining trees at the end of the study period (autumn 2019) was four per plot. Additionally, one population had missing seed source information, one population (Ogle County, IL) had no remaining trees at the start of the study period, and 10 plots contained no remaining trees. Therefore, we removed a population from our analysis if it had high mortality (fewer than 3 trees or fewer than 2 plots remaining at the end of the study period), leaving a total of 398 trees across 83 plots and 28 populations (mean = 4.5 trees per plot). The final list of seed source locations is available in **Table S3**, and their spatial distribution is in **Figs 2.2 and S2.5**. For more details on the establishment of the test site, see reference (39).

Phenology observations

Beginning in autumn 2013 and continuing through autumn 2019, phenology was observed every 2-7 days during the spring and autumn seasons. Observations were made by walking through the middle of each plot and making visual observations by eye or with binoculars as the stages necessitated [following (40)]. Each observation represented the average phenological stage (phenophase) across all trees in the plot. Spring phenology was recorded in four phenophases. The first phenophase was the bud swell stage, when dormant buds began swelling at the beginning of the season. The second phenophase was the bud opening stage (hereafter “bud burst”), when buds were visibly opening. The third phenophase was the leaf unfolding stage, when small leaves unfold

and become visible before the fourth phenophase of leaf growth, where leaves grow to their final size. The first three phenophases were recorded at 10%, 50% and 90% thresholds, and the fourth phenophase was recorded at 25%, 50%, 75%, and 100% thresholds (due to the more linear growth rate of leaves). Autumn phenology was recorded into two co-occurring stages (as opposed to progressive). The autumn phenophases were leaf coloration (percent leaves changed color) and leaf fall (percent leaves lost from the canopy). Both autumn phenophases were recorded at 10%, 50%, and 90% thresholds. Leaf coloration was also recorded at a 100% threshold, but leaf fall was not since northern red oak often retains a small portion of leaves throughout the winter. In total, we had 282 observation days during the study period (114 spring observation days across six seasons and 168 autumn observation days across seven seasons).

We calculated the day of year (DOY) of specific observed phenological transitions (hereafter, “phenological events”). In the spring, we were interested in the timing of bud burst as the end to the dormant season and the timing of leaf out as the beginning of the growing season. We defined the DOY of bud burst as the first observation when 50% or more of the canopy had reached the bud swell stage (first spring phenophase). Although the bud swell stage indicates the end of the dormant period, detection of swollen buds is more difficult than detecting the emergence of leaves, so we also analyzed the timing of leaf out, which we defined as the DOY of the first observation when the 90% or more of the leaves had unfolded (end of the third spring phenophase). In the autumn, we were interested in the timing of senescence as the end of the growing season and beginning of the winter dormant season. We used the simultaneous observations of leaf color and leaf fall to calculate DOY of leaf senescence by taking the first observation when both leaf color was above 50% and leaf fall was above 10%. All phenological events were recorded as day of year for comparison across years. For each phenological event, we calculated the difference between the observed DOY and the mean within-population DOY across all years to represent the shift in phenology due to climate change and other variables.

Climate and weather data

We aimed to assess the effects of local environmental conditions on the timing of phenological events. Hourly weather station data was downloaded from the two closest weather stations (Purdue University Airport, KLAf, about 9.3 km from the test site, and Purdue Agronomy Center for Research and Education, ACRE, about 16.0 km from the test site) from the Indiana

State Climate Office (<https://ag.purdue.edu/indiana-state-climate/>) for all years of the study period (January 1, 2013 through December 31, 2019). We averaged the KLAf and ACRE weather station data when both stations had recorded temperature measurements, and we used the only available record when either station had missing data. We used the hourly weather station data to calculate daily maximum (T_{\max}) and minimum (T_{\min}) temperature, and we used these values to calculate growing degree days (GDD) for spring observations using the formula: $GDD = \max(\frac{T_{\max} - T_{\min}}{2} - T_{\text{base}}, 0)$, where T_{base} is a fixed value of 5°C, and GDD is given a value of 0 when the average of T_{\max} and T_{\min} is less than T_{base} [following (41)]. We also calculated chilling degree days (CDD) for autumn observations (due to the lack of GDD accumulation in mid-to-late autumn) using the formula: $CDD = \max(T_{\text{base}} - \frac{T_{\max} - T_{\min}}{2}, 0)$, where T_{base} is a fixed value at 20°C (26, 42). Higher values of CDD indicate colder autumn weather and higher values of GDD indicate warmer spring weather. To quantify differences across the seven autumn and six spring seasons, we measured accumulated GDD from the 1st of February each year to the date of bud burst and leaf out and accumulated CDD from the 1st of August each year to the date of senescence (43). This allowed us to calculate how different a given day of year was relative to the other years in the study period. For example, October 16, 2013, the first observed date of senescence, had accumulated 7.27 CDD units more than the average accumulated CDD on October 16 (i.e., 7.27 CDD units colder than average).

We aimed to assess the effects of historic climate at the seed source on the timing phenological events. Bioclimatic variables (BIOCLIM) are commonly used biologically relevant variables often used in species distribution modeling to identify differences in climatic niche of populations of widespread species (29). There exist many BIOCLIM variables—19 in the WorldClim dataset (29)—that represent precipitation and temperature magnitude and variability and the interaction between precipitation and temperature. We accessed WorldClim BIOCLIM variables using the “getData()” function in the R package “raster” (44). A full list and description of BIOCLIM variables is available in **Table S2**, with more details available at (45). We also aimed to test if phenologically-relevant measures of average springtime growing degree days were better predictors of phenology than BIOCLIM variables. Daily gridded temperature data from Daymet were downloaded using the R package “daymetr” for each of our 28 seed sources for 30 years (1980-2009). GDD and CDD were calculated for each day, daily averages were calculated for the

30 years, and daily averages were summed for winter (January through March) and spring (March through May).

Quantifying sensitivity of phenology to climate change

Differences in environmental conditions (accumulated GDD and CDD) are hypothesized to shift phenology. We assessed the sensitivity of northern red oak using linear regression. We fit models in a hierarchical fashion [following (46) and (47)], first modeling the shift in a phenological event (e.g. shift in the DOY for population j in year i relative to the mean DOY for population j across all years) as a function of environmental conditions (shifts in accumulated CDD and GDD for autumn and spring phenophases, respectively) at the common garden (climate sensitivity, “CS” models). Then, we modeled the slope of the CS models as a function of seed source climate (19 BIOCLIM variables) to identify which populations from different climates had higher/lower sensitivity to changing environmental conditions.

Assessing impact of shifting phenology on growing season length and productivity

Diameter at breast height (DBH) is commonly used to measure tree growth, and allometric scaling equations can be used to estimate above ground biomass from DBH (32). All trees within the test site were measured in January 2013 before the beginning of the study period, and all trees were re-measured in February 2020 after the end of the study period. Some trees had negative or abnormally large growth rates (identified as a gap between 1.1 cm year⁻¹ and 2.7 cm year⁻¹ DBH change between measurements) that were likely measurement errors; therefore, we removed trees with negative or larger than 1.2 cm year⁻¹ growth rates from basal area and biomass calculations, leaving a total of 346 trees in our analysis of productivity (**Table S3**). We estimated total aboveground biomass (kg) using the allometric equation (32): $biomass = e^{-2.0127 + 2.4342 \ln(DBH)}$ for 2020 and 2013, and then we subtracted 2020 biomass from 2013 biomass and divided by $N_{year} = 7$ growing seasons between measurements to calculate annual accumulated biomass (kg year⁻¹). We also calculated periodic annual increment of basal area (PAI, cm² year⁻¹) based on DBH (cm): $PAI = \frac{\pi \left(\frac{DBH_{2020}}{2} \right)^2 - \pi \left(\frac{DBH_{2013}}{2} \right)^2}{N_{year}}$, where $N_{year} = 7$ growing seasons between measurements. We summed tree-level productivity measures to the population level and

used linear regression and a Pearson correlation test to compare population-level annual accumulated biomass to PAI.

We also aimed to measure the effects of shifting phenology on the length of growing season and leaf longevity. We calculated growing season length (GSL) as the number of days between leaf out and senescence and modeled mean GSL as a function of leaf out and bud burst sensitivity using linear regression. We used a correlation test between shift in leaf out and shift in autumn senescence to determine whether red oak has a fixed leaf longevity. A strong negative correlation would indicate that gaining days in the spring would lead to losing days in the autumn due to a fixed leaf longevity. Finally, we used linear regression to determine the relationship between bud burst and leaf out sensitivity and our two measures of productivity (biomass and PAI). We included a quadratic term to determine if a linear or hump-shape relationship predominated. All analyses in this project were performed in R version 3.6.1 (48) using packages “rgdal” (49) and “raster” (44) for geospatial analysis and “stats” (48), “car” (50), and “MuMIn” (51) for linear regression and model selection.

2.7.2 Supplementary Figures and Tables

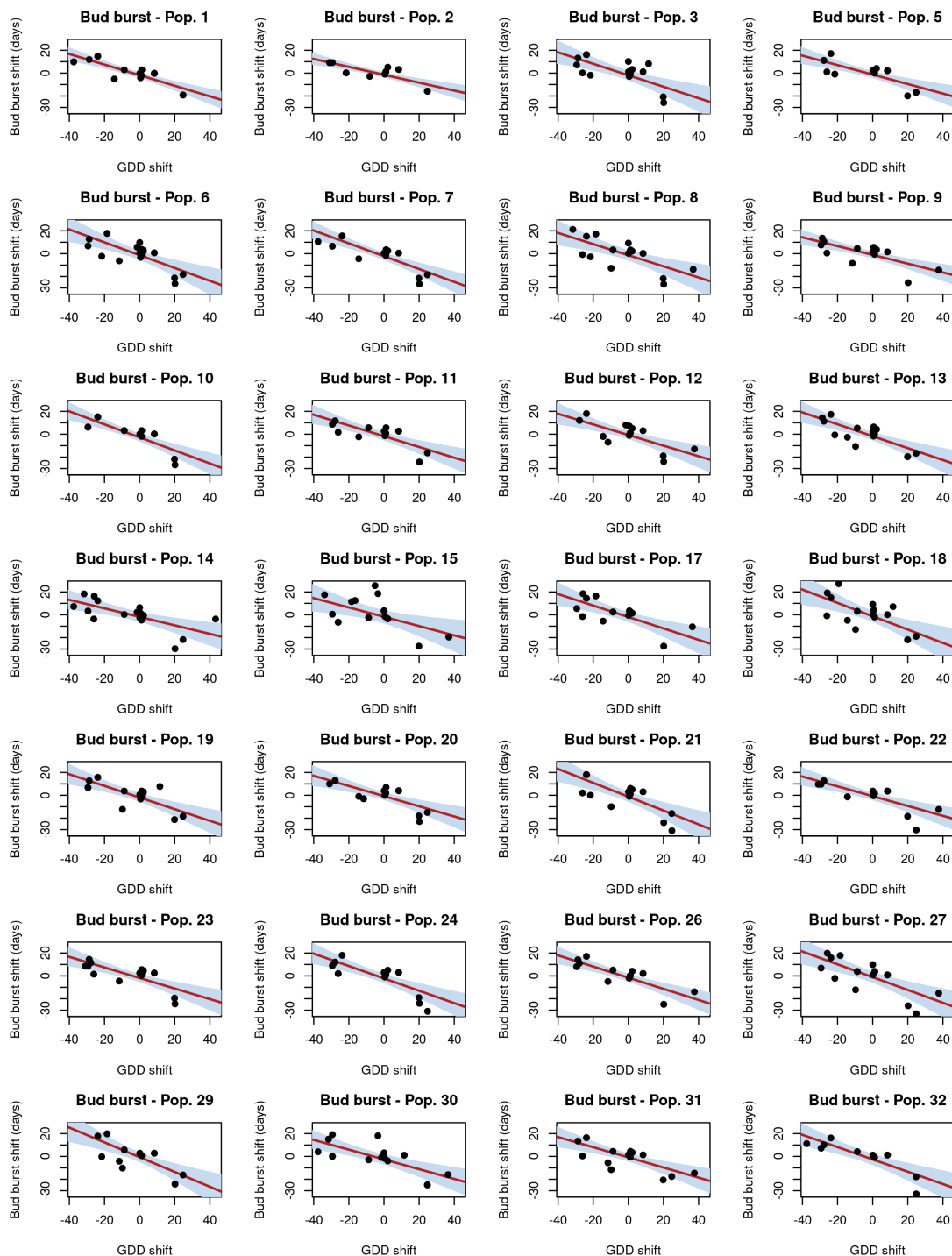


Fig. S2.1. Scatterplots of phenological shifts as a function of changes in environmental conditions. Each scatterplot represents one of the 28 populations. Regression line color indicates direction and significance: significant negative trend in red, non-significant trend in gray. Negative trends indicate an advancement of spring or delay of autumn in warmer years. Blue area represents 95% confidence interval. Each dot represents one replicate in one year.

Figure S2.1 continued

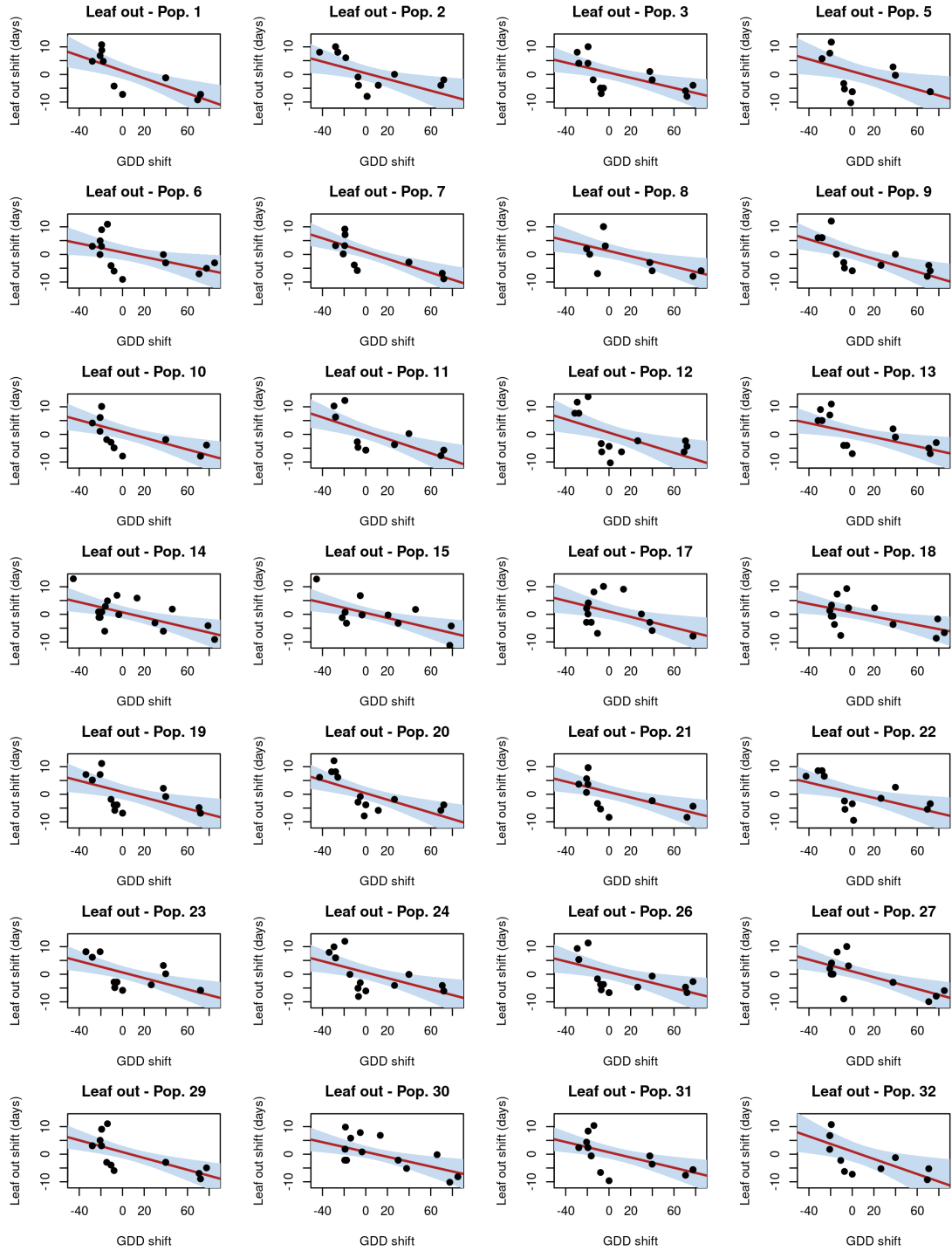
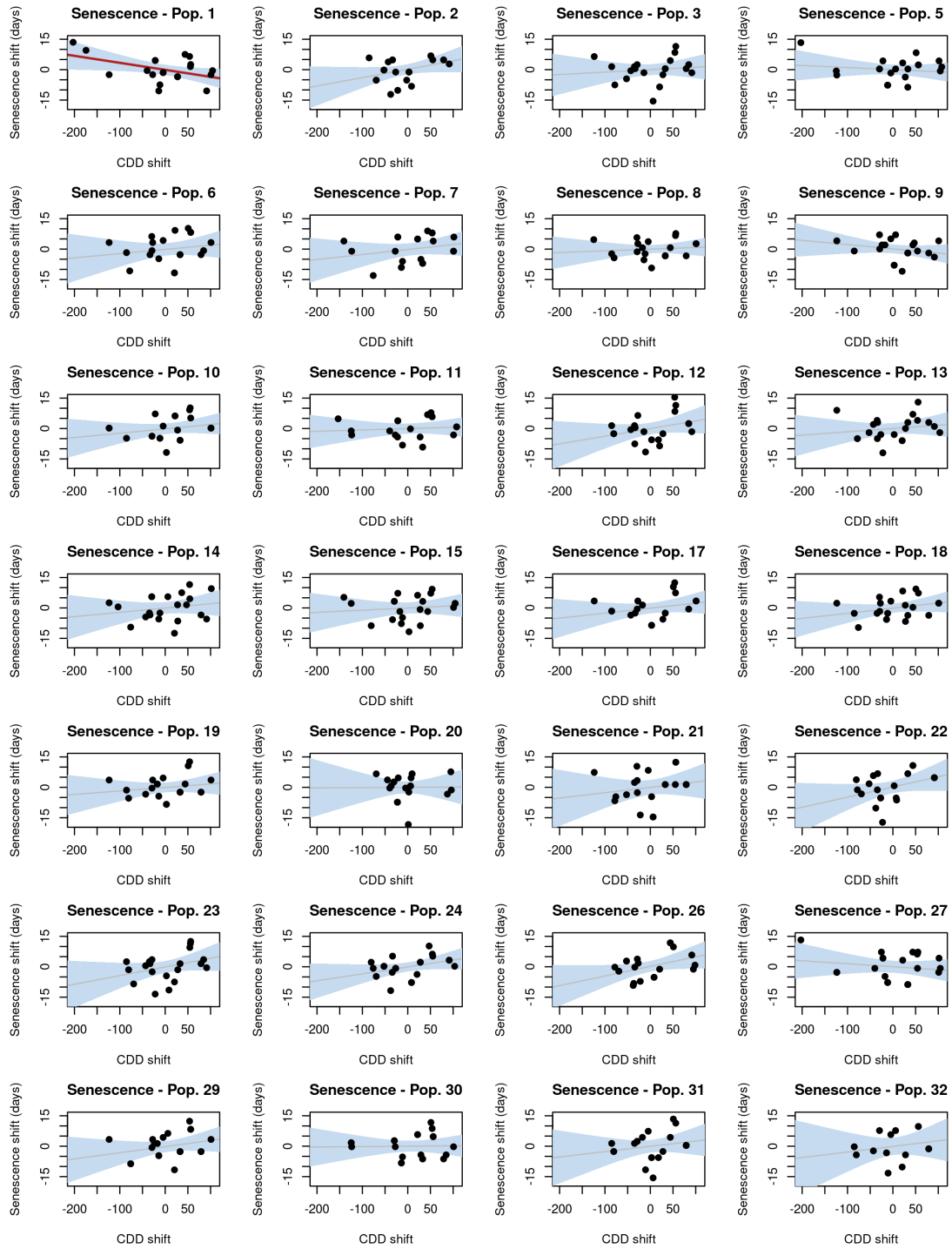


Figure S2.1 continued



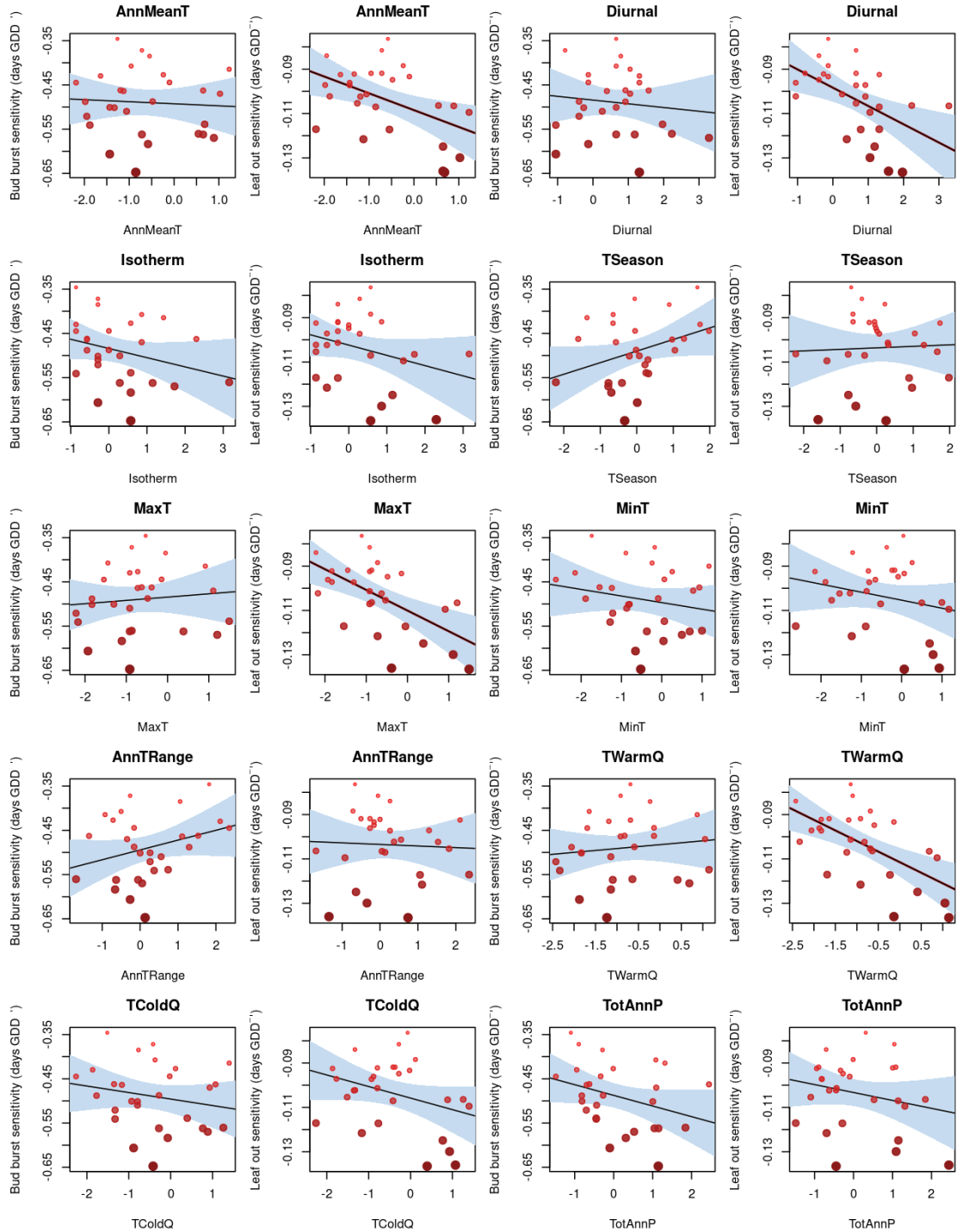
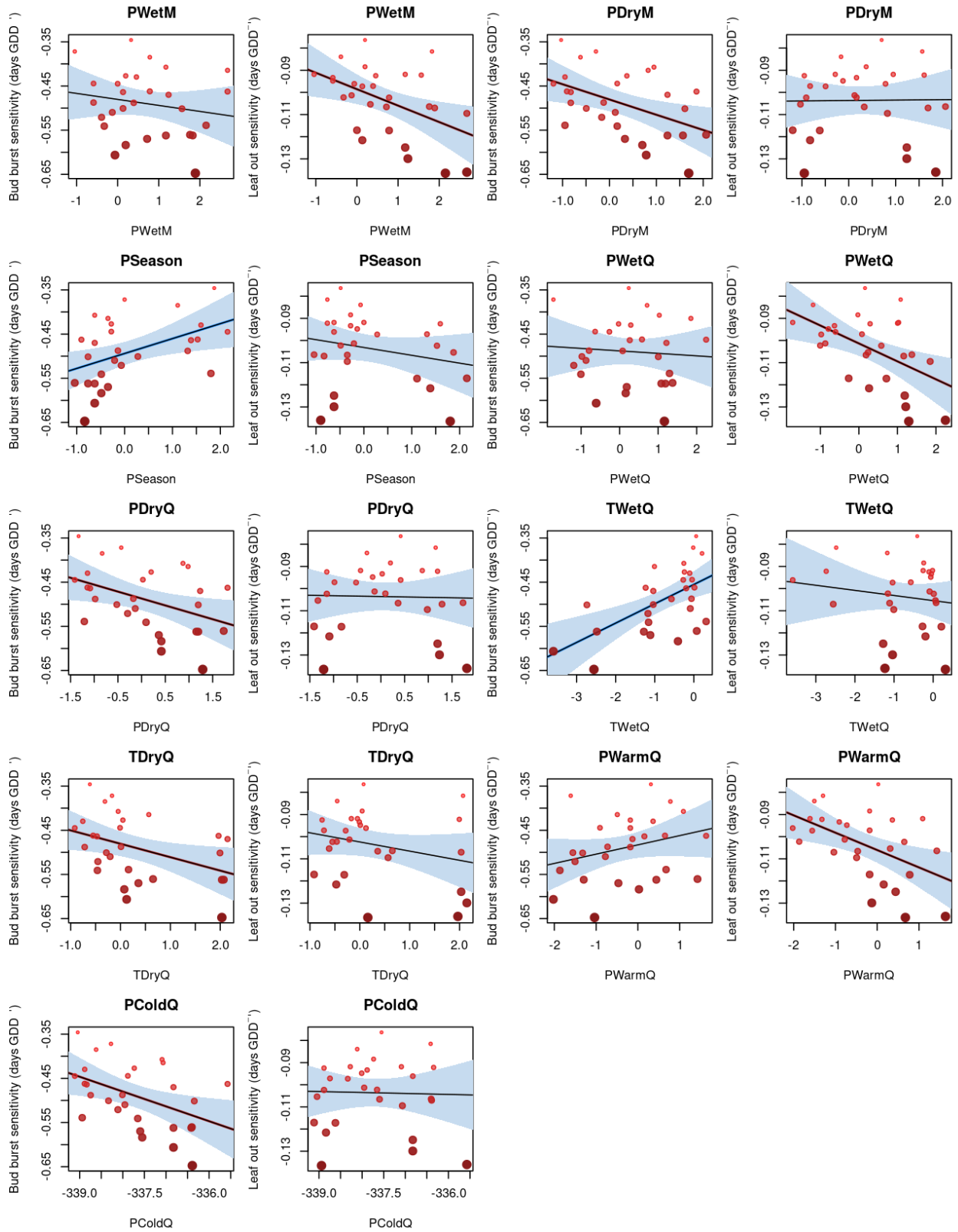


Fig. S2.2. Scatterplots of bioclimatic predictors of bud burst and leaf out sensitivity. Bud burst and leaf out sensitivity were modeled as a function of seed source BIOCLIM predictors. Circles represent individual populations, with color and size representing significance of sensitivity. BIOCLIM variables were standardized by subtracting the value at the common garden and dividing by the standard deviation. Blue areas represent 95% confidence intervals. Color of regression line indicates significance of the relationship: red = significant negative; blue = significant positive; black = non-significant. Negative coefficient values are interpreted as an increase in the BIOCLIM variable leads to an increase in sensitivity (more negative sensitivity value); conversely, positive coefficient values are interpreted as an increase in the BIOCLIM variable leads to a decrease in sensitivity (less negative sensitivity value).

Figure S2.2 continued



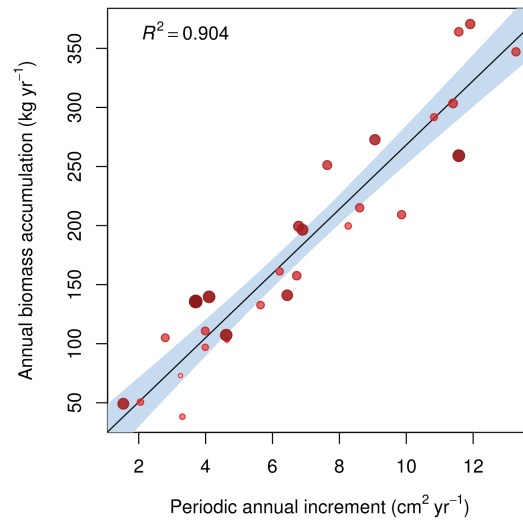


Fig. S2.3. Relationship between measures of productivity. X axis = periodic annual increment (PAI) measured as the annual change in basal area during the study period. Y axis = annual biomass accumulation measured as the change in estimated biomass between 2013 and 2020 based on the allometric scaling equation for oak species (30). Colors and dot size reflect leaf out sensitivity as shown in Fig 2.2.

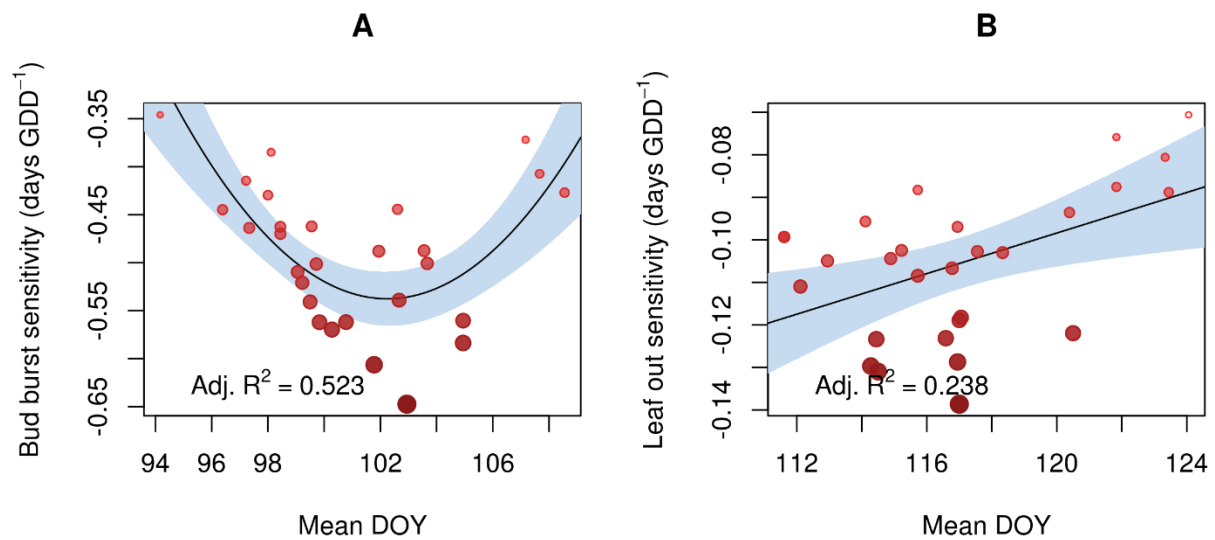


Fig. S2.4. Bud burst and leaf out sensitivity as a function of mean DOY of (A) bud burst and (B) leaf out. Populations that break bud early or late tend to have less sensitivity to climate change, but populations that leaf out early are generally more sensitive to climate change than populations that leaf out late.

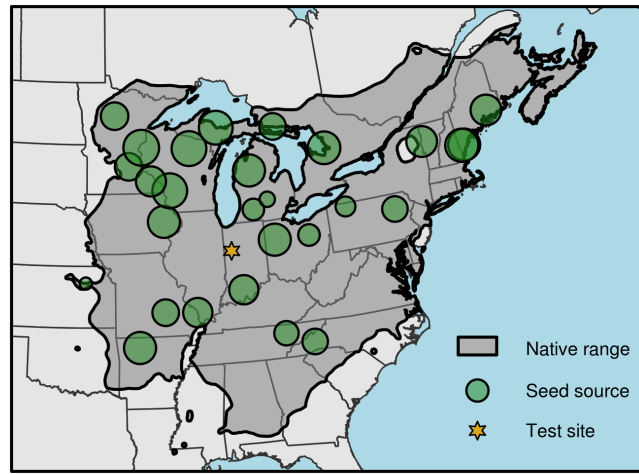


Fig. S2.5. Map of study area. Gray area indicates the native range of *Quercus rubra* based on Little (37). Green circles indicate seed source locations of the 28 populations used in this study, and size is proportional to the survival of original population of 48 trees. Gold star indicates location of the common garden site at Martell Forest, West Lafayette, IN.

Table S2.1. Mean day of phenological events and climate sensitivity values. Max and min shift values in parentheses. Bolded sensitivity values were statistically significant ($P < 0.05$), and asterisks indicate level of significance of advances (negative values) or delays (positive values) in response to increased GDD in spring or CDD in autumn: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Populations are ordered from north to south.

Mean day of year (min, max shift)				Sensitivity (slope coefficient values)		
Pop. ID	Bud burst	Leaf out	Senescence	Bud burst (Days GDD ⁻¹)	Leaf out (Days GDD ⁻¹)	Senescence (Days CDD ⁻¹)
20	98 (-23, 13)	111.6 (-6.6, 9.4)	284.3 (-18.3, 7.7)	-0.445***	-0.099*	0.001
13	99.7 (-19.7, 17.3)	115.2 (-8.2, 11.8)	298 (-12, 13)	-0.521***	-0.102**	0.016
24	99 (-31, 18)	114.9 (-7.9, 10.1)	295.8 (-11.8, 10.2)	-0.541***	-0.104**	0.034
22	98.3 (-30.3, 12.7)	112.1 (-7.1, 10.9)	294.2 (-17.2, 10.8)	-0.430***	-0.111**	0.050
26	99.9 (-24.9, 17.1)	115.7 (-10.7, 11.3)	293.2 (-9.2, 11.8)	-0.488***	-0.108*	0.047
2	98.8 (-15.8, 9.2)	111.6 (-6.6, 9.4)	296.2 (-12.2, 6.8)	-0.346***	-0.099**	0.041
3	100.8 (-25.8, 16.2)	116.9 (-5.9, 10.1)	300.5 (-15.5, 11.5)	-0.501***	-0.097**	0.012
21	98.9 (-30.9, 18.1)	117 (-6, 12)	299.6 (-14.6, 12.4)	-0.606***	-0.119**	0.026
17	102.6 (-27.6, 18.4)	120.4 (-9.4, 11.6)	303.6 (-8.6, 12.4)	-0.501***	-0.094*	0.025
19	101.3 (-21.3, 15.7)	115.7 (-6.7, 9.3)	303.4 (-8.4, 12.6)	-0.510***	-0.088*	0.017
23	99.5 (-24.5, 14.5)	114.1 (-9.1, 8.9)	299.5 (-13.5, 12.5)	-0.462***	-0.096*	0.043
12	98.9 (-23.9, 18.1)	112.9 (-7.9, 10.1)	300.6 (-11.6, 15.4)	-0.464***	-0.105*	0.038
6	101.3 (-26.3, 17.7)	118.3 (-7.3, 10.7)	303.8 (-11.8, 10.2)	-0.562***	-0.103*	0.021
29	99.2 (-24.2, 19.8)	117.6 (-6.6, 11.4)	303.7 (-11.7, 12.3)	-0.647***	-0.103**	0.030
14	104.7 (-29.7, 18.3)	123.4 (-9.4, 11.6)	304.5 (-12.5, 11.5)	-0.372**	-0.089**	0.021
8	101.8 (-26.8, 21.2)	121.8 (-7.8, 11.2)	304.3 (-9.3, 7.7)	-0.488**	-0.088*	0.008
9	100.4 (-25.4, 13.6)	114.5 (-7.5, 12.5)	303 (-11, 7)	-0.385***	-0.131**	-0.021
15	107.5 (-27.5, 25.5)	124.1 (-9.1, 8.9)	306.8 (-11.8, 9.2)	-0.407**	-0.071	0.011
18	101.9 (-21.9, 27.1)	121.8 (-7.8, 11.2)	304.7 (-9.7, 9.3)	-0.584**	-0.076*	0.025
30	107.9 (-24.9, 19.1)	123.3 (-8.3, 9.7)	307.3 (-8.3, 11.7)	-0.427***	-0.081*	0.002
31	100.6 (-20.6, 16.4)	116.8 (-7.8, 12.2)	300.6 (-15.6, 13.4)	-0.444***	-0.107*	0.026
32	100.8 (-32.8, 16.2)	116.6 (-7.6, 12.4)	302.3 (-13.3, 9.7)	-0.539***	-0.123*	0.027
7	101.5 (-26.5, 15.5)	117.1 (-8.1, 11.9)	308 (-13, 9)	-0.562***	-0.118**	0.024
10	101.8 (-26.8, 15.2)	116.9 (-7.9, 12.1)	306.8 (-11.8, 10.2)	-0.570***	-0.129**	0.021
11	99.3 (-24.3, 11.7)	114.3 (-5.3, 10.7)	310.2 (-9.2, 7.8)	-0.470***	-0.130***	0.007
1	102.2 (-19.2, 14.8)	117 (-10, 12)	309.5 (-10.5, 13.5)	-0.463***	-0.139**	-0.035*
5	99.9 (-19.9, 17.1)	114.4 (-9.4, 14.6)	309.7 (-8.7, 13.3)	-0.415***	-0.123**	-0.010
27	101.2 (-33.2, 19.8)	120.5 (-9.5, 10.5)	309.8 (-8.8, 13.2)	-0.560***	-0.122**	-0.015

Table S2.2 Bioclimatic predictors and their effect on climate change sensitivity. WorldClim BIOCLIM variables and Daymet accumulated growing degree days were used as predictors of bud burst and leaf out sensitivity. See references (29, 30, 45) for more detailed descriptions of the BIOCLIM and Daymet data. Significant slope coefficients in bold, with asterisks indicating significance of relationship: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

			Bud burst				Leaf out		
Variable (abbreviation)	Category	Description	Slope (+/- 95% CI)	R ²	AIC weight	Slope (+/- 95% CI)	R ²	AIC weight	
BIOCLIM (AnnMeanT)	1	Temperature	Annual mean temperature	-0.005 (+/-0.030)	<0.01	0.002	-0.008** (+/-0.006)	0.23**	0.020
BIOCLIM (Diurnal)	2	Temperature	Annual mean diurnal range	-0.008 (+/-0.030)	0.01	0.002	-0.008** (+/-0.006)	0.27**	0.044
BIOCLIM (Isotherm)	3	Temperature	Isothermality	-0.021 (+/-0.029)	0.08	0.006	-0.005 (+/-0.006)	0.09	0.002
BIOCLIM (TSeason)	4	Temperature	Temperature seasonality	0.026 (+/-0.028)	0.13	0.012	0.001 (+/-0.006)	<0.01	0.001
BIOCLIM 5 (MaxT)		Temperature	Maximum temperature of warmest month	0.007 (+/-0.030)	0.01	0.002	-0.009*** (+/-0.005)	0.35***	0.204
BIOCLIM 6 (MinT)		Temperature	Minimum temperature of coldest month	-0.015 (+/-0.029)	0.04	0.003	-0.004 (+/-0.006)	0.05	0.001
BIOCLIM (AnnTRange)	7	Temperature	Annual temperature range	0.022 (+/-0.028)	0.09	0.007	0.002 (+/-0.006)	<0.01	0.001
BIOCLIM (TwarmQ)	10	Temperature	Mean temperature of warmest quarter	0.009 (+/-0.030)	0.01	0.002	-0.010*** (+/-0.005)	0.36**	0.289
BIOCLIM (TColdQ)	11	Temperature	Mean temperature of coldest quarter	-0.015 (+/-0.029)	0.04	0.003	-0.005 (+/-0.006)	0.11	0.003
BIOCLIM (TotAnnP)	12	Precipitation	Total annual precipitation	-0.024 (+/-0.028)	0.11	0.009	-0.004 (+/-0.006)	0.05	0.001
BIOCLIM (PWetM)	13	Precipitation	Total precipitation of wettest month	-0.014 (+/-0.029)	0.03	0.003	-0.009* (+/-0.006)	0.22*	0.017
BIOCLIM (PDryM)	14	Precipitation	Total precipitation of driest month	-0.035* (+/-0.026)	0.22*	0.056	0.000 (+/-0.006)	<0.01	0.001
BIOCLIM (PSeason)	15	Precipitation	Precipitation seasonality	0.034* (+/-0.027)	0.21*	0.048	0.005 (+/-0.006)	0.05	0.001
BIOCLIM (PWetQ)	16	Precipitation	Total precipitation of wettest quarter	-0.006 (+/-0.030)	<0.01	0.002	-0.008** (+/-0.005)	0.26**	0.036
BIOCLIM (PDryQ)	17	Precipitation	Total precipitation of driest quarter	-0.031* (+/-0.027)	0.18*	0.028	-0.000 (+/-0.006)	<0.01	0.001
BIOCLIM (TWetQ)	8	Temp.- precip. interaction	Mean temperature of wettest quarter	0.044*** (+/-0.024)	0.35***	0.737	-0.002 (+/-0.006)	0.02	0.001
BIOCLIM (TDryQ)	9	Temp.- precip. interaction	Mean temperature of driest quarter	-0.030* (+/-0.027)	0.17*	0.024	-0.004 (+/-0.006)	0.07	0.001
BIOCLIM (PWarmQ)	18	Temp.- precip. interaction	Total precipitation of warmest quarter	0.021 (+/-0.029)	0.08	0.006	-0.008** (+/-0.006)	0.25**	0.027
BIOCLIM (PColdQ)	19	Temp.- precip. interaction	Total precipitation of coldest quarter	-0.034* (+/-0.027)	0.21*	0.045	-0.000 (+/-0.006)	<0.01	0.001
Daymet GDD	spring	Temperature	Mean spring (March-May) accumulated growing degree days	0.007 (+/-0.030)	0.01	0.002	-0.010*** (+/-0.005)	0.37**	0.352

Table S2.3. Seed source locations and number of trees. N_{alive} indicates number of trees remaining at the end of the study period. N_{DBH} indicates number of trees with reliable diameter at breast height (DBH) measurements in both 2013 and 2020 (some trees were removed from the analysis with suspected measurement errors). Populations are ordered from north to south, and population ID (Pop. ID) reflects original population ID number from plantation establishment (38).

Pop. ID	State/ Province	County	Year planted	Lat.	Lon.	N_{alive}	N_{DBH}
20	MN	Cass	1962	47.33	-94.50	12	10
13	MD	Marquette	1962	46.50	-87.33	21	18
24	ONT	Algoma	1962	46.25	-83.33	11	11
22	WI	Pierce	1963	45.75	-92.67	25	24
26	WI	Oneida	1962	45.58	-89.33	23	19
2	MN	Carver	1962	44.83	-93.58	12	9
3	ME	Penobscot	1962	44.83	-68.50	16	13
21	ONT	Simcoe	1962	44.83	-80.00	19	18
17	MI	Missaukee	1962	44.25	-85.33	18	17
19	NY	Essex	1962	44.17	-73.33	16	13
23	MN	Winona	1963	44.08	-92.08	15	12
12	WI	Vernon	1963	43.58	-90.83	23	20
6	ME	York	1962	43.50	-70.58	18	15
29	ME	York	1962	43.50	-70.75	20	19
14	MI	Ingham	1964	42.75	-84.33	4	3
8	MI	Kalamazoo	1964	42.33	-85.33	7	5
9	IA	Boone	1963	42.08	-91.33	18	16
15	PA	Warren	1964	41.83	-79.25	6	5
18	PA	Luzerne	1964	41.25	-76.08	10	9
30	OH	Wayne	1963	40.75	-81.92	7	6
31	OH	Allen	1962	40.75	-84.17	18	16
32	KS	Riley	1963	39.17	-96.50	3	3
7	IN	Orange	1962	38.50	-86.50	14	13
10	MO	Dent	1963	37.67	-91.50	11	8
11	IL	Jackson	1962	37.58	-89.50	14	12
1	TN	Anderson	1962	36.17	-84.17	9	6
5	AR	Newton	1963	36.00	-93.17	18	16
27	NC	Buncombe	1964	35.58	-82.50	10	10
TOTAL						389	346

CHAPTER 3. COMMUNITY-LEVEL RESPONSES TO CLIMATE CHANGE IN FORESTS OF THE EASTERN UNITED STATES

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3.1 Abstract

Aim: Climate change has impacted forest ecosystems, leading to species-level tree migration. However, climate change impacts on forest communities are mostly unknown. Here, we assess changes to forest communities at three scales: within community changes in species composition, individual community spatial shifts, and changes across all communities.

Location: Eastern United States

Major taxa studied: Forest tree species

Methods: Using a region-wide forest inventory dataset from the USDA Forest Service's Forest Inventory and Analysis Program with over 70,000 plots, we identified forest communities using the Latent Dirichlet Allocation method. We analyzed species composition changes within communities and assessed community-level spatial shifts over the last three decades to quantify individual community responses to climate change. We utilized the distribution of forest communities across climate conditions to predict where communities could migrate to during the study period and compared climate-predicted shifts to observed community shifts. Changes across all communities were modeled as a function of climate and non-climate variables using generalized linear mixed-effects models.

Results: We identified 12 regional forest communities of the eastern United States, which varied in their stability of species composition over the study period. All communities experienced relatively short yet significant shifts in their spatial distribution (median = 8.0 km dec⁻¹). Historic climate and changes in seasonal temperature variability were the best predictors of change across all communities. However, the distance and direction of individual community migration was

poorly predicted by climate change, and the observed direction was often opposite of the predicted direction.

Main conclusions: Forest communities shifted their distributions over the last three decades, but climate change outpaced the rate of community migration. Continued lags between climate change and forest community responses and the lack of migration in the direction predicted by climate change may lead to the inability of forests to keep up with changing climate.

Keywords: Climate change, forest communities, Forest Inventory and Analysis, Latent Dirichlet Allocation, spatial shifts, tree migration

3.2 Introduction

Forest ecosystems across the United States (U.S.) are threatened by human disturbance (Riitters, Coulston, & Wickham, 2012; Vanderwel & Purves, 2014), invasion of nonnative plants and pests (Fei, Morin, Oswalt, & Liebhold, 2019; Oswalt et al., 2015), and climate change (Fei et al., 2017; Iverson & Prasad, 1998). Among these major threats, climate change has been shown to cause tree species to shift their distributions. Often, species have moved to higher latitudes or elevations in response to temperature change (Lenoir, Gégout, Marquet, De Ruffray, & Brisse, 2008; Woodall et al., 2009; Zhu, Woodall, & Clark, 2012), but westward movement has also been observed in response to precipitation change (Fei et al., 2017). Changes in the distribution of forest species can have severe consequences for ecosystem functioning; however, changes at the community level—impacting not only the species composition but also the interactions among species—may be even more important to ecosystem functioning (Loreau et al., 2001; Symstad, Tilman, Willson, & Knops, 1998). Understanding the effects of climate change and other large-scale threats to forest communities is important for predicting the future sustainability of forests and the services they provide.

Ecologists have attempted to define communities for over a century, yet communities are dynamic, and their stability is increasingly questioned due to climate change. Early attempts at defining communities, such as Clements (1916) and Gleason (1926), revealed multiple conflicting views of ecological communities. Clements argued that communities acted as superorganisms that matured into a climax community determined by regional macroclimate, whereas Gleason argued that communities were artificial groupings of overlapping species distributions created by

individualistic responses to environmental gradients. In addition to the difficulty of defining communities, Braun (1950) identified large-scale, sub-continental patterns of forest species distributions, which Davis (1983) showed were the result of post-glaciation migrations of individual species over the last five millennia. As a result of these migration patterns, distinct forest regions emerged that were considered mostly stable in the recent past (Braun, 1950), but their current and future stability is questionable given decade-scale tree species migrations in response to recent climate change (e.g., Fei et al., 2017; Woodall et al., 2009; Zhu et al., 2012) that rival the distance of these historic millennium-scale post-glaciation migrations.

In addition to difficulty defining communities, data availability and computational complexity often limited earlier attempts at describing and analyzing changes to ecological communities. Many early studies were based on limited, local-scale samples and used simplified statistical tests or relied on anecdotal evidence. The availability of large-scale datasets (e.g., Forest Inventory and Analysis from the USDA Forest Service; FIA) containing tens of thousands to millions of observations and the advancements in analytical techniques for big data (e.g., Bayesian statistics and machine learning) have allowed researchers to confirm the patterns in species co-existence observed by earlier studies and provide greater detail about these communities (Dyer, 2006; Peters et al., 2014). However, these large-scale community analyses still have underlying problems related to the abundance and complexity of data. First, many multivariate methods rely on the creation of a distance matrix in multidimensional species space to determine if they exhibit different species compositions (Costanza, Coulston, & Wear, 2017; Legendre & Legendre, 2012). These approaches can be influenced by the abundance of non-overlapping species (i.e., the “double-zero” problem), where patterns are driven by the lack of species co-occurrence (Legendre & Legendre, 2012). As such, distance metrics used in multivariate analyses need to be carefully considered in order to minimize these effects (Dyer, 2006). Multivariate methods are good at detecting abrupt changes between communities, but may fail to detect differences when transitions between communities occur slowly (Valle, Baiser, Woodall, & Chazdon, 2014). In addition, the creation and analysis of a distance matrix for tens of thousands of samples can become computationally unfeasible (e.g., a distance matrix between 80,000 samples, the approximate size of the FIA database for the eastern U.S., contains 6.4 billion entries). Second, irregular sampling density can cause community delineations to be biased by areas where forests are more abundant. Regions such as the southern Appalachian Mountains or the upper Midwest that have large regions of continuous forest with many sampling sites in the FIA database can drive the patterns found in

traditional clustering and multivariate methods. Thus, the results of these methods may provide great detail about one region but little detail about a more sparsely forested or sampled region. There is a need to address these problems by using different models of species coexistence.

Here, we take a multiple-lens view of forest community changes over time by assessing changes at multiple scales: (1) within community changes in species composition, (2) spatial shifts of individual communities, and (3) changes in composition and dominance across all communities. We first needed to identify forest communities, so we used the Latent Dirichlet Allocation (LDA) topic model (Blei, Ng, & Jordan, 2003; Valle et al., 2014) to identify forest communities within two datasets (T1, 1980s and T2, 2010s), each containing over 70,000 FIA plots. As such, communities in this study are similar to those considered in traditional local-scale ecological studies, but are more generalized given the large amount of data used to identify consistent patterns in species associations. The resulting communities, therefore, represent regional species assemblages or regional forest types similar to those defined by Braun (1950), Costanza et al. (2017), or Dyer (2006). Our first assessment of forest community changes (1) was to analyze: (a) changes in species rank within a community (i.e., changes in dominant species of the community), (b) changes in the contribution of species to a community (i.e., shifts in the proportion/abundance of each species in each community), and (c) the gain or loss of species over time. These analyses would reveal if new assemblages of species are formed or if the species composition of existing communities is shifting. Our second assessment of forest community changes (2) was to test if communities were shifting their geographic distributions, and if the community migrations were tracking with climate change. Given recent knowledge of spatial shifts at the species level (Fei et al., 2017; Zhu et al., 2012), we aimed to test if forest communities were also shifting their distributions in response to climate change. Finally, our third assessment of forest community changes (3) was to identify areas with high levels of community change and test if these areas were also experiencing greater levels of climate change. By taking this multiple-lens view of forest community responses to climate change, we can better understand the ways in which forest communities change over time and can use this information to address the future sustainability of forest communities in a continuously changing global climate.

3.3 Methods

3.3.1 Forest inventory data

The USDA Forest Service’s Forest Inventory and Analysis (FIA) program is a nationwide sampling effort of approximately one plot per 2428 hectares (6000 acres) of forested land, containing approximately 130,000 plots nationwide and approximately 80,000 plots in the eastern U.S. We selected FIA data from the eastern U.S., encompassing 37 states and four ecoregions (Cleland et al., 2007): the Northern Hardwood Region (NHR), the Central Hardwood Region (CHR), the Forest-Prairie Transition Region (FPTR), and the Southern Pine-Hardwood Region (SPHR) (**Table S3.1, Fig S3.1**). We compiled two datasets (T1 and T2) to assess changes over the last three decades. Before the early 2000s, the FIA program utilized a periodic sampling protocol, in which states completed sampling every 10 to 15 years. More recently, a panel system for FIA sampling has been used, where each year partial sampling is completed, and states report sampling every 5 to 7 years when all plots in the state have been sampled. Therefore, the year of completion varied across the eastern U.S. for both time periods. For the first period (T1), we used the first measurement available in 1980 or later (a full periodic sample from each state completed in a single year from 1980 to 1995). For the second period (T2), we used measurements from sampling that concluded in 2015 to 2017 (the compiled sampling that was carried out over the previous 5 to 7 years). The median interval between T1 and T2 sampling periods in each state was 31 years.

Ideally, we would have used data for all species available in the FIA database. However, some species were aggregated to the genus level in certain states’ surveys at T1. For example, coastal states from Virginia to Florida have *Celtis* genus-level records at T1 but have *Celtis occidentalis* and *Celtis laevigata* recorded separately at T2. Similarly, some genera (such as the *Carya* genus) were identified to the genus level at T1 across most of the range. Therefore, we assigned species with only genus-level samples at T1 to their genus-level species code even when species-level data were collected at T2. Similarly, ash species (*Fraxinus* species) were aggregated to the genus level to reduce the effects of uncertainty from known identification issues (e.g., overlapping ranges of species with similar morphological characteristics). Additional species that were not aggregated to the genus level were considered rare and removed from the dataset if they occurred in fewer than 300 plots (following Fei et al., 2017). The final species list included 138 species of interest (out of approximately 263 species in the FIA database for the eastern U.S.) that were aggregated into 85 new species or genus labels (hereafter “species”; **Table S3.2**).

We utilized three metrics to measure species abundance in each plot: relative basal area, relative stem density, and importance value (average of relative basal area and relative density). These metrics were derived for all stems and for two separate size classes: < 5.1 cm DBH (hereafter, saplings) and > 5.1 cm DBH (hereafter, trees). The use of relative metrics allowed each plot to be weighted equally (i.e., the sum of importance values for all species in each plot is equal). All values were rounded up to the nearest integer percentage to accommodate for the LDA model (which was built using integer word counts) and to avoid removing species from samples where they had low abundance (with a metric value between 0% and 0.5%). The plot-level data were used to fit the LDA model. However, to account for the spatial mismatch between T1 and T2 (i.e., not all plots inventoried at T1 were re-inventoried at T2, or *vice versa*), we aggregated plot-level results to a 1452 km² hexagon tessellation following Fei et al. (2017). To reduce the potential biases in our analysis of spatial shifts caused by hexagons with few FIA plots (i.e., dramatic community turnover due to mismatch in sampling), we selected hexagons that contained > 10 FIA plots at both T1 and T2. A final total of 89,231 plots at T1 and 75,715 plots T2 fell into 1813 hexagons with > 10 FIA plots.

3.3.2 Identifying forest communities with the Latent Dirichlet Allocation model

The Latent Dirichlet Allocation topic model is a Bayesian hierarchical model that was developed to identify topics in text data based on the frequency and co-occurrence of words across hundreds to thousands of documents (Blei et al., 2003). It has been widely used for text-mining uses (e.g., Tirunillai & Tellis, 2014), but has recently been expanded to other uses in the natural sciences such as remote sensing, vegetation classification, and community detection (Damgaard, 2015; Tang et al., 2013; Valle et al., 2014). For community detection, the analogy to traditional text-mining is quite clear: communities (or topics) are based on the frequency and co-occurrence of species (or words) across hundreds to thousands of plots (or documents). The LDA model is a Bayesian hierarchical model that assumes a generative process to forest (or document) sampling (or creation) (Blei et al., 2003; Valle et al., 2014). This assumption means that first a forest (or document) selects a number of communities (or topics) to include in the sample following a Dirichlet distribution. Then, for each community (or topic) a number of species (or words) related to the community (or topic) is chosen. The posterior distributions of the LDA model contain two main

components: (1) the proportion of each community in each sample (or each topic in each document) and (2) the proportion of each species in each community (or each word in each topic).

We ran the LDA model on the T1 data using the built-in Gibbs sampler in the “topicmodels” package in R (Grün & Hornik, 2011), with 5000 iterations and a 500 iteration burn-in period. The LDA model requires specifying the number of groups *a priori*. Since we did not have *a priori* knowledge of the exact number of communities in the FIA data, we used an iterative approach, increasing the number of communities, k , by 1 from 2 to 50. We used the plot-level data with importance value for all stems to fit the LDA model. The models were evaluated for goodness of fit and complexity using a suite of four metrics (Arun, Suresh, Veni Madhavan, & Narasimha Murthy, 2010; Cao, Xia, Li, Zhang, & Tang, 2009; Deveaud, SanJuan, & Bellot, 2014; Griffiths & Steyvers, 2004) from the “ldatuning” package in R (Nikita, 2016). The value k is chosen by maximizing two of the metrics (Deveaud et al., 2014; Griffiths & Steyvers, 2004) and minimizing the other two (Arun et al., 2010; Cao et al., 2009); therefore, we included possible values of k that were at these maximum and minimum values of the four metrics. Due to the asymptotic nature of the metrics, we also included break points indicated by multivariate adaptive regression splines (MARS regression; Friedman, 1991) using the “earth” package in R (Milborrow, 2017). Finally, we used the posterior distributions from the candidate models to evaluate an ecologically-based metric, the number of species with proportion $> 1/n_{\text{species}}$ in each community, to remove models that contained communities that were comprised of only one species. To test if there were differences between input data type (i.e., relative basal area, relative density, or importance value for saplings, adults, or all stems), we used the best fit model to initialize new models with different input data and tested for differences in species composition using Mantel tests using the “ade4” package in R (Dray & Dufour, 2007). After identifying the best-fit model from the T1 data, we used the posterior distributions to initialize the T2 model. Doing so allowed the species composition of the communities to begin aligned with the T1 communities but then progressively change to fit the T2 data, reflecting the way that communities naturally change over time. We compared species composition between T1 and T2 to identify communities that changed dominant species or lost/gained species.

To visualize the distribution of identified communities and calculate measures of community change over time, we aggregated our results to the 1452 km² hexagon tessellation (**Fig S3.1**) by taking the average community proportion across all plots within a hexagon. We then created regional forest community maps for T1 and T2 by mapping the community with the highest

proportion in each hexagon. We used these maps to identify hexagons where the dominant community type changed between T1 and T2 and create a transition matrix containing the proportion of hexagons changing from one dominant community type to another over the study period. Non-forested areas were masked out using the 2011 National Land Cover Database for visualization purposes only (<https://www.mrlc.gov/data>). A GIS shape file with the posterior distribution of communities in each hexagon and a spreadsheet of the posterior distribution of species in each community are available at <https://www.doi.org/10.4231/GCE5-ZY59>.

3.3.3 Climate and non-climate forest condition data

The PRISM climate dataset (4 km resolution) was used to create climate normals for 30 years leading up to the T1 FIA sampling (1951-1980, hereafter, “historic climate conditions”) and 30 years during the study period (1986-2015, hereafter, “study period conditions”; PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu/>). The PRISM dataset contains monthly mean, maximum, and minimum temperature, and monthly accumulated precipitation. We calculated the mean of monthly mean temperature (MAT), the minimum of monthly minimum temperature (TMIN), the maximum of monthly maximum temperature (TMAX), and the sum of monthly precipitation (TAP) across the twelve months in each year. We also calculated climate variability by taking the standard deviation (SD) of monthly precipitation (PSD), SD of monthly minimum temperature (TMINS), SD of monthly maximum temperature (TMAXSD), and temperature range (annual maximum temperature minus annual minimum temperature, TRANGE). Therefore, TRANGE, TMINS, and TMAXSD are measures of seasonal temperature variability, and PSD is a measure of seasonal precipitation variability. Temperature and precipitation conditions are closely linked to drought severity (Hu & Willson, 2000; McEwan, Dyer, & Pederson, 2011), so we used Palmer Drought Severity Index (PDSI) data (from the same two periods, 1951-1980 and 1986-2015) to test whether drought severity was a better predictor of community change than the PRISM-derived temperature and precipitation variables (available at <https://wrcc.dri.edu/wwdt/>). Then, we averaged each variable across 30 years before and during the study period (1951-1980 and 1986-2015, respectively). We calculated the difference between historic climate conditions and study period conditions for each variable to use as indicators of climate change (hereafter, “climate change variables”).

A variety of non-climate factors can influence forest dynamics, and we aimed to test forest developmental stage, nitrogen deposition, and fire frequency as potential drivers of community change (hereafter, “non-climate variables”). As we do not have reliable information on tree or stand age, we used hexagon-level total basal area (BA) at T1 (across all species in all plots in each hexagon) as a proxy for forest developmental stage following Fei et al. (2017). We also calculated hexagon-level total basal area at T2 and took the difference between T1 and T2 as a measure of forest development over the study period. Nitrogen deposition data (NDEP) during a portion of the study period (2000-2015) were aggregated at the hexagon level (available at <http://nadp.slh.wisc.edu/>) following Jo, Fei, Oswalt, Domke, and Phillips (2019). We used the kernel density tool in ArcGIS (V.10.4, Esri Inc., USA) on fire occurrence point data during a majority of the study period (1992-2015) as a proxy for fire frequency within each hexagon (Jo et al., 2019; Short, 2017). We natural-log transformed fire frequency (LOG(FIRE)) to normalize the predictor. Maps of predictor variables are available in **Fig S3.2**.

3.3.4 Analysis of individual community changes over time

To assess changes in the distribution of communities over time, we computed a proportion-weighted community centroid and community area for T1 and T2. We used the proportion of the community in each hexagon to weight the XY coordinates of the hexagon centroid, and took the difference in community centroid between the two time periods to assess distance and direction of movement of the centroid (following Fei et al., 2017). This approach allowed shifts in abundance within the community to influence the community’s centroid, even if the spatial extent did not change. We assessed the significance of the change in latitude, longitude, and overall shift distance using randomization tests by randomly disassociating the XY coordinates with the community proportion and recalculating the centroid shifts. We then repeated the randomization process 1000 times and calculated a *P* value for each community (i.e., the proportion of random shifts larger than the observed shift). All *P* values were corrected for multiple testing using the Benjamini-Hochberg method (P_{BH}) (Benjamini & Hochberg, 1995), and shifts were considered significant when $P_{BH} \leq 0.05$. We also assessed changes in community spatial coverage by weighting the hexagon area by the community proportion at T1 and T2. We used randomization tests to assess the significance of changes in community area by randomly reassigning community proportions to T1 or T2 and recalculating the difference in proportion-weighted area between the randomly

assigned T1 and T2 groups. This process was repeated 1000 times to test how extreme the observed expansions or contractions were relative to random increases or decreases in area.

For each community, we tested if climate change predicts shifts in its distribution. We first calculated the relative frequency of the community under each of the nine historic climate conditions (eight PRISM-derived variables and PDSI). Then, a kernel density tool (density.default in the “stats” package in R) (R Core Team, 2019) was used to create a smoothed probability of occurrence distribution across each of the historic climate conditions. Locations with study period conditions within the range of observed historic climate conditions were assigned the corresponding probability of occurrence for each of the eight PRISM climate variables and PDSI. The probability of occurrence was averaged across the nine variables to generate a probability of occurrence in each hexagon for each community based solely on climate. Then, we calculated the climate-predicted centroids for the communities by weighting each hexagon’s XY coordinates by the probability of occurrence and compared these centroids to the observed T2 centroids.

3.3.5 Analysis of change across communities

The communities in each hexagon are compositional data; that is, the proportion of all communities in a hexagon sums to one, which leads to lack of independence between the communities (i.e., if the proportion of $k-1$ out of the k communities is known, the proportion of the k th community can be derived as 1 minus the sum of the $k-1$ community proportions). To reduce the issue of violating independence and identify which forest regions are changing the most, we calculated the Jensen-Shannon Divergence (JSD; Hall, Jurafsky, & Manning, 2008; Lin, 1991) between the k -dimensional community composition at T1 and T2 using the “philentropy” package in R (Drost, 2018). JSD is a measure of dissimilarity between compositional data or probability distributions based on Kullback-Liebler divergence (Lin, 1991). It is calculated by taking the Shannon entropy of the average of the T1 and T2 community proportions and subtracting the average of the Shannon entropy of T1 and T2 community proportions: $JSD = H\left(\frac{X_{T1} + X_{T2}}{2}\right) - \frac{H(X_{T1}) + H(X_{T2})}{2}$, where H is the Shannon entropy: $H = -\sum_i p_i \log_2 p_i$, and X_{T1} and X_{T2} are vectors of community proportions in a hexagon at T1 and T2, respectively (Lin, 1991). We then square root transformed JSD to calculate Jensen-Shannon Distance ($JSD_{T1,T2}$), which is a distance metric that is symmetric and approximately normal, but bounded by $[0, 1]$ (Lin, 1991).

To test the importance of drivers of community composition, we modeled $JSD_{T1,T2}$ as a function of initial climate conditions, climate change variables, and non-climate variables. Theoretically, $JSD_{T1,T2}$ is approximately normal but bounded by $[0,1]$; however, we found that our measures of $JSD_{T1,T2}$ were slightly right skewed, so we fit generalized linear mixed-effects models (GLMMs) with a beta distribution and logit link (which better fits our $JSD_{T1,T2}$ values) using the “glmmTMB” package in R (Brooks et al., 2017). Due to collinearity between predictor variables (**Fig S3.2**), we fit each model with two predictor variables: the historic climate condition and the change between historic and study period conditions. Fire frequency and nitrogen deposition only contained data during the study period, so we fit these GLMMs as univariate models. ANOVA revealed significant differences in $JSD_{T1,T2}$ across the 12 communities ($F_{11,1801} = 15.93, P < 0.001$), so we included random slopes and a random intercepts for the dominant community at T1 in our GLMMs. However, models that included random slopes failed to converge (due to some communities being dominant in only a few hexagons), so we used a random intercept only. Since the predictor variables were standardized, coefficient values are a measure of effect size: a predictor with a larger coefficient value indicates that it more strongly influences the response. A total of 1757 hexagons were used in the GLMMs due to hexagons with missing climate and non-climate data (hexagons with missing data outlined in **Fig 3.4**). All analyses were conducted in R version 3.6.1 (R Core Team, 2019), and all maps were projected to Albers Equal Area Conic projection. A full list of R packages used in these analyses is available in **Table S3.3**.

3.4 Results

3.4.1 Assessment of communities identified by LDA

Using the LDA model on Forest Inventory and Analysis data, we identified 12 dominant forest communities in the eastern U.S. (**Table 3.1, Fig 3.1**). Model selection via an iterative approach identified a candidate set of models with values of k , the number of communities in the model, ranging from 12 to 43 (out of possible k values from 2 to 50). However, when we applied an ecologically based metric, the number of species with proportion in the community $>1/n_{\text{species}}$ ($>1/85$), the $k = 12$ community model was chosen because it did not include any communities comprised of only one species. Models with varying inputs (relative density, relative basal area, and importance value for saplings, trees, and all stems) generally agreed in species composition

and were not significantly different from one another (Mantel test correlation $r > 0.99$, $P < 0.01$ for all tests). Therefore, results shown are based on the model including importance value of all stems; it was the most generalized community, incorporating density, basal area, and all size classes.

Since the LDA model does not incorporate spatial constraints on the communities, clustering of communities in a specific region would indicate the model is generating meaningful communities. Indeed, the observed communities were centered on a specific geographic region (**Figs 3.1 and S3.3**). Likewise, we used the species composition of each community to assess if it aligned with previous knowledge of the forest communities in these different regions. We found similarities between our communities and those from Braun (1950), Dyer (2006), and Costanza et al. (2017) (see Discussion) indicating the that LDA model was identifying meaningful ecological communities. The spatial and ecological consistency of the communities indicated that further analysis using communities as a unit was justified.

3.4.2 Community compositional shift between T1 and T2

Generally, communities were identifiably similar between T1 and T2, and correlation tests revealed significant correlation between T1 and T2 species composition for all communities ($r = 0.67-0.99$, $P < 0.001$ for all tests). Three main community groups were observed in terms of their compositional shifts, although the groupings are not mutually exclusive. The first group of communities (Communities 5, Oak-hickory; 6, Beech-maple; 8, Yellow poplar-oak; 9, Red maple; 10, Poplar-aspen; and 12, Spruce-tamarack) remained stable over the study period, with only minor shifts in species composition or gain/loss of minor component species (**Table 3.1**). For example, Community 6 (Beech-maple) only lost the bottom two species in the community and had no changes in dominance, and Community 9 (Red maple) had very minor changes in the relative proportion of red maple (*Acer rubrum*) vs. willow species (*Salix* species). The second group of communities (Communities 2, Central woodlot; 7, Pine-sweetgum; and 11, Southern lowland) gained or lost major species over time. Community 11 (Southern lowland) gained oak species (*Quercus nigra*, *Quercus laurifolia*, and *Quercus virginiana*) from Community 7 (Pine-sweetgum), and Community 2 (Central woodlot) lost Virginia pine (*Pinus virginiana*), the second highest proportion species in Community 2 at T1. All other communities except Communities 1 (Cherry-oak) and 9 (Red maple) gained or lost species; however, these gains and losses were generally a

minor component of the community. The third community group (Communities 1, Cherry-oak; 4, Pine-sweetgum; and 11, Southern lowland) shifted the dominant species in the community. For example, Community 1 (Cherry-oak) switched from being dominated by red oak (*Quercus rubra*) to being dominated by cherry species (*Prunus* species), and Community 4 (Pine-tupelo-oak) switched from being dominated by shortleaf pine (*Pinus echinata*) to being dominated by blackgum (*Nyssa sylvatica*). The most dramatic shift in species composition occurred in Community 11 (Southern lowland) which switched from being dominated by slash pine (*Pinus elliottii*) to a species new in the community, water oak (*Quercus nigra*).

3.4.3 Shifts in communities' spatial distributions

We found that there was large variability in the distance communities shifted over the last three decades. Compared to the species-level (i.e., observed shifts from Fei, et al. 2017), community-level shifts in spatial distribution were relatively short, ranging from 3.6 to 24.6 km dec⁻¹ with a median of 8.0 km dec⁻¹ (**Table 3.2**). All communities had significant shift distances when tested with randomization tests (**Fig 3.2a**). The forest community with the largest spatial shift, Community 11 (Southern lowland), was centered in the Southern Pine Hardwood Region (SPHR). This community shifted its centroid 24.6 km dec⁻¹ to the southwest (Benjamini-Hochberg adjusted P value, $P_{BH} < 0.001$). Communities 2 (Central woodlot), 3 (Conifer-birch), and 4 (Pine-tupelo-oak) also had relatively large shift distances (24.2, 21.2, and 21.5 km dec⁻¹, respectively, $P_{BH} < 0.001$ for all three communities) (**Table 3.2**). The community with the smallest shift, Community 1 (Cherry-oak) had a marginally significant southeastward shift (3.6 km dec⁻¹, $P_{BH} = 0.045$).

The shift direction also varied across the 12 communities (**Table 3.2, Fig 3.2b**). Half of the communities shifted eastward (five significant, Communities 1, Cherry-oak, 2.8 km dec⁻¹, $P_{BH} = 0.035$; 3, Conifer-birch, 21.2 km dec⁻¹, $P_{BH} < 0.001$; 4, Pine-tupelo-oak, 11.3 km dec⁻¹, $P_{BH} < 0.001$; 5, Oak-hickory, 2.5 km dec⁻¹, $P_{BH} = 0.035$; and 8, Yellow poplar-oak, 3.7 km dec⁻¹, $P_{BH} = 0.015$) and the other half shifted westward (five significant, Communities 2, Central-woodlot, 23.2 km dec⁻¹, $P_{BH} < 0.001$; 6, Beech-maple, 11.4 km dec⁻¹, $P_{BH} < 0.001$; 9, Red maple, 6.7 km dec⁻¹, $P_{BH} < 0.001$; 11, Southern lowland, 12.2 km dec⁻¹, $P_{BH} < 0.001$; and 12, Spruce-tamarack, 6.4 km dec⁻¹, $P_{BH} < 0.001$). A total of five communities shifted northward (four significant, Communities 2, Central woodlot, 6.9 km dec⁻¹, $P_{BH} = 0.002$; 4, Pine-tupelo-oak, 18.3 km dec⁻¹, $P_{BH} < 0.001$; 5, Oak-hickory, 5.8 km dec⁻¹, $P_{BH} < 0.001$; and 7, Pine-sweetgum, 8.6 km dec⁻¹, $P_{BH} < 0.001$), and

seven communities shifted southward (four significant, Communities 6, Beech-maple, 6.9 km dec^{-1} , $P_{BH} < 0.001$; 8, Yellow poplar-oak, 4.2 km dec^{-1} , $P_{BH} = 0.009$; 10, Poplar-aspen, 6.4 km dec^{-1} , $P_{BH} < 0.001$; and 11, Southern lowland, 21.4 km dec^{-1} , $P_{BH} < 0.001$).

Additionally, eight communities expanded their area of coverage, and four communities contracted their area of coverage (**Table 3.2**). Of the eight expansions, four communities significantly gained spatial coverage (Communities 1, Cherry-oak, $4578 \text{ km}^2 \text{ dec}^{-1}$, $P_{BH} = 0.03$; 9, Red maple, $3423 \text{ km}^2 \text{ dec}^{-1}$, $P_{BH} = 0.026$; 11, Southern lowland, $13,759 \text{ km}^2 \text{ dec}^{-1}$, $P_{BH} < 0.001$; and 12, Spruce-tamarack, $2903 \text{ km}^2 \text{ dec}^{-1}$, $P_{BH} = 0.003$), and of the four contractions, two communities significantly lost spatial coverage (Communities 4, Pine-tupelo-oak $-11,506 \text{ km}^2 \text{ dec}^{-1}$, $P_{BH} < 0.001$; and 5, Oak-hickory, $-17,089 \text{ km}^2 \text{ dec}^{-1}$, $P_{BH} < 0.001$) (**Table 3.2**). The largest increase in community area was Community 11 (Southern lowland), which increased by $13,759 \text{ km}^2 \text{ dec}^{-1}$, a 26.7% expansion in area ($P_{BH} < 0.001$). The largest decrease in area was Community 5 (Oak-hickory), which decreased by $17,089 \text{ km}^2 \text{ dec}^{-1}$, a 15.6% contraction in area ($P_{BH} < 0.001$). Community 2 (Central woodlot) had the smallest change in area, increasing by $175 \text{ km}^2 \text{ dec}^{-1}$ (0.2% expansion), and Community 6 (Beech-maple) had a similar decrease in area ($-205 \text{ km}^2 \text{ dec}^{-1}$, 0.2% contraction).

Observed T2 locations of communities were predicted well by climate conditions during the study period (**Fig S3.4a and S3.4b**) but shifts in the communities were smaller than predicted by climate change except for Community 6 (Beech-maple; **Fig 3.3**). Climate-predicted longitude was moderately associated with observed longitude of the 12 communities ($R^2 = 0.278$), and the slope of the association was no different than the 1:1 line (slope = 1.14, $P = 0.826$, **Fig S3.4a**). However, the relationship between observed and predicted latitude was very strong ($R^2 = 0.96$) and significantly smaller than the 1:1 line (slope = 0.84, $P < 0.001$, **Fig S3.4b**), indicating that the predicted locations are generally farther from the center of the study region than observed. In contrast, there were very low R^2 values between predicted and observed shifts in distance in latitude and longitude, with slopes close to 0 and far from the 1:1 line ($R^2 = 0.02$ and 0.05 , and slope = 0.047 and -0.06 for latitude and longitude, respectively, **Figs 3.3, S3.4c and S3.4d**). The map depicting observed and predicted shifts (**Fig 3.3**) showed many communities shifting different directions than predicted by climate change, and only three communities had the same observed and predicted shift direction (**Table 3.2**).

3.4.4 Across community responses to climate and non-climate factors

We assessed changes in all communities collectively across the study region to identify where forest communities are changing most rapidly and compare those areas to a variety of climate and non-climate factors. Areas in the southern portion of the study region tended to have the largest changes in community composition over time (i.e., the largest $JSD_{T1,T2}$; **Fig 3.4a**). Our GLMMs with climate and non-climate predictors of $JSD_{T1,T2}$ showed that eight PRISM-derived historic climate conditions were significant predictors of community change over time (TAP, PSD, MAT, TMAX, TMIN, TRANGE, TMAXSD, TMINSD; $P_{BH} < 0.001$ for all eight), but PDSI was only marginally significant ($P_{BH} = 0.047$; **Fig 3.4b**). Of the nine climate variables, only changes in temperature variability (TRANGE, TMINSD, TMAXSD; $P_{BH} < 0.001$ for all three) and MAT ($P_{BH} = 0.025$) were significant (**Fig 3.4b**). Of the non-climate variables we tested, only basal area (BA, a proxy for forest developmental stage) was significant ($P_{BH} < 0.001$ for initial BA and $P_{BH} = 0.004$ for change in BA). Areas that had forests that were initially older or that had increases in basal area (forests that progressively got older over the study period) tended to be more stable over time.

About one-quarter of hexagons showed turnover in the dominant community type in (24.6%, 446 out of 1813 hexagons, **Fig 3.5**), even though correlation tests revealed overall community composition was consistent between T1 and T2 across all 12 communities ($r = 0.80$ to 0.97 , $P < 0.001$ for all tests). The map of change in dominant community between T1 and T2 (**Fig 3.5a**) showed that areas changing from one community to another tended to occur along the boundaries of the T1 communities (e.g., along the northern and southern edges of Community 7, Pine-sweetgum, in the SPHR, or the boundary between Communities 8, Yellow poplar-oak, and 5, Oak-hickory, in the CHR). Hexagons dominated by Communities 3 (Conifer-birch), 7 (Pine-sweetgum), 11 (Southern lowland), and 12 (Spruce-tamarack) at T1 were most frequently classified under the same dominant community at T2 (86.2%, 90.0%, 91.5% and 100.0%, respectively) (**Fig 3.5b**).

3.5 Discussion

We showed that the LDA model works for identifying meaningful communities of co-occurring species at a regional scale. In general, the 12 communities aligned with previous studies of forest communities. The boundaries of our regional forest community maps (**Fig 3.1**) were

quite similar to those found in Dyer (2006) and Braun (1950). Similarly, the species composition and distribution of some of our communities aligned closely with those identified by Costanza et al. (2017). For example, the Balsam fir-quaking aspen community identified by Costanza et al. (2017) is similar in species composition and spatial distribution to Community 3 (Conifer-birch). A benefit of the LDA model is that it provides relative frequency of each forest community within each sample versus other methods that assign a single dominant community type to each sample (Valle et al., 2014). This allows for the analysis of community dynamics across the entire study area, including areas where a community is a minor component (e.g., community centroids were weighted by the community proportion in all hexagons, not just the hexagons where it was dominant). However, our maps in **Fig 3.1** and analysis of dominant community change (**Fig 3.5**) only indicate the community with the highest proportion in each hexagon sampling unit; that is, many samples contained multiple community types (median number of communities with proportion $>1/12$ in each hexagon = 4; minimum = 1; maximum = 8).

Given the wide range of responses to climate change at the species level (e.g., Fei et al., 2017; Woodall et al., 2009; Zhu et al., 2012), we expected to find communities responding to climate change with different spatial dynamics. For example, we found a wide range of spatial shifts, such as the Southern lowland community (Community 11) which had large southwest shift and large increase in area versus Communities 1 (Cherry-oak) and 8 (Yellow poplar-oak) which had highly stable spatial distributions (both showing marginally significant southeastern shifts and small increases in area). The dramatic shifts in Community 11 are likely due to increases in the slash pine (*Pinus elliottii*) component of this community in this region (Fox, Jokela, & Allen, 2007; Knott, Desprez, Oswalt, & Fei, 2019) and the addition of *Quercus* species over the study period. On the other hand, Communities 1 (Cherry-oak) and 8 (Yellow poplar-oak) have contrasting mechanisms for stability: the Cherry-oak community is most commonly found as a mid-to-late successional component of forests in the CHR and NHR versus the Yellow poplar-oak community which is dominated by yellow poplar (*Liriodendron tulipifera*), a disturbance dependent species that can grow under a wide range of conditions and create a stable community where it dominates multi-tree canopy openings (Burns & Honkala, 1990).

In addition to variability in the spatial dynamics of the communities, we also expected to find variability in the amount of changes to the species composition of the communities. Again, Community 11 (Southern lowland) was most dynamic, gaining oak species (*Quercus nigra*, *Quercus laurifolia*, and *Quercus virginiana*) at T2 from Community 7 (Pine-sweetgum). On the

other hand, Communities 6 (Beech-maple) and 9 (Red maple) were highly stable in species composition. While they both had significant spatial shifts (indeed, Community 6 was the only community that shifted farther than climate predicted), the stability of their species composition is not surprising given that Beech-maple forests are considered to be a climax community (Braun, 1950) and red maple (*Acer rubrum*) has consistently increased over recent decades (Fei & Steiner, 2007).

The strongest predictors of community change over time were related to historic climate conditions and changes in seasonal temperature variability. In general, forests that had the greatest changes in community composition tended to have wetter and warmer historic climate, higher precipitation variability, or lower seasonal temperature variability (**Fig 3.4b**). In addition, forests that decreased in seasonal temperature variability over the study period tended to have larger changes over time. Measures of precipitation change were not significant in relationship to community spatial shifts despite species-level migration in response to precipitation change (Fei et al., 2017), and measures of temperature change (MAT) were less significant than measures of temperature variability change. The nature of the relationship between seasonal temperature variability and $JSD_{T1,T2}$ (areas with larger climate variability and areas that increased in climate variability led to more stable communities) generally supports the hypothesis that fluctuations in temperature can act as stabilizing processes in vegetation dynamics (Lloret, Escudero, Iriondo, Martínez-Vilalta, & Valladares, 2012).

Although the non-climate variables we tested play an important role in local forest dynamics, they generally lack strong relationships with community change at the regional scale (the largest of three scales studied in this research), which aligns with the view of Ricklefs (1987) that regional-scale processes are more important than local-scale processes. Fire frequency is often considered an important disturbance metric in forest ecosystems, especially at the stand level (Briggs, Knapp, & Brock, 2002; Hutchinson, Sutherland, & Yaussy, 2005; Nowacki & Abrams, 2008), but was found to have little effect on the overall changes to forest communities at the regional scale (**Fig 3.4b**). In addition, nitrogen deposition was found to have a non-significant effect on forest community change despite the regulatory influence of the nitrogen and carbon cycles—and the mycorrhizal communities that influence these cycles—in forest ecosystems (Jo et al., 2019; Lovett, Weathers, & Arthur, 2002; Pellegrini et al., 2017). Areas with initially higher total basal area or that gained basal area—generally associated with older forests—were found to be more stable over time, consistent with comparisons of old-growth forests to younger forests

(Fralish, Crooks, Chambers, & Harty, 1991); however the relationship was weaker than the effect of climate.

Previous studies at the local scale have shown dramatic within-site turnover in forest communities as a response to climate change (Feeley, Davies, Perez, Hubbell, & Foster, 2011; Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010; Ozier, Groninger, & Ruffner, 2006). At the regional scale, about 25% of the study region experienced turnover in the dominant community (**Fig 3.5**), with some communities losing dominance at higher rates than other communities. This trend was also indicated by the significant community shift distances but lack of directionality—as one community moves out of an area, another fills in behind, leading to a lack of consistent directional shifts.

The rate of change in communities is likely lagging behind climate change. Although we showed many dramatic changes in species composition, spatial distribution, and turnover in dominant community type, climate change outpaced the rate of community migration (**Fig 3.3**). However, this is not surprising since there are expected to be significant time lags between climate change and community-level responses (Bertrand et al., 2011). It is possible that communities have not yet accumulated enough species-level responses (e.g., increased mortality in unsuitable areas or differential recruitment rates across the region) to produce a community-wide response to climate change, especially over a relatively short study period. Our study encompassed three decades of forest inventory data, but more direct response to climate change may emerge when considering a longer time interval.

A second reason for climate lags is the resilience of complex systems. Generally, with increased complexity there is a greater resilience to stressors (Loreau et al., 2001; Symstad et al., 1998). With these complex communities comprised of multiple species, it is likely that species with large responses are balanced out by others with small responses, and the diversity and plasticity of traits within a community can allow it to compensate for climate change. Additionally, climate effects may be masked out by other unaccounted factors such as trait variability (e.g., variation in the dispersal ability of the component species), invasive species, and disturbances (such as deer browse and land use change) that differentially affect communities (Côté, Rooney, Tremblay, Dussault, & Waller, 2004; Jo, Potter, Domke, & Fei, 2018; Knott et al., 2019; Oswalt et al., 2015).

There are a few caveats of our study that need to be considered, especially when utilizing the results of our study for management and extrapolation to other regions. First, our results are

aggregated to a larger scale (i.e., the 1452 km² hexagon tessellation) than most management occurs. This is important for managers who intend to use our results as an indicator of changes beyond their local plot-level observations. Managers should consider the dynamics of the various regional communities represented in their forests when making decisions, but they also should recognize that the trends in regional forest communities may not always reflect the variability in local-scale forest dynamics. Second, it is also important to consider the location of our study. Forest communities near the coast (hard boundaries) may tend to shift inland, and forest communities along the soft boundaries of our study area (i.e., Canada and the central U.S.) may have shifted into these regions but are not observable in the FIA data used in this study. Likewise, our analysis of climate-predicted shifts was limited to climate data within the study region boundaries, and it is likely that some communities (especially those near the Canadian border) will find suitable climate outside of the study area. However, many of the northern communities did not move as far north as predicted by climate change even when limited to the study area, so extending our modeling approach to include potentially suitable climate in Canada might further increase the divergence between observed and predicted shifts. Finally, although we found many significant shifts in eastern U.S. communities, communities in other locations (e.g., in other parts of North America or on other continents) may be more or less stable than found in our study area; however, to our knowledge, there have not been studies similar to ours in other areas of North America or globally.

The consistently significant shifts in forest communities can serve as a warning sign of the continued impact of anthropogenic activities. Although we detected changes in forest communities within three decades that surpasses rates of change observed during times of historic climate change (e.g., century to millennium time scales of post-glaciation migration; Davis, 1983), climate change is currently outpacing the rate of community migration. Forest communities not only migrated shorter distances than climate change predicted, but also shifted in directions opposite of climate change. This is alarming in that forest communities are unable to keep up with neither the pace nor direction of climate change. Future analyses incorporating individual species traits within a community can help elucidate the susceptibility of certain ecosystem functions to climate change. In addition, understanding other potential threats to forest communities, such as invasive species, specific management practices, and other climate-related factors, can help further quantify the sustainability of forest ecosystems and the services they provide. Nevertheless, our analysis presents one of the first attempts at quantifying the redistribution of regional forest

communities, and our results can aid in the monitoring and management of forest ecosystems in a rapidly changing global environment.

Data Accessibility

The original FIA data used in this project are available through the USDA Forest Service (<https://www.fia.fs.fed.us/>). The climate data are available through the PRISM Climate Group, Oregon State University (for temperature and precipitation; <http://prism.oregonstate.edu/>) and the West Wide Drought Tracker (for PDSI; <https://wrcc.dri.edu/wwdt/>). Nitrogen deposition data are available from the National Atmospheric Deposition Program <http://nadp.slh.wisc.edu/>), and fire frequency data are available from Short (2017). More details about the publicly available data are in Methods Sections 3.3.2 and 3.3.3. GIS shapefiles of the hexagon-level output for mapping individual communities or creating maps of the top communities and a full list of community species compositions are available through the Purdue University Research Repository (PURR, <https://www.doi.org/10.4231/GCE5-ZY59>).

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3.6 Figures and Tables

Table 3.1 Top species in each community at the two sampling periods. Species are only included if their proportion is $>1/n_{\text{species}}$ ($>1/85$). Species proportion in each community in parentheses. Asterisks indicate species that were present in the community at one sampling period but not the other.

Community	Time	Species
1: Cherry-oak	T1	<i>Quercus rubra</i> (0.360), <i>Prunus</i> spp. (0.286), <i>Pinus strobus</i> (0.177), <i>Tsuga canadensis</i> (0.126), <i>Betula lenta</i> (0.051)
	T2	<i>Prunus</i> spp. (0.318), <i>Quercus rubra</i> (0.238), <i>Pinus strobus</i> (0.216), <i>Tsuga canadensis</i> (0.148), <i>Betula lenta</i> (0.081)
2: Central woodlot	T1	<i>Ulmus</i> spp. (0.346), <i>Pinus virginiana</i> (0.117)*, <i>Sassafras albidum</i> (0.095), <i>Quercus laevis</i> (0.069)*, <i>Celtis</i> spp. (0.061), <i>Robinia pseudoacacia</i> (0.054), <i>Juglans nigra</i> (0.046), <i>Acer negundo</i> (0.043), <i>Platanus occidentalis</i> (0.034), <i>Cercis canadensis</i> (0.032), <i>Acer saccharinum</i> (0.029), <i>Quercus muehlenbergii</i> (0.021), <i>Gleditsia triacanthos</i> (0.014), <i>Populus deltoides</i> (0.013), <i>Maclura pomifera</i> (0.012)
	T2	<i>Ulmus</i> spp. (0.382), <i>Celtis</i> spp. (0.108), <i>Acer negundo</i> (0.088), <i>Juglans nigra</i> (0.072), <i>Sassafras albidum</i> (0.067), <i>Robinia pseudoacacia</i> (0.052), <i>Platanus occidentalis</i> (0.047), <i>Acer saccharinum</i> (0.040), <i>Cercis canadensis</i> (0.036), <i>Quercus muehlenbergii</i> (0.025), <i>Gleditsia triacanthos</i> (0.023), <i>Maclura pomifera</i> (0.023), <i>Populus deltoides</i> (0.020), <i>Quercus imbricaria</i> (0.012)*
3: Conifer-birch	T1	<i>Abies balsamea</i> (0.343), <i>Betula papyrifera</i> (0.260), <i>Thuja occidentalis</i> (0.183), <i>Populus grandidentata</i> (0.096), <i>Picea glauca</i> (0.052), <i>Picea rubens</i> (0.046), <i>Betula alleghaniensis</i> (0.021)
	T2	<i>Abies balsamea</i> (0.371), <i>Thuja occidentalis</i> (0.131), <i>Betula alleghaniensis</i> (0.113), <i>Betula papyrifera</i> (0.106), <i>Picea rubens</i> (0.098), <i>Populus grandidentata</i> (0.075), <i>Picea glauca</i> (0.059), <i>Acer pensylvanicum</i> (0.048)*
4: Pine-tupelo-oak	T1	<i>Pinus echinata</i> (0.316), <i>Nyssa sylvatica</i> (0.235), <i>Pinus palustris</i> (0.195), <i>Quercus falcata</i> (0.165), <i>Diospyros virginiana</i> (0.066), <i>Quercus lyrata</i> (0.022)
	T2	<i>Nyssa sylvatica</i> (0.318), <i>Pinus echinata</i> (0.199), <i>Pinus palustris</i> (0.179), <i>Quercus falcata</i> (0.163), <i>Diospyros virginiana</i> (0.074), <i>Quercus lyrata</i> (0.031), <i>Quercus laevis</i> (0.030)*
5: Oak-hickory	T1	<i>Carya</i> spp. (0.302), <i>Quercus alba</i> (0.294), <i>Quercus velutina</i> (0.160), <i>Quercus stellata</i> (0.134), <i>Juniperus virginiana</i> (0.076), <i>Quercus marilandica</i> (0.035)*
	T2	<i>Carya</i> spp. (0.322), <i>Quercus alba</i> (0.287), <i>Juniperus virginiana</i> (0.144), <i>Quercus velutina</i> (0.123), <i>Quercus stellata</i> (0.114)
6: Beech-maple	T1	<i>Acer saccharum</i> (0.372), <i>Fraxinus</i> spp. (0.302), <i>Fagus grandifolia</i> (0.120), <i>Tilia</i> spp. (0.078), <i>Ostrya virginiana</i> (0.066), <i>Betula alleghaniensis</i> (0.045)* <i>Acer pensylvanicum</i> (0.014)*
	T2	<i>Acer saccharum</i> (0.351), <i>Fraxinus</i> spp. (0.310), <i>Fagus grandifolia</i> (0.182), <i>Ostrya virginiana</i> (0.093), <i>Tilia</i> spp. (0.065)
7: Pine-sweetgum	T1	<i>Pinus taeda</i> (0.472), <i>Liquidambar styraciflua</i> (0.298), <i>Quercus nigra</i> (0.108)*, <i>Quercus laurifolia</i> (0.054)*, <i>Quercus virginiana</i> (0.027)*, <i>Quercus phellos</i> (0.027), <i>Quercus pagoda</i> (0.015)*
	T2	<i>Pinus taeda</i> (0.674), <i>Liquidambar styraciflua</i> (0.301), <i>Quercus phellos</i> (0.026)
8: Yellow poplar-oak	T1	<i>Liriodendron tulipifera</i> (0.279), <i>Quercus prinus</i> (0.186), <i>Pinus banksiana</i> (0.162), <i>Pinus resinosa</i> (0.118), <i>Oxydendrum arboreum</i> (0.112), <i>Quercus coccinea</i> (0.109), <i>Pinus rigida</i> (0.023)
	T2	<i>Liriodendron tulipifera</i> (0.330), <i>Quercus prinus</i> (0.178), <i>Pinus resinosa</i> (0.131), <i>Oxydendrum arboreum</i> (0.092), <i>Pinus virginiana</i> (0.084)*, <i>Quercus coccinea</i> (0.080), <i>Pinus banksiana</i> (0.066), <i>Pinus rigida</i> (0.024)

Table 3.1 continued

9: Red maple	T1	<i>Acer rubrum</i> (0.964), <i>Salix</i> spp. (0.036)
	T2	<i>Acer rubrum</i> (0.959), <i>Salix</i> spp. (0.041)
10: Poplar-aspen	T1	<i>Populus tremuloides</i> (0.804), <i>Populus balsamifera</i> (0.105), <i>Quercus macrocarpa</i> (0.091),
	T2	<i>Populus tremuloides</i> (0.715), <i>Quercus macrocarpa</i> (0.121), <i>Populus balsamifera</i> (0.069), <i>Betula papyrifera</i> (0.056)*, <i>Fraxinus</i> spp. (0.038)*
11: Southern lowland	T1	<i>Pinus elliotii</i> (0.539), <i>Magnolia virginiana</i> (0.114), <i>Taxodium ascendens</i> (0.101), <i>Pinus serotina</i> (0.078), <i>Taxodium distichum</i> (0.051), <i>Persea borbonia</i> (0.049), <i>Nyssa aquatica</i> (0.041), <i>Gordonia lasianthus</i> (0.023)
	T2	<i>Quercus nigra</i> (0.302)*, <i>Pinus elliotii</i> (0.279), <i>Quercus laurifolia</i> (0.108)*, <i>Magnolia virginiana</i> (0.075), <i>Taxodium ascendens</i> (0.049), <i>Taxodium distichum</i> (0.047), <i>Quercus virginiana</i> (0.042)*, <i>Persea borbonia</i> (0.030), <i>Nyssa aquatica</i> (0.028), <i>Gordonia lasianthus</i> (0.020), <i>Pinus serotina</i> (0.019)
12: Spruce-tamarack	T1	<i>Picea mariana</i> (0.383), <i>Larix laricina</i> (0.213), <i>Carpinus caroliniana</i> (0.212), <i>Ilex opaca</i> (0.102), <i>Quercus michauxii</i> (0.025), <i>Betula populifolia</i> (0.024), <i>Quercus palustris</i> (0.020)
	T2	<i>Picea mariana</i> (0.274), <i>Carpinus caroliniana</i> (0.220), <i>Larix laricina</i> (0.195), <i>Ilex opaca</i> (0.137), <i>Quercus pagoda</i> (0.072)*, <i>Betula populifolia</i> (0.026), <i>Quercus palustris</i> (0.023), <i>Quercus shumardii</i> (0.021)*, <i>Quercus michauxii</i> (0.020)

Table 3.2 Shifts in forest communities over the last three decades. Shifts were measured by movement of community centroid and changes in community spatial coverage. Positive values of latitude and longitude shift represent northward and eastward movement, respectively; conversely, negative values represent southward and westward movement. Predicted direction based on expected shifts due to climate change (bolded communities had the same observed and predicted shift direction). Percentage change in area in parentheses. Asterisks indicate significant Benjamini-Hochberg adjusted P values (P_{BH}) when tested by randomization tests: * $P_{BH} \leq 0.05$; ** $P_{BH} \leq 0.01$; *** $P_{BH} \leq 0.001$.

Community	Lat. shift (km dec ⁻¹)	Lon. shift (km dec ⁻¹)	Observed direction	Predicted direction	Dist. shift (km dec ⁻¹)	Area change (km ² dec ⁻¹)
1: Cherry-oak	-2.3	2.8*	Southeast	Northwest	3.6*	4578* (+7.1%)
2: Central woodlot	6.9**	-23.2***	Northwest	Northeast	24.2***	175 (+0.2%)
3: Conifer-birch	0.2	21.2***	Northeast	Northwest	21.2***	1259 (+2.5%)
4: Pine-tupelo-oak	18.3***	11.3***	Northeast	Northeast	21.5***	-11506*** (-18.5%)
5: Oak-hickory	5.8***	2.5*	Northeast	Northeast	6.3***	-17089*** (-15.6%)
6: Beech-maple	-6.9***	-11.4***	Southwest	Northeast	13.3***	-205 (-0.2%)
7: Pine-sweetgum	8.6***	-3.1	Northwest	Northeast	9.1***	1830 (+1.8%)
8: Yellow poplar-oak	-4.2**	3.7*	Southeast	Southwest	5.6***	2878 (+5.0%)
9: Red maple	-1.7	-6.7***	Southwest	Northwest	6.9***	3423* (+5.1%)
10: Poplar-aspen	-6.4***	+0.0	Southeast	Northeast	6.4***	-2005 (-4.7%)
11: Southern lowland	-21.4***	-12.2***	Southwest	Southwest	24.6***	13759*** (+26.7%)
12: Spruce-tamarack	-2.3	-6.4***	Southwest	Northwest	6.8***	2903** (+7.7%)

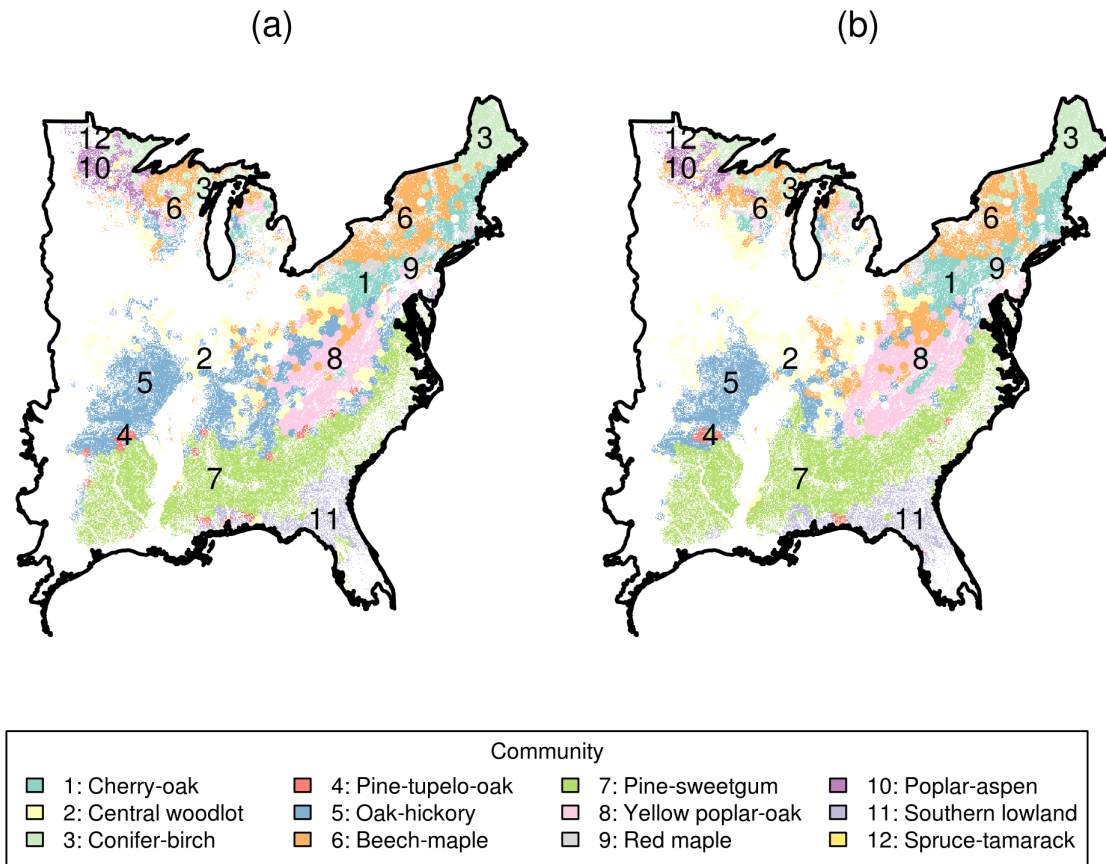


Fig. 3.1 Maps of 12 regional forest communities across the eastern U.S. Hexagon sampling units are mapped according to the community with the highest proportion in each hexagon at (a) T1 and (b) T2. Non-forested areas are masked out by the 2011 National Land Cover Database for visualization purposes only (<https://www.mrlc.gov/data>). Community 12 (Spruce-tamarack) was the dominant community in only eight hexagons at T1 and 11 hexagons at T2 and therefore does not show clearly on the maps. Maps are projected to Albers Equal Area Conic projection. Species composition of the 12 communities can be found in **Table 3.1**, and map showing the difference between T1 and T2 can be found in **Fig 3.5**. GIS shapefiles of these maps available for download from <https://www.doi.org/10.4231/GCE5-ZY59>.

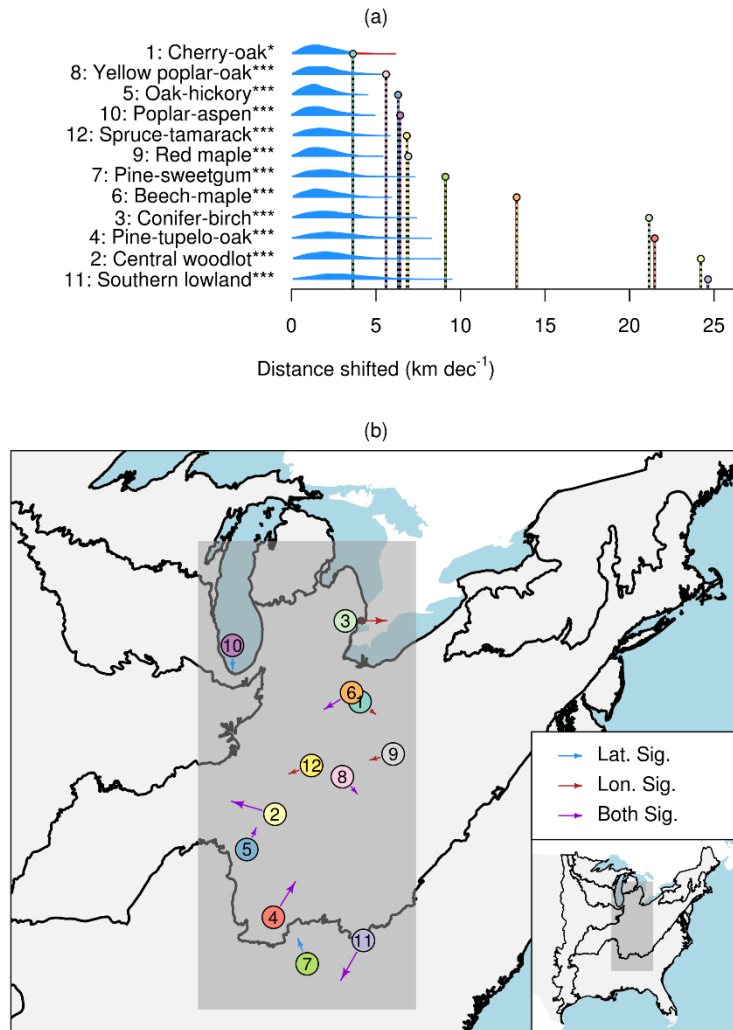


Fig. 3.2. Centroid shift of forest communities. (a) Frequency distribution of randomized centroid shifts (blue area) and observed shift distance (dashed lines). Proportion of frequency distribution greater than observed shift distance in red. Asterisks indicate significant Benjamini-Hochberg adjusted P values (P_{BH}): * $P_{BH} \leq 0.05$; ** $P_{BH} \leq 0.01$; *** $P_{BH} \leq 0.001$. (b) Direction and distance of forest community shifts. Arrow colors represent significance of distribution shifts. Map is projected to Albers Equal Area Conic projection, and inset map shows location displayed relative to the study area (white areas included for display purposes only).

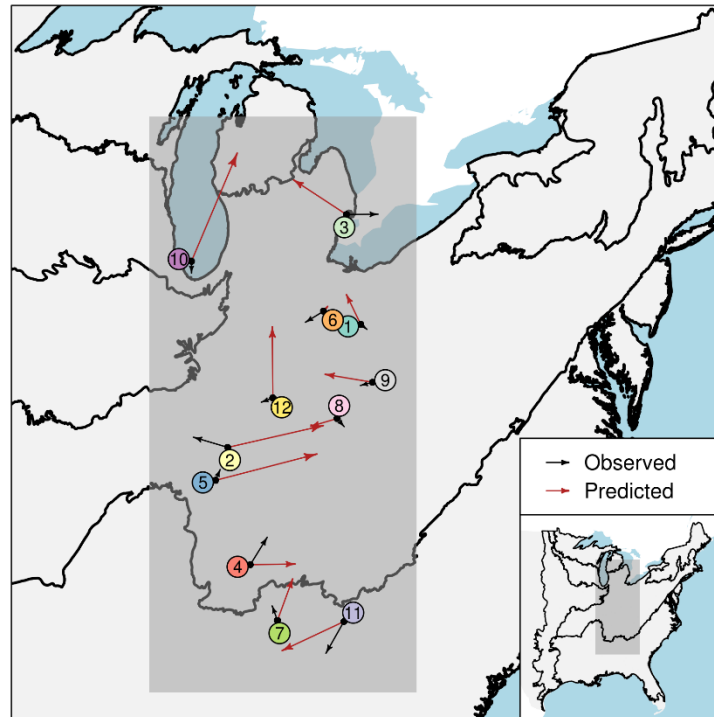


Fig. 3.3. Predicted vs. observed shifts in forest communities. Black dots represent community centroids at T1, and arrows represent climate-predicted (red) and observed (black) shifts in community centroid. All predicted shifts are larger than observed shifts except Community 6 (Beech-maple). Inset map indicates location of community centroids within the study area. White areas outside of study area included for display purposes only. Map is projected to Albers Equal Area Conic projection. See **Fig 3.2** for significance of observed community shifts.

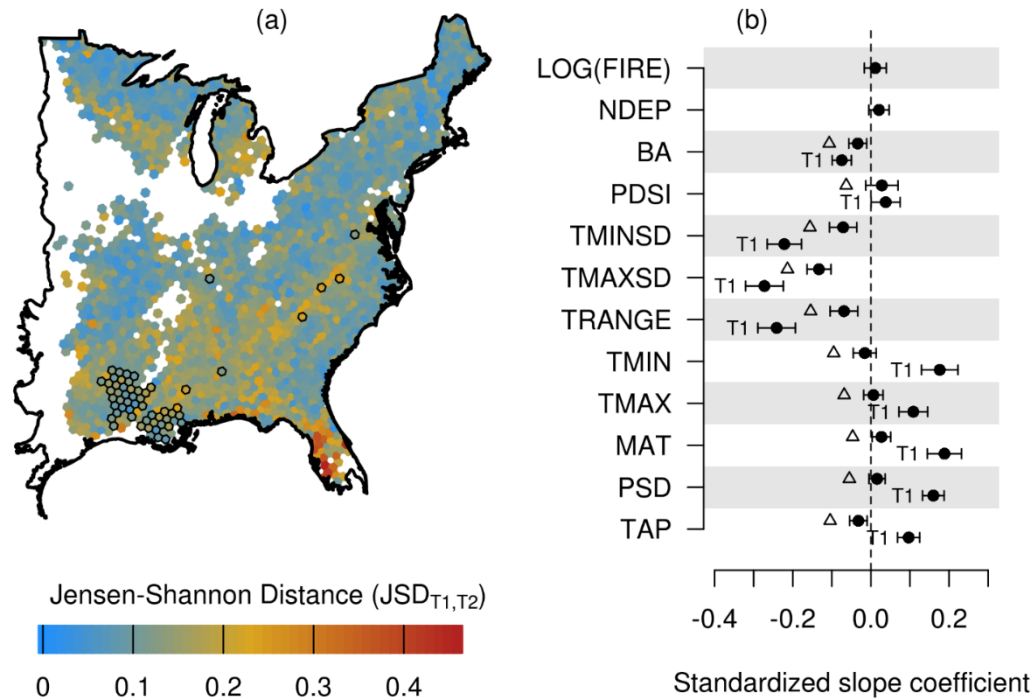


Fig. 3.4 Changes in forest communities and associated factors. (a) Response variable from GLMMs: change in community composition measured by Jensen-Shannon Distance in $k = 12$ -dimensional community space between T1 and T2 ($JSD_{T1,T2}$). Areas in red have greater dissimilarity in community composition between T1 and T2. Hexagons with black borders were removed from the analysis due to missing data. Map is projected to Albers Equal Area Conic projection. (b) Predictors of community composition change over the last three decades. Dots represent standardized slope coefficient estimates from GLMMs with a beta distribution and logit link function. Shading indicates individual models. All models except fire frequency and nitrogen deposition (LOG(FIRE) and NDEP, respectively) contained the historic climate conditions (indicated by “T1”) and change between the historic and study period conditions (indicated by “Δ”). Bars represent 95% confidence intervals, and those that cross the vertical line at zero are considered non-significant. LOG(FIRE) = fire frequency; NDEP = nitrogen deposition; BA = basal area; PDSI = Palmer Drought Severity Index; TMINSD = standard deviation (SD) of minimum monthly temperature; TMAXSD = SD of maximum monthly temperature; TRANGE = annual temperature range; TMIN = annual minimum temperature; TMAX = annual maximum temperature; MAT = mean annual temperature; PSD = SD of monthly precipitation; TAP = total annual precipitation.

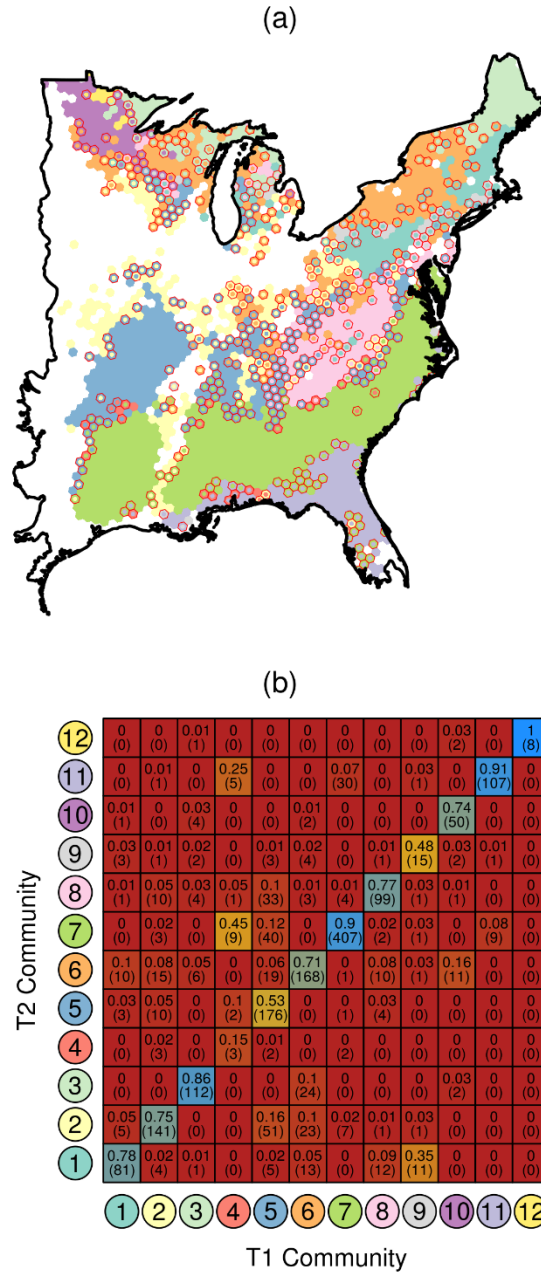


Fig. 3.5 Change in dominant forest communities between T1 and T2. (a) Hexagons with red borders indicate where the dominant community at T2 differs from the dominant community at T1. Hexagon outer color represents dominant community at T1 and inner point color represents dominant community at T2. Map is projected to Albers Equal Area Conic projection. (b) Transition matrix between T1 and T2. Each box contains the proportion of hexagons with dominant community at T1 (x-axis) transitioning to dominant community at T2 (y-axis). Number of hexagons in each transition in parentheses. Colors represent higher proportions (red = low, blue = high). A total of 446 out of 1813 hexagons (24.6%) changed dominance between T1 and T2.

3.7 References

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3.8 Supplementary Tables and Figures

Table S3.1 States with Forest Inventory and Analysis data included in this study, including sampling years (T1 and T2) and the interval between them. The median sampling years were 1985 and 2017 for T1 and T2, respectively, with a median interval of 31 years. See **Fig S3.1** for a map of the study location.

State	Sampling year		Interval (years)
	T1	T2	
Alabama	1982	2017	35
Arkansas	1988	2017	29
Connecticut	1985	2017	32
Delaware	1986	2017	31
Florida	1980	2015	35
Georgia	1982	2016	34
Illinois	1985	2017	32
Indiana	1986	2017	31
Iowa	1990	2017	27
Kansas	1981	2016	35
Kentucky	1988	2015	27
Louisiana	1984	2015	31
Maine	1995	2017	22
Maryland	1986	2017	31
Massachusetts	1985	2017	32
Michigan	1980	2017	37
Minnesota	1990	2017	27
Mississippi	1987	2016	29
Missouri	1989	2017	28
Nebraska	1983	2017	34
New Hampshire	1983	2017	34
New Jersey	1987	2016	29
New York	1993	2016	23
North Carolina	1984	2017	33
North Dakota	1980	2017	37
Ohio	1991	2016	25
Oklahoma	1986	2016	30
Pennsylvania	1989	2016	27
Rhode Island	1985	2017	32
South Carolina	1986	2016	30
South Dakota	1980	2017	37
Tennessee	1980	2015	35
Texas	1986	2016	30
Vermont	1983	2017	34
Virginia	1985	2016	31
West Virginia	1989	2017	28
Wisconsin	1983	2017	34

Table S3.2 List of species used in this study. Some species were aggregated to the genus level (such as *Carya* spp.) when trees were identified only to the genus level in either the T1 or T2 samples. SPCD = species code from the Forest Inventory and Analysis database.

SPCD	Common name	Scientific name	Aggregated SPCD	Aggregated common name	Aggregated scientific name
12	Balsam Fir	<i>Abies balsamea</i>	12	Balsam Fir	<i>Abies balsamea</i>
68	Eastern Redcedar	<i>Juniperus virginiana</i>	68	Eastern Redcedar	<i>Juniperus virginiana</i>
71	Tamarack	<i>Larix laricina</i>	71	Tamarack	<i>Larix laricina</i>
94	White Spruce	<i>Picea glauca</i>	94	White Spruce	<i>Picea glauca</i>
95	Black Spruce	<i>Picea mariana</i>	95	Black Spruce	<i>Picea mariana</i>
97	Red Spruce	<i>Picea rubens</i>	97	Red Spruce	<i>Picea rubens</i>
105	Jack Pine	<i>Pinus banksiana</i>	105	Jack Pine	<i>Pinus banksiana</i>
110	Shortleaf Pine	<i>Pinus echinata</i>	110	Shortleaf Pine	<i>Pinus echinata</i>
111	Slash Pine	<i>Pinus elliottii</i>	111	Slash Pine	<i>Pinus elliottii</i>
115	Spruce Pine	<i>Pinus glabra</i>	115	Spruce Pine	<i>Pinus glabra</i>
121	Longleaf Pine	<i>Pinus palustris</i>	121	Longleaf Pine	<i>Pinus palustris</i>
125	Red Pine	<i>Pinus resinosa</i>	125	Red Pine	<i>Pinus resinosa</i>
126	Pitch Pine	<i>Pinus rigida</i>	126	Pitch Pine	<i>Pinus rigida</i>
128	Pond Pine	<i>Pinus serotina</i>	128	Pond Pine	<i>Pinus serotina</i>
129	Eastern White Pine	<i>Pinus strobus</i>	129	Eastern White Pine	<i>Pinus strobus</i>
131	Loblolly Pine	<i>Pinus taeda</i>	131	Loblolly Pine	<i>Pinus taeda</i>
132	Virginia Pine	<i>Pinus virginiana</i>	132	Virginia Pine	<i>Pinus virginiana</i>
221	Baldcypress	<i>Taxodium distichum</i>	221	Baldcypress	<i>Taxodium distichum</i>
222	Pondcypress	<i>Taxodium ascendens</i>	222	Pondcypress	<i>Taxodium ascendens</i>
241	Northern White-Cedar	<i>Thuja occidentalis</i>	241	Northern White-Cedar	<i>Thuja occidentalis</i>
261	Eastern Hemlock	<i>Tsuga canadensis</i>	261	Eastern Hemlock	<i>Tsuga canadensis</i>
313	Boxelder	<i>Acer negundo</i>	313	Boxelder	<i>Acer negundo</i>
315	Striped Maple	<i>Acer pensylvanicum</i>	315	Striped Maple	<i>Acer pensylvanicum</i>
316	Red Maple	<i>Acer rubrum</i>	316	Red Maple	<i>Acer rubrum</i>
317	Silver Maple	<i>Acer saccharinum</i>	317	Silver Maple	<i>Acer saccharinum</i>
318	Sugar Maple	<i>Acer saccharum</i>	318	Sugar Maple	<i>Acer saccharum</i>
330	Buckeye, Horsechestnut	<i>Aesculus</i> spp.	330	Buckeye, Horsechestnut	<i>Aesculus</i> spp.
371	Yellow Birch	<i>Betula alleghaniensis</i>	371	Yellow Birch	<i>Betula alleghaniensis</i>
372	Sweet Birch	<i>Betula lenta</i>	372	Sweet Birch	<i>Betula lenta</i>
375	Paper Birch	<i>Betula papyrifera</i>	375	Paper Birch	<i>Betula papyrifera</i>
379	Gray Birch	<i>Betula populifolia</i>	379	Gray Birch	<i>Betula populifolia</i>
391	Am Hornbeam, Musclemwood	<i>Carpinus caroliniana</i>	391	Am Hornbeam, Musclemwood	<i>Carpinus caroliniana</i>
400	Hickory Spp.	<i>Carya</i> spp.	400	Hickory Spp.	<i>Carya</i> spp.
401	Water Hickory	<i>Carya aquatica</i>	400	Hickory Spp.	<i>Carya</i> spp.
402	Bitternut Hickory	<i>Carya cordiformis</i>	400	Hickory Spp.	<i>Carya</i> spp.
403	Pignut Hickory	<i>Carya glabra</i>	400	Hickory Spp.	<i>Carya</i> spp.
404	Pecan	<i>Carya illinoensis</i>	400	Hickory Spp.	<i>Carya</i> spp.
405	Shellbark Hickory	<i>Carya laciniosa</i>	400	Hickory Spp.	<i>Carya</i> spp.
406	Nutmeg Hickory	<i>Carya myristiciformis</i>	400	Hickory Spp.	<i>Carya</i> spp.
407	Shagbark Hickory	<i>Carya ovata</i>	400	Hickory Spp.	<i>Carya</i> spp.
408	Black Hickory	<i>Carya texana</i>	400	Hickory Spp.	<i>Carya</i> spp.
409	Mockernut Hickory	<i>Carya alba</i>	400	Hickory Spp.	<i>Carya</i> spp.
410	Sand Hickory	<i>Carya pallida</i>	400	Hickory Spp.	<i>Carya</i> spp.
411	Scrub Hickory	<i>Carya floridana</i>	400	Hickory Spp.	<i>Carya</i> spp.
412	Red Hickory	<i>Carya ovalis</i>	400	Hickory Spp.	<i>Carya</i> spp.
413	Southern Shagbark Hickory	<i>Carya carolinae-septentrionalis</i>	400	Hickory Spp.	<i>Carya</i> spp.
460	Hackberry Spp.	<i>Celtis</i> spp.	460	Hackberry Spp.	<i>Celtis</i> spp.
461	Sugarberry	<i>Celtis laevigata</i>	460	Hackberry Spp.	<i>Celtis</i> spp.
462	Hackberry	<i>Celtis occidentalis</i>	460	Hackberry Spp.	<i>Celtis</i> spp.
463	Nettleleaf Hackberry	<i>Celtis laevigata</i>	460	Hackberry Spp.	<i>Celtis</i> spp.
471	Eastern Redbud	<i>Cercis canadensis</i>	471	Eastern Redbud	<i>Cercis canadensis</i>
521	Common Persimmon	<i>Diospyros virginiana</i>	521	Common Persimmon	<i>Diospyros virginiana</i>
531	American Beech	<i>Fagus grandifolia</i>	531	American Beech	<i>Fagus grandifolia</i>
540	Ash Spp.	<i>Fraxinus</i> spp.	540	Ash Spp.	<i>Fraxinus</i> spp.
541	White Ash	<i>Fraxinus americana</i>	540	Ash Spp.	<i>Fraxinus</i> spp.
543	Black Ash	<i>Fraxinus nigra</i>	540	Ash Spp.	<i>Fraxinus</i> spp.
544	Green Ash	<i>Fraxinus pennsylvanica</i>	540	Ash Spp.	<i>Fraxinus</i> spp.
545	Pumpkin Ash	<i>Fraxinus profunda</i>	540	Ash Spp.	<i>Fraxinus</i> spp.
546	Blue Ash	<i>Fraxinus quadrangulata</i>	540	Ash Spp.	<i>Fraxinus</i> spp.
547	Velvet Ash	<i>Fraxinus velutina</i>	540	Ash Spp.	<i>Fraxinus</i> spp.

Table S3.2 continued

548	Carolina Ash	<i>Fraxinus caroliniana</i>	540	Ash Spp.	<i>Fraxinus</i> spp.
549	Texas Ash	<i>Fraxinus texensis</i>	540	Ash Spp.	<i>Fraxinus</i> spp.
552	Honeylocust	<i>Gleditsia triacanthos</i>	552	Honeylocust	<i>Gleditsia triacanthos</i>
555	Loblolly-Bay	<i>Gordonia lasianthus</i>	555	Loblolly-Bay	<i>Gordonia lasianthus</i>
591	American Holly	<i>Ilex opaca</i>	591	American Holly	<i>Ilex opaca</i>
602	Black Walnut	<i>Juglans nigra</i>	602	Black Walnut	<i>Juglans nigra</i>
611	Sweetgum	<i>Liquidambar styraciflua</i>	611	Sweetgum	<i>Liquidambar styraciflua</i>
621	Yellow-Poplar	<i>Liriodendron tulipifera</i>	621	Yellow-Poplar	<i>Liriodendron tulipifera</i>
641	Osage-Orange	<i>Maclura pomifera</i>	641	Osage-Orange	<i>Maclura pomifera</i>
651	Cucumbertree	<i>Magnolia acuminata</i>	651	Cucumbertree	<i>Magnolia acuminata</i>
653	Sweetbay	<i>Magnolia virginiana</i>	653	Sweetbay	<i>Magnolia virginiana</i>
691	Water Tupelo	<i>Nyssa aquatica</i>	691	Water Tupelo	<i>Nyssa aquatica</i>
693	Blackgum	<i>Nyssa sylvatica</i>	693	Blackgum	<i>Nyssa sylvatica</i>
701	E. Hophornbeam	<i>Ostrya virginiana</i>	701	E. Hophornbeam	<i>Ostrya virginiana</i>
711	Sourwood	<i>Oxydendrum arboreum</i>	711	Sourwood	<i>Oxydendrum arboreum</i>
721	Redbay	<i>Persea borbonia</i>	721	Redbay	<i>Persea borbonia</i>
731	Sycamore	<i>Platanus occidentalis</i>	731	Sycamore	<i>Platanus occidentalis</i>
741	Balsam Poplar	<i>Populus balsamifera</i>	741	Balsam Poplar	<i>Populus balsamifera</i>
742	Eastern Cottonwood	<i>Populus deltoides</i>	742	Eastern Cottonwood	<i>Populus deltoides</i>
743	Bigtooth Aspen	<i>Populus grandidentata</i>	743	Bigtooth Aspen	<i>Populus grandidentata</i>
746	Quaking Aspen	<i>Populus tremuloides</i>	746	Quaking Aspen	<i>Populus tremuloides</i>
760	Cherry/Plum Spp.	<i>Prunus</i> spp.	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
761	Pin Cherry	<i>Prunus pensylvanica</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
762	Black Cherry	<i>Prunus serotina</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
763	Chokecherry	<i>Prunus virginiana</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
764	Peach	<i>Prunus persica</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
765	Canada Plum	<i>Prunus nigra</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
766	Wild Plum	<i>Prunus americana</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
769	Allegheny Plum	<i>Prunus alleghaniensis</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
770	Chickasaw Plum	<i>Prunus angustifolia</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
771	Sweet Cherry	<i>Prunus avium</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
772	Sour Cherry	<i>Prunus cerasus</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
773	European Plum	<i>Prunus domestica</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
774	Mahaleb Plum	<i>Prunus mahaleb</i>	760	Cherry/Plum Spp.	<i>Prunus</i> spp.
802	White Oak	<i>Quercus alba</i>	802	White Oak	<i>Quercus alba</i>
804	Swamp White Oak	<i>Quercus bicolor</i>	804	Swamp White Oak	<i>Quercus bicolor</i>
806	Scarlet Oak	<i>Quercus coccinea</i>	806	Scarlet Oak	<i>Quercus coccinea</i>
812	Southern Red Oak	<i>Quercus falcata</i>	812	Southern Red Oak	<i>Quercus falcata</i>
813	Cherrybark Oak	<i>Quercus pagoda</i>	813	Cherrybark Oak	<i>Quercus pagoda</i>
817	Shingle Oak	<i>Quercus imbricaria</i>	817	Shingle Oak	<i>Quercus imbricaria</i>
819	Turkey Oak	<i>Quercus laevis</i>	819	Turkey Oak	<i>Quercus laevis</i>
820	Laurel Oak	<i>Quercus laurifolia</i>	820	Laurel Oak	<i>Quercus laurifolia</i>
822	Overcup Oak	<i>Quercus lyrata</i>	822	Overcup Oak	<i>Quercus lyrata</i>
823	Bur Oak	<i>Quercus macrocarpa</i>	823	Bur Oak	<i>Quercus macrocarpa</i>
824	Blackjack Oak	<i>Quercus marilandica</i>	824	Blackjack Oak	<i>Quercus marilandica</i>
825	Swamp Chestnut Oak	<i>Quercus michauxii</i>	825	Swamp Chestnut Oak	<i>Quercus michauxii</i>
826	Chinkapin Oak	<i>Quercus muehlenbergii</i>	826	Chinkapin Oak	<i>Quercus muehlenbergii</i>
827	Water Oak	<i>Quercus nigra</i>	827	Water Oak	<i>Quercus nigra</i>
830	Pin Oak	<i>Quercus palustris</i>	830	Pin Oak	<i>Quercus palustris</i>
831	Willow Oak	<i>Quercus phellos</i>	831	Willow Oak	<i>Quercus phellos</i>
832	Chestnut Oak	<i>Quercus prinus</i>	832	Chestnut Oak	<i>Quercus prinus</i>
833	Northern Red Oak	<i>Quercus rubra</i>	833	Northern Red Oak	<i>Quercus rubra</i>
834	Shumard Oak	<i>Quercus shumardii</i>	834	Shumard Oak	<i>Quercus shumardii</i>
835	Post Oak	<i>Quercus stellata</i>	835	Post Oak	<i>Quercus stellata</i>
837	Black Oak	<i>Quercus velutina</i>	837	Black Oak	<i>Quercus velutina</i>
838	Live Oak	<i>Quercus virginiana</i>	838	Live Oak	<i>Quercus virginiana</i>
901	Black Locust	<i>Robinia pseudoacacia</i>	901	Black Locust	<i>Robinia pseudoacacia</i>
920	Willow Spp.	<i>Salix</i> spp.	920	Willow Spp.	<i>Salix</i> spp.
921	Peachleaf Willow	<i>Salix amygdaloides</i>	920	Willow Spp.	<i>Salix</i> spp.
922	Black Willow	<i>Salix nigra</i>	920	Willow Spp.	<i>Salix</i> spp.
923	Diamond Willow	<i>Salix eriocephala</i>	920	Willow Spp.	<i>Salix</i> spp.
925	Coastal Plain Willow	<i>Salix caroliniana</i>	920	Willow Spp.	<i>Salix</i> spp.
926	Balsam Willow	<i>Salix pyrifolia</i>	920	Willow Spp.	<i>Salix</i> spp.
927	White Willow	<i>Salix alba</i>	920	Willow Spp.	<i>Salix</i> spp.
929	Weeping Willow	<i>Salix sepulcralis</i>	920	Willow Spp.	<i>Salix</i> spp.
931	Sassafras	<i>Sassafras albidum</i>	931	Sassafras	<i>Sassafras albidum</i>
950	Basswood Spp.	<i>Tilia</i> spp.	950	Basswood Spp.	<i>Tilia</i> spp.
951	American Basswood	<i>Tilia americana</i>	950	Basswood Spp.	<i>Tilia</i> spp.

Table S3.2 continued

952	White Basswood	<i>Tilia americana</i> var. <i>heterophylla</i>	950	Basswood Spp.	<i>Tilia</i> spp.
953	Carolina Basswood	<i>Tilia americana</i> var. <i>caroliniana</i>	950	Basswood Spp.	<i>Tilia</i> spp.
970	Elm Spp.	<i>Ulmus</i> spp.	970	Elm Spp.	<i>Ulmus</i> spp.
971	Winged Elm	<i>Ulmus alata</i>	970	Elm Spp.	<i>Ulmus</i> spp.
972	American Elm	<i>Ulmus americana</i>	970	Elm Spp.	<i>Ulmus</i> spp.
973	Cedar Elm	<i>Ulmus crassifolia</i>	970	Elm Spp.	<i>Ulmus</i> spp.
974	Siberian Elm	<i>Ulmus pumila</i>	970	Elm Spp.	<i>Ulmus</i> spp.
975	Slippery Elm	<i>Ulmus rubra</i>	970	Elm Spp.	<i>Ulmus</i> spp.
976	September Elm	<i>Ulmus serotina</i>	970	Elm Spp.	<i>Ulmus</i> spp.
977	Rock Elm	<i>Ulmus thomasi</i>	970	Elm Spp.	<i>Ulmus</i> spp.

Table S3.3 R packages used in this project. All analyses were conducted in R 3.6.1 (R Core Team 2019).

Package	Purpose	Citation
<i>ade4</i>	Mantel tests	Dray and Dufour (2007)
<i>glmmTMB</i>	Generalized linear mixed-effects models with beta distribution	Brooks et al. (2017)
<i>earth</i>	Identifying potential best-fit models from <i>ldatuning</i>	Milborrow (2017)
<i>ldatuning</i>	Evaluating the Latent Dirichlet Allocation model output	Nikita (2016)
<i>MuMIn</i>	Assessing model fit	Bartoń (2018)
<i>philentropy</i>	Computing Jensen-Shannon Divergence	Drost (2018)
<i>raster</i>	GIS – raster layers	Hijmans (2018)
<i>RColorBrewer</i>	Graphics – color schemes	Neuwirth (2014)
<i>rgdal</i>	GIS – shapefiles	Bivand et al. (2018)
<i>scales</i>	Graphics – color scales	Wickham (2018)
<i>shape</i>	Graphics – arrows	Soetaert (2018)
<i>sp</i>	GIS – shapefiles	Pebesma and Bivand (2005)
<i>topicmodels</i>	Running the Latent Dirichlet Allocation model	Grün and Hornik (2011)

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- Bivand, R., T. Keitt, and B. Rowlingson. 2018. rgdal: Bindings for the geospatial data abstraction library.
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- Neuwirth, E. 2014. RColorBrewer: ColorBrewer palettes.
- Nikita, M. 2016. ldatuning: Tuning of the Latent Dirichlet Allocation models parameters.
- Pebesma, E., and R. Bivand. 2005. Classes and methods for spatial data in R.
- R Core Team. 2019. R: A language and environment for statistical computing.
- Soetaert, K. 2018. shape: Functions for plotting graphical shapes, colors.
- Wickham, H. 2018. scales: Scale functions for visualization.

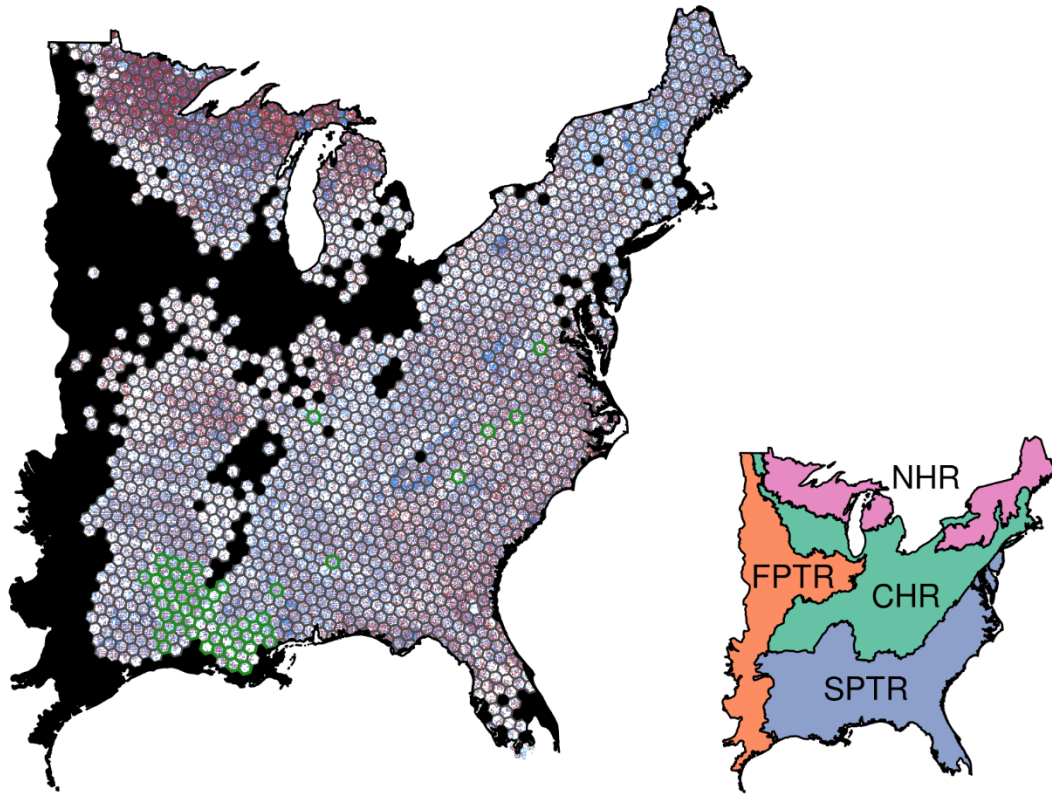


Figure S3.1 Study area including hexagon tessellation and plot locations. Dots represent approximate locations of Forest Inventory and Analysis plots for T1 (red) and T2 (blue). The gray hexagon tessellation was used to aggregate the LDA results for calculating community shifts. Black hexagons either contained no data or contained < 10 plots and were removed from the analysis. Green border indicates hexagons that were used to fit the LDA model and calculate community shifts but were removed from the analysis of climate and non-climate drivers due to missing data. Inset map shows the four ecoregions of the eastern U.S.: the Northern Hardwood Region (NHR, pink color), the Central Hardwood Region (CHR, green color), the Forest-Prairie Transition Region (FPTR, orange color), and the Southern Pine-Hardwood Region (SPHR, blue color). See **Table S3.1** for state-level sampling information.

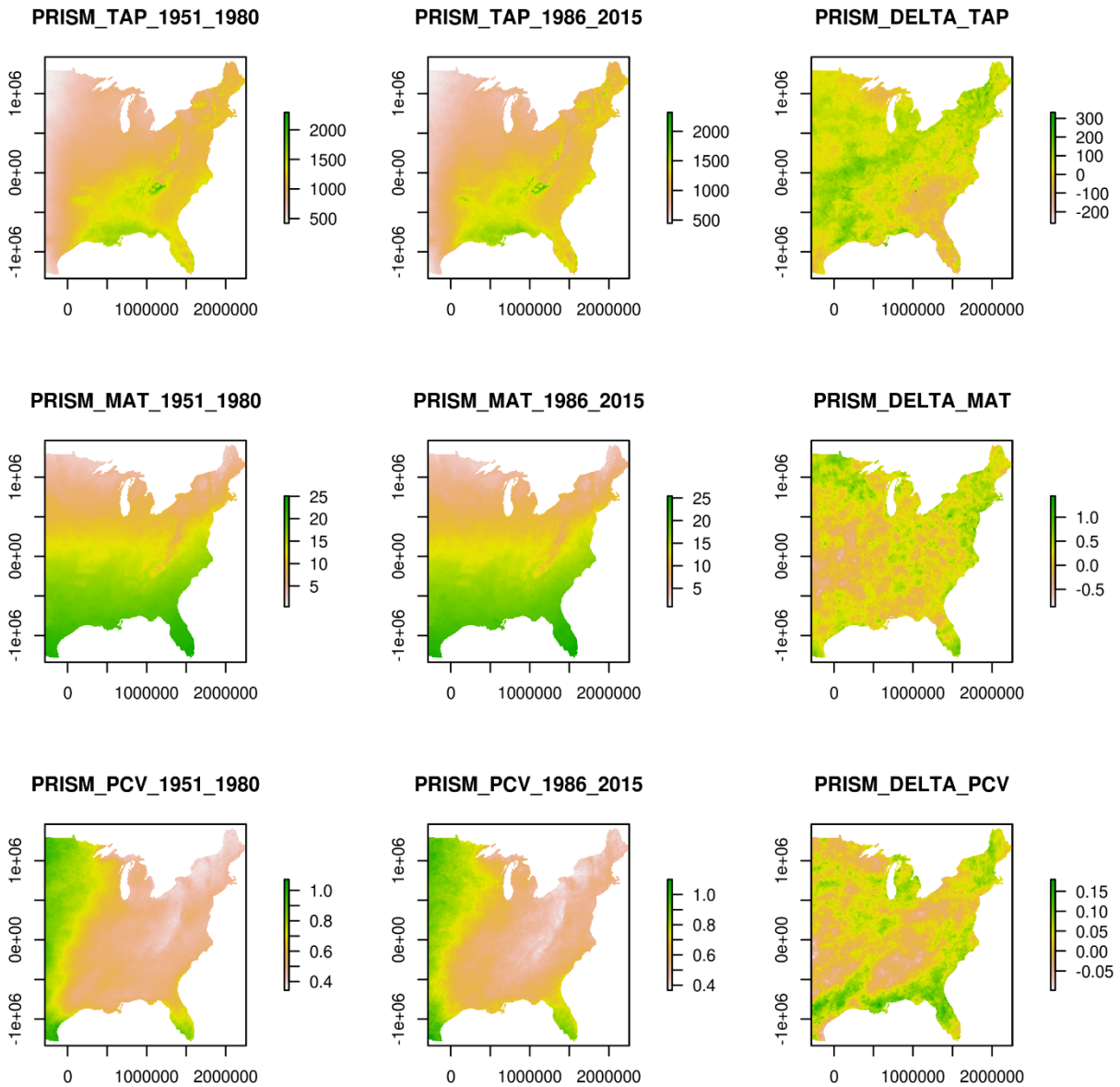


Figure S3.2. Climate and non-climate variables used in this study. Units are millimeters for TAP and PSD, and °C for MAT, TMAX, TMIN, TRANGE, TMAXSD, TMINSD. Coefficient of variation of monthly precipitation (PCV) was removed from the final analysis due to interpretability (PCV is unit-less). PRISM-derived variables (earth tones) are at 4 km resolution. Total basal area, PDSI, NDEP, and fire frequency (blue) were aggregated to the 1452 km² hexagon level.

Figure S3.2 continued

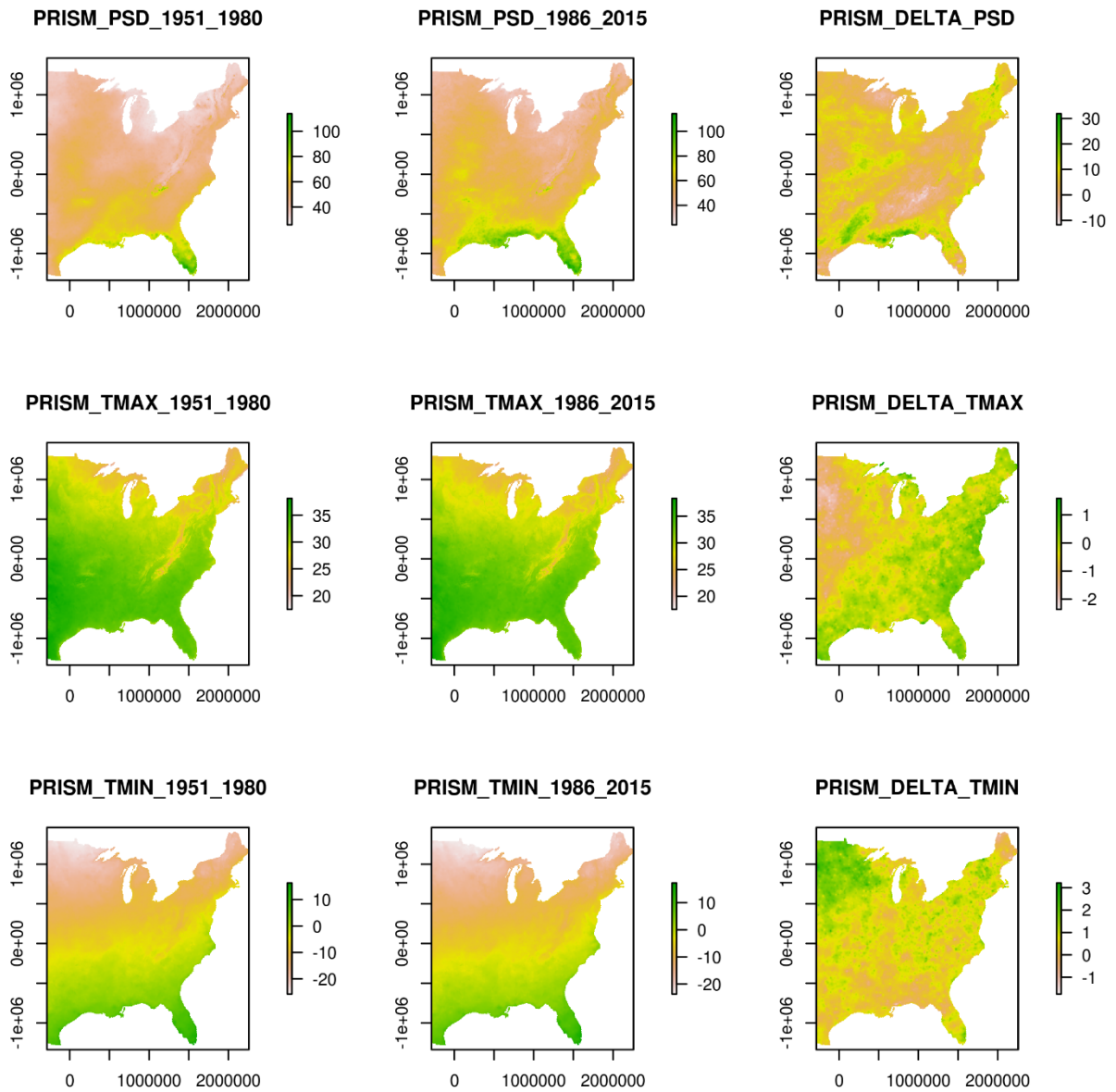
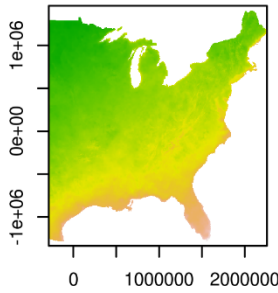
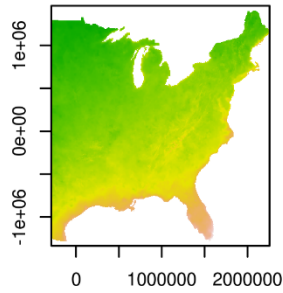


Figure S3.2 continued

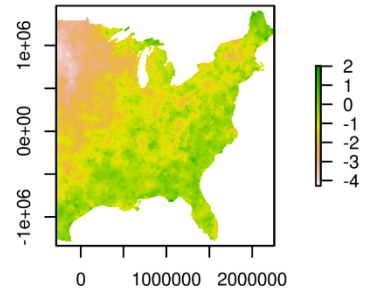
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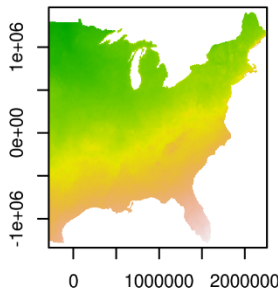
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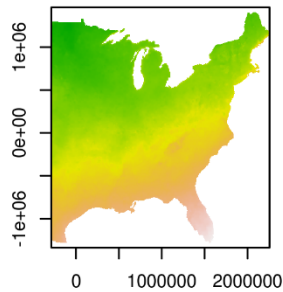
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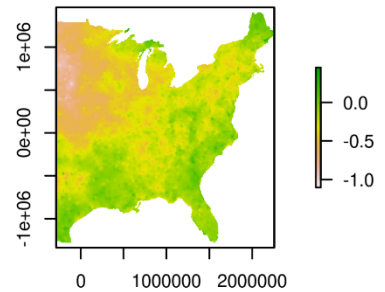
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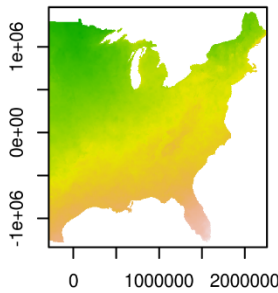
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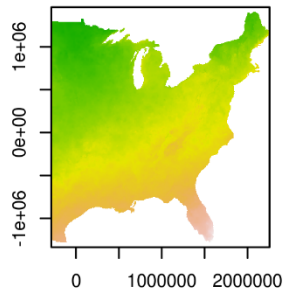
PRISM_DELTA_TMAXSD



PRISM_TMINSD_1951_1980



PRISM_TMINSD_1986_2015



PRISM_DELTA_TMINSD

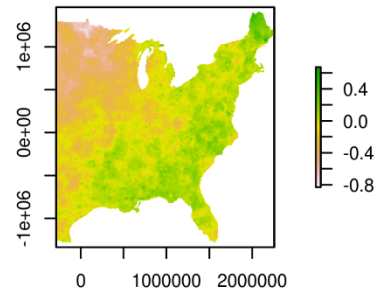
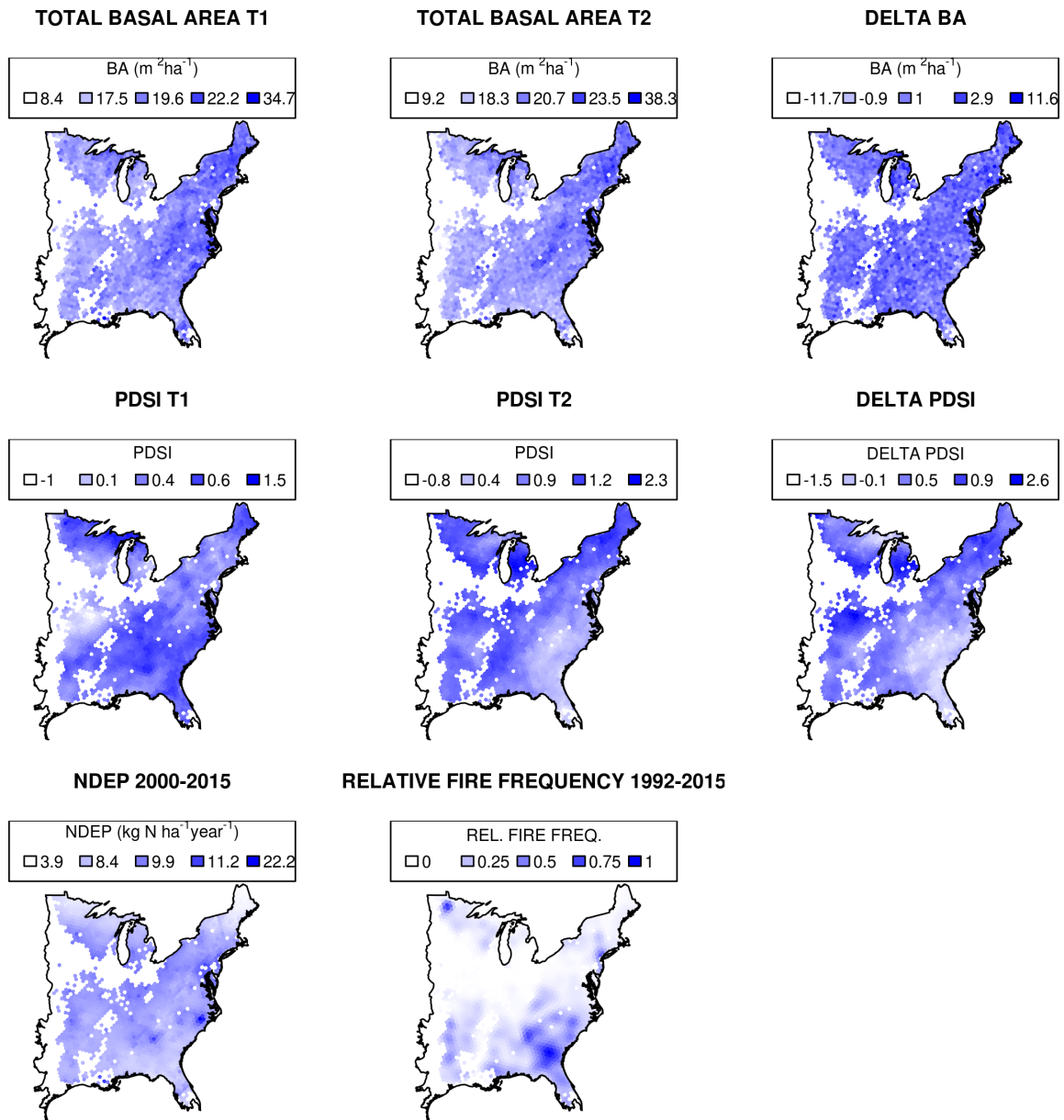


Figure S3.2 continued



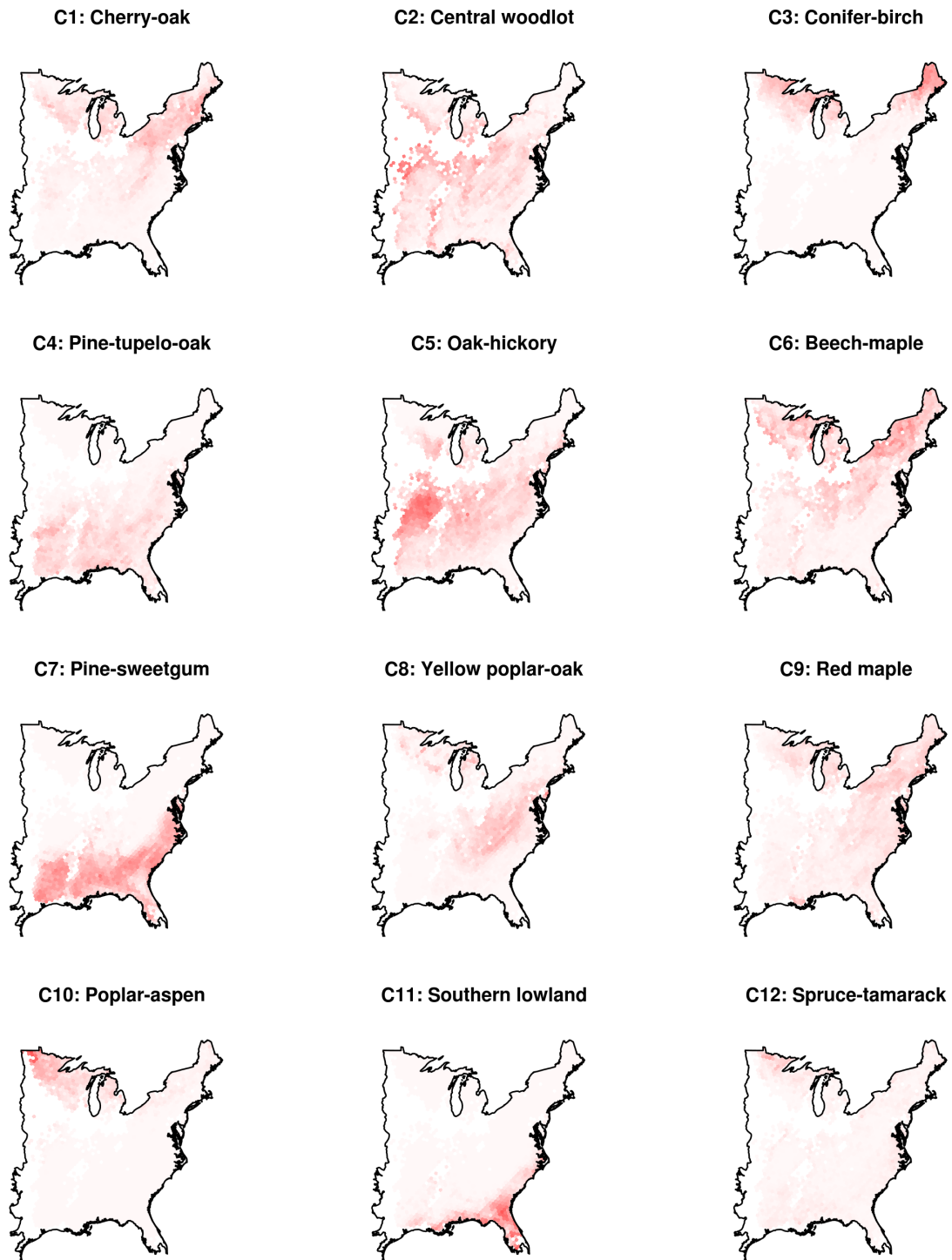


Figure S3.3 Maps of regional forest communities at T1. Darker red indicates a higher proportion of the sampling unit comprised of the community; however, colors are normalized to a 0-1 color intensity scale for display purposes. Due to high correlations between T1 and T2 ($r = 0.80-0.97$, $P < 0.001$ for all communities), only the T1 distribution is shown. A GIS layer containing the community composition at both T1 and T2 is available at <https://www.doi.org/10.4231/GCE5-ZY59>

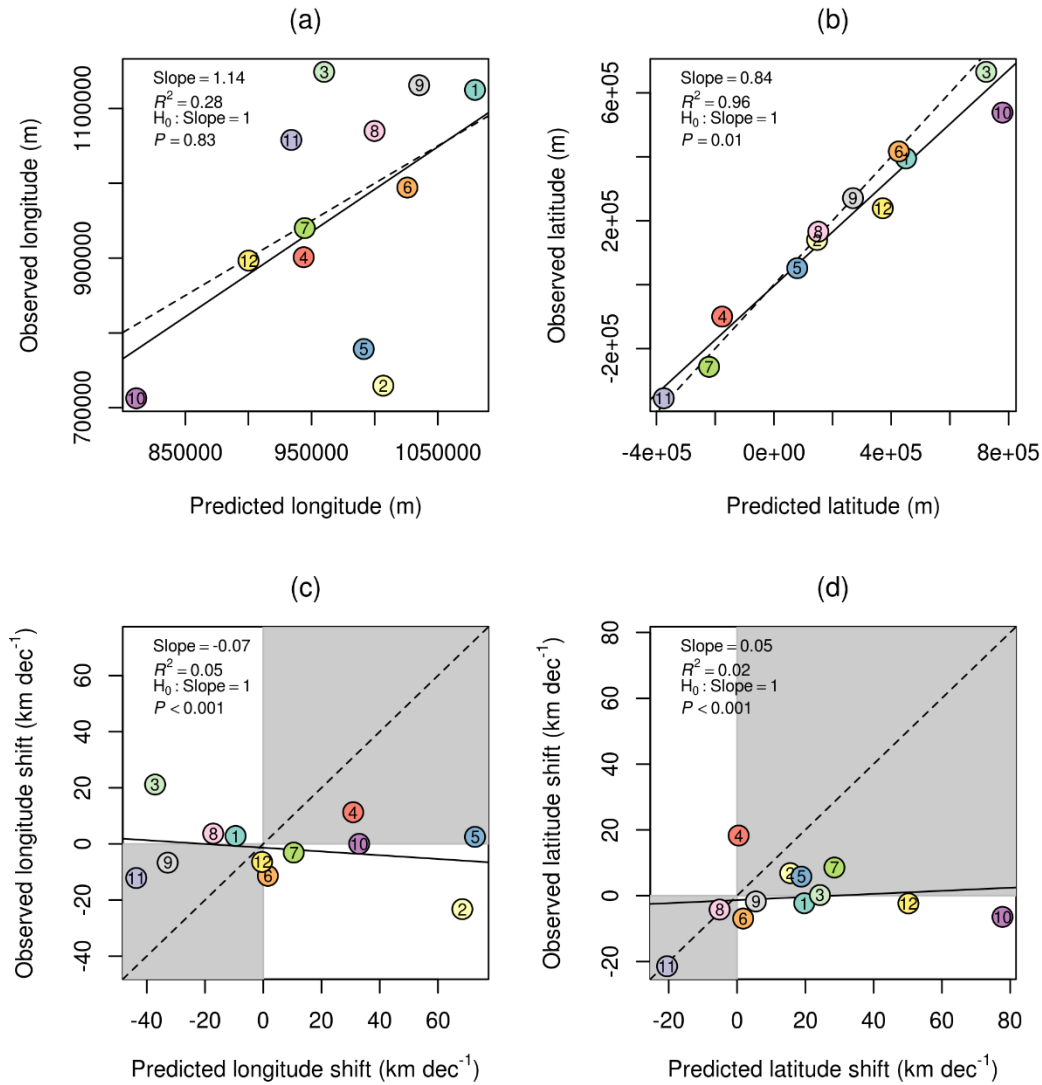


Figure S3.4 Climate predicted vs. observed locations and shifts of forest communities. Nine climate variables were used to identify climate conditions where the communities were located at T1 and predict locations that aligned with these conditions at T2. (a and b) Predicted vs. observed community centroids in longitude (a) and latitude (b). (c and d) Predicted vs. observed shifts in community centroid in longitude (c) and latitude (d). Dashed lines indicate 1:1 line and solid lines indicate regression lines. R^2 values indicate fit of the regression line. P values indicate significant differences of the regression line from the 1:1 line. Slope > 1 in (a) indicates climate predicted T2 centroids are more central to the study region than observed T2 centroids in longitude. Slope < 1 in (b) indicates climate predicted T2 centroids are more poleward than observed T2 centroids in latitude. Slope < 1 in (c) and (d) indicates climate predicted shifts are farther than observed shifts. Gray rectangles (c) and (d) indicate communities where predicted and observed shifts are in the same direction.

CHAPTER 4. CONCLUSIONS

The purpose of this research was to assess the impacts of climate change on eastern U.S. forests. By studying the phenology of northern red oak at a common garden across multiple years, I was able to quantify the phenology sensitivity of widespread populations. This analysis revealed consistent bud burst and leaf out responses to warmer spring temperatures but the inability for populations to extend their growing season into fall during warmer years. Pairing phenological observations with diameter at breast height measurements showed that phenological sensitivity does not positively correlate with estimates of productivity; rather, local populations with intermediate leaf out sensitivity had the highest productivity. By studying large-scale responses of forest communities using FIA data, I showed that forest communities are shifting in three main ways: shifts in species composition of the communities, shifts in spatial distribution of the communities, and changes across all communities that aligned with warmer, wetter, more temperature-variable climates. This second study revealed that although communities are shifting their spatial distributions as a result of species-level migration, climate change predicted communities to move farther than the observed shifts and often in a different direction.

The outcomes of my research provide insight into the sustainability of forests. For example, previous studies have shown that oak forests have been in decline over the last few decades (Knott et al., 2019; Nowacki & Abrams, 2008). My research on phenology highlights how populations of northern red oak have differential responses to warming, with some populations able to shift their phenology in response to warming more quickly. However, this study also revealed the locally adapted populations have the highest productivity, indicating that populations that are relocated under climate change (either natural dispersal/recruitment or human-mediated assisted migration) may be less productive than local populations. Similarly, my research on forest communities showed that the oak-hickory community, one of the most widespread communities of the eastern U.S., had dramatic decreases in spatial coverage over the last three decades. Taken together, these studies expand on previous studies by providing additional evidence of the decline in oak forests. Given the economic and ecological importance of oak species, these findings can serve as a warning sign of the potential impacts on the sustainability of oak forests under continued climate change.

Forests respond to climate change at many spatial (local to global), temporal (near real-time to millennia), and organizational scales (individuals to communities). In this dissertation I aimed to address multiple scales, from the population-level shifts in phenology to species- and community-level tree migrations. The processes I studied have direct and indirect effects on ecosystem functioning, climate feedbacks, and human wellbeing (Parmesan & Yohe, 2003; Pecl et al., 2017). Small changes in phenology and community composition can likely lead to changes in the overall structure and functioning of forest ecosystems. These observed responses to climate change in the recent past are a warning sign of the impacts that future climate change—which may be greater than already observed climate change—may have on forest ecosystems and ultimately bring into question the overall sustainability of forests under climate change.

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 - Cross-scale analyses of forest ecosystem dynamics
 - Novel modeling approaches to investigate ecological patterns and processes at landscape-to macro-scales
-

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PEER-REVIEWED PUBLICATIONS

Published and accepted

* indicates co-first authorship; ** indicates undergraduate co-author

Machine learning to understand big data in ecology

LaRue, E., Rohr, J., **Knott, J.**, Dodds, W., Dahlin, K., Thorp, J., Johnson, J., Rodriguez-Gonzalez, M., Hardiman, B., Keller, M., Fahey, R., SanClements, M., Atkins, J., Tromboni, F., Chandra, S., Parker, G., Rose, K., Liu, J., & Fei, S. (In Press). The evolution of macrosystems biology. *Frontiers in Ecology and the Environment*.

Knott, J., LaRue, E., Ward, S., McCallen, E., Ordonez, K., Wagner, F., Jo, I., Elliott, J.**, & Fei, S. (2019). A roadmap for exploring the thematic content of ecology journals. *Ecosphere* 10(8):e02801.

McCallen, E.*, **Knott, J.***, Nunez-Mir, G., Taylor, B., Jo, I., & Fei, S. (2019). Trends in ecology: shifts in ecological research themes over the past four decades. *Frontiers in Ecology and the Environment* 17(2):109-116.

Responses of biodiversity to global change

Knott, J., Jenkins, M., Oswalt, C., & Fei, S. (2020). Community-level responses to climate change in forests of the eastern United States. *Global Ecology and Biogeography*.

Knott, J.*, Desprez, J. M.*, Fei, S., & Oswalt, C. M. (2019). Shifts in forest composition in the eastern United States. *Forest Ecology and Management* 433:176-183.

Guo, Q., Fei, S., Shen, Z., Iannone, B. V., **Knott, J.**, & Chown, S. L. (2018). A global analysis of elevational distribution of nonnative versus native plants. *Journal of Biogeography* 45:793-803.

Fei, S., Desprez, J. M., Potter, K. M., Jo, I., **Knott, J.**, & Oswalt, C. M. (2017). Divergence of species responses to climate change. *Science Advances*, 3(5), e1603055.

Teaching ecology and evolution

Buteyn, N., Oh, Y.I., **Knott, J.**, Stephens, P., Konyndyk, J., Tenney, J., Wilstermann, A., Fynewever, H., & Koetje, D. (2019). Exploring neutraceuticals to enhance scientific literacy: aligning with *Vision and Change*. *American Biology Teacher* 81(3):176-185

PRESENTATIONS

(All presentations are sole presenter unless noted otherwise)

Invited presentations

2020. **Center for Science of Information virtual seminar series**, Purdue University. Invited online presentation, “Using big data to address forest responses to climate change.”

2018. **Biology Department Seminar**, Calvin College, Grand Rapids, MI. Invited Oral Presentation, “Species and community responses to climate change in eastern US forests.”

Oral presentations

2019. **Forest Inventory and Analysis Stakeholders Science Meeting**, Knoxville, TN. Oral Presentation, “Distributional shifts of regional forest communities in the eastern U.S.”

2019. **Purdue GIS Day**, Purdue University. Lightning Talk, “Distributional shifts of regional forest communities of the eastern United States.”

2019. **Symposium on Data Science and Statistics**, Bellevue, WA. Oral Presentation, “Are forest communities impacted by climate change?”

2019. **Quantitative Ecology Group Meeting**, Purdue University. Oral Presentation, “Trends in ecology: Exploring four decades of ecological literature.”

2019. **U.S. Chapter of the International Association for Landscape Ecology (US-IALE) Annual Meeting**, Ft. Collins, CO. Oral Presentation, “Is climate change driving distributional shifts of forest tree communities?”

2018. **Central Hardwood Forest Conference**, Bloomington, IN. Oral Presentation, “Assessing impacts of climate change on phenology in a common garden.”

2018. **US-IALE Annual Meeting**, Chicago, IL. Oral Presentation, “Red oak phenology in a common garden.”

2018. **Quantitative Ecology Group Meeting**, Purdue University. Oral Presentation, “Decomposing forest communities using a topic modeling approach.”

2017. **Ecological Sciences and Engineering Symposium**, Purdue University (People’s Choice Award). Three Minute Thesis Competition, “Assessing impacts of climate change on forest communities.”

2017. **North America Colleges and Teachers of Agriculture meeting**, Purdue University. Oral presentation, “Climate change impacts on red oak phenology in a common garden study.” Co-presenter: Ben Taylor.

2017. **Quantitative Ecology Group Meeting**, Purdue University. Oral Presentation, “Introduction to automated content analysis with Leximancer.” Co-presenter: Gabriela Nunez-Mir.

2016. **Ecological Sciences and Engineering Symposium**, Purdue University (1st Place). Three Minute Thesis Competition, “Assessing the impacts of climate change on red oak phenology.”
2015. **Michigan Academy of Science, Arts, and Letters**, Andrews University, Berrien Springs, MI. Oral Presentation, “Forty years of forest change in the Calvin College Ecosystem Preserve.”

Poster presentations

2019. **Ecological Society of America Annual Meeting**, Louisville, KY. Poster Presentation, “Is your research blooming or wilting? An exploration of four decades of ecological literature.”
2019. **Symposium on Data Science and Statistics**, Bellevue, WA. E-poster Presentation, “Identifying forest communities using machine learning techniques.” Co-presenters: Trenton Ford and Chathurangi Pathiravasan.
2018. **Purdue GIS Day**, Purdue University (3rd place). Poster Presentation, “Shifts in forest composition in the eastern United States.”
2018. **Purdue Forestry and Natural Resources Research Symposium**, Purdue University (Honorable Mention). Poster Presentation, “Assessing impacts of climate change on phenology using a common garden study.”
2017. **Purdue GIS Day**, Purdue University (1st Place). Poster Presentation, “Assessing impacts of climate change on phenology using a common garden study.”
2017. **Office of Interdisciplinary Graduate Programs Spring Reception**, Purdue University. Poster Presentation, “What’s trending in ecology? An automated content analysis of the top concepts in ecology.”
2017. **International Biogeography Society Biennial Meeting**, Tucson, AZ. Poster Presentation, “Assessing impacts of climate change on phenology using a common garden study.”
2016. **Ecological Society of America Annual Meeting**, Ft. Lauderdale, FL. Poster Presentation, “Assessing impacts of climate change on phenology using a common garden study.”
2016. **Office of Interdisciplinary Graduate Programs Spring Reception**, Purdue University. Poster Presentation, “Assessing human health in Rio De Janeiro, Brazil using the World Urban Database (WUDAPT) framework.” Co-presenters: Rachel Scarlett, Leah Sandler, Renee Obringer, and Janelle Cronin.
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AWARDS AND SCHOLARSHIPS

Awards

2020. **Outstanding Graduate Teaching Assistant for the College of Agriculture, Purdue University.**
2019. **Ecological Society of America W.S. Cooper Award**
2019. **Purdue College of Agriculture Graduate Student Spotlight**
2018. **Purdue GIS Poster Competition**, Third place.
2018. **Purdue Forestry and Natural Resources Poster Competition**, Honorable mention.
2017. **Purdue GIS Day Poster Competition**, First place.
2017. **Purdue Ecological Sciences and Engineering Symposium Three Minute Thesis Competition**, People’s choice award.
2016. **Purdue Ecological Sciences and Engineering Symposium Three Minute Thesis Competition**, First place.

Scholarships and funding

2019. **Purdue Climate Change Research Center Travel Award**, \$500.

2019-2020. **Charles H. Michler Scholarship**, \$5000 for outstanding graduate student researcher in forest biology.

2019. **American Statistical Association Student Travel Award**, \$265.

2019. **NASA-MSU Professional Enhancement Award**, \$700.

2018-Present. **Center for Science of Information interdisciplinary research fund**, \$6000.
Project: Identifying forest communities using machine learning techniques. Co-PIs: Trenton Ford (University of Notre Dame) and Chathurangi Pathiravasan (Southern Illinois University).

2018-2019. **Fischer Forestry Fund Graduate Scholarship**, \$3500.

2018. **US-IALE Student Travel Award**, \$700.

2017-2018. **Charles H. Michler Scholarship**, \$3700 for outstanding graduate student researcher in forest biology.

2016. **Purdue Climate Change Research Center Travel Award**, \$1500.

PROFESSIONAL EXPERIENCE

2018-Present. **Research assistant**, Department of Forestry and Natural Resources, Purdue University.

2015-2018. **USDA NIFA National Needs Fellow**, Department of Forestry and Natural Resources, Purdue University.

2014. **Summer research fellow**, Calvin College. Forty years of forest development in the Calvin College ecosystem preserve. Advisor: Dr. Randy VanDragt.

2013. **Summer research fellow**, Calvin College. Teaching ecology and evolution through the lens of *Vision and Change*. Advisor: Dr. David Koetje.

TEACHING

2020. **Outstanding Graduate Teaching Assistant for the College of Agriculture**, Purdue University.

2019 (Fall). **Teaching assistant** for FNR 64700 Quantitative Methods for Ecologists. Provided help sessions and office hours for graduate students; created and graded homework assignments. Instructor: Robert Swihart.

2018 and 2019 (Spring). **Teaching assistant and guest lecturer** for FNR 38400 Statistical Methods for Natural Resources. Instructed and aided during lab; presented guest lectures on regression analysis; provided office hours for students. Instructor: Robert Swihart.

2018 (Fall). **Certificate of Foundations in College Teaching awardee**, Purdue University.

2017 and 2018 (Fall). **Instructor** for FNR 59800-18 Introduction to R Programming. Created and delivered hands-on lectures; provided help during co-instructor lectures; created and graded assignments and individual projects. Co-instructors: (2017) Gabriela Nunez-Mir, Insu Jo, and Emily McCallen; (2018) Samuel Ward, Elizabeth LaRue, and Insu Jo.

2017 (Fall). **Instructor** for FNR 59800-19 Introduction to Automated Content Analysis. Created and delivered hands-on lectures; provided help during co-instructor lectures; aided students with individual ACA projects. Co-instructors: Gabriela Nunez-Mir, Emily McCallen, and Benjamin Taylor.

MENTORING, SERVICE, AND PROFESSIONAL MEMBERSHIP

2017-Present. **Undergraduate student mentor** for five Forestry/Wildlife/Natural Resources and Environmental Science undergraduate students (Ali Gilchrist, Amy Hanners, Avery Cook, Rachel Brummet, and Erica Mueller) and one Statistics Living-Learning Community undergraduate student (Jessica Gilbert).

2016-Present. **Graduate student peer mentor** for four Ecological Sciences and Engineering and three Forestry and Natural Resources graduate students (Leonardo Bertasello, Patricia Nease, Songhao Wu, Zackary Delisle, Akane Ota, Kyle Richardville, and Joshua Tellier).

2016. **Speakers Committee Chair**, Ecological Sciences and Engineering Symposium.
Coordinated keynote speaker, group discussion leaders, and panelists.

Reviewer for *Global Ecology and Conservation* and *The Landscape Journal*.

Member of the Ecological Society of America (ESA), the International Biogeography Society (IBS), and the International Association for Landscape Ecology-North America (IALE-NA, formerly US-IALE).
