CLIMATE CHANGE

Divergence of species responses to climate change

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Climate change can have profound impacts on biodiversity and the sustainability of many ecosystems. Various studies have investigated the impacts of climate change, but large-scale, trait-specific impacts are less understood. We analyze abundance data over time for 86 tree species/groups across the eastern United States spanning the last three decades. We show that more tree species have experienced a westward shift (73%) than a poleward shift (62%) in their abundance, a trend that is stronger for saplings than adult trees. The observed shifts are primarily due to the changes of subpopulation abundances in the leading edges and are significantly associated with changes in moisture availability and successional processes. These spatial shifts are associated with species that have similar traits (drought tolerance, wood density, and seed weight) and evolutionary histories (most angiosperms shifted westward and most gymnosperms shifted poleward). Our results indicate that changes in moisture availability have stronger near-term impacts on vegetation dynamics than changes in temperature. The divergent responses to climate change by trait- and phylogenetic-specific groups could lead to changes in composition of forest ecosystems, putting the resilience and sustainability of various forest ecosystems in question.

INTRODUCTION

Climate change can have profound impacts on biodiversity and the sustainability of various ecosystems (1, 2). Many studies have investigated the impacts of global temperature rise and suggested that species will migrate poleward (higher latitude) and upward (higher elevation) (3–7). However, climate change incorporates both temperature and precipitation (8), and the responses to climate change are likely to be trait-specific (9, 10).

In the last 30 years, the mean annual temperature (MAT) in the eastern United States has increased about 0.16°C on average, with the northern region undergoing the highest temperature increase (Fig. 1A). Precipitation patterns have also changed, with an increase of more than 150-mm total annual precipitation (TAP) in the central United States and a large reduction in the southeast (Fig. 1B). The combined shifts in precipitation patterns and increasing temperatures have resulted in widespread droughts, as measured by the Palmer Drought Severity Index (PDSI) in the southeastern region of the study area (fig. S1), which can be detrimental to various ecosystems (11–13). Therefore, taking only temperature into consideration is likely to result in an underestimation of the impacts of climate change on species distributions (14–16).

In addition, variations in physiological traits (for example, thermal tolerance) can result in trait-specific responses to climate change (10, 17). Pollen records indicated that different tree species had differential patterns of migration and range shifts in response to changes in the late Quaternary climate (18). These different patterns were likely driven by trait dissimilarities among species. For example, gymnosperms generally have slower juvenile maximum growth rate than angiosperms (19), nearly all gymnosperms are wind-pollinated whereas many angiosperms are insect-pollinated, and gymnosperms have greater hydraulic safety margins than angiosperms in response to drought (11). Tremendous variability also exists within the gymnosperm and angiosperm tree lineages in response to different environmental conditions because of their varying functional traits (20). Hence, the realized current and near-term, broadscale climate change impacts on vegetation dynamics will likely be trait- and lineage-specific.

For tree species, upward and poleward shifts have been observed, but with some inconsistencies. Upward shifts of trees, primarily in response to temperature change, have been observed in a wide range of studies (4, 21), but downward shifts have also been observed as a result of tracking moisture (22). Poleward shifts of tree species have also been observed worldwide but with some exceptions (7, 15). For example, Woodall et al. (23) found that in the eastern United States, the mean latitude of seedlings shifted greater than 20 km north for the northern species, whereas southern species did not move; Zhu et al. (24) found no indication of tree range expansion.

The impacts of climate change on trees can be complicated, as different combinations of alterations in temperature and precipitation can result in different impacts (15) and different tree species can have different responses to climate change (25). To complicate things further, species range shift can also be affected by other nonclimatic factors. In particular, successional processes, influenced by various types of disturbances (or lack of disturbances) along with land use changes, could play an important role in species recruitment, dispersal, and abundance change (26, 27).

Here, we analyzed the distributions of 86 tree species/groups across the eastern United States over the last three decades to (i) investigate the magnitude and directionality of their responses to climate change while accounting for successional processes and (ii) provide a mechanistic understanding of the observed spatial shift. Past studies have primarily focused on the leading and trailing edges of species distributions (14). We used tree abundance data to quantify species response to climate change because quantitative changes within species ranges are more informative (6), can be considerable without any observable changes in overall range extent (28), and are likely to represent intermediate states in species range shifts (14, 29). We hypothesized that (i) young trees have more prominent responses to climate change than adult trees and (ii) species that experience similar responses to climate change share similar physiological traits and evolutionary histories.

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RESULTS

Spatial patterns of shift

We observed a prominent westward and poleward shift in abundance for most tree species in the eastern United States during the last 30 years (Fig. 2). Of the 86 species studied, 73% shifted their abundance centers westward, of which 65% were statistically significant (*P* < 0.05), whereas 62% shifted poleward, of which 55% were significant (table S1A). The median longitudinal rate for species that shifted westward (15.4 km per decade) was 40% larger than the median latitudinal rate for species that shifted poleward (11.0 km per decade). The primary direction of species abundance shift was northwest (37% of the species), and the least common direction was southeast (2%).

Further examination of tree abundances within the four cardinal quadrants of each species distribution range indicates that the observed spatial shifts are primarily due to changes in subpopulations at the leading edges (Fig. 3). In general, subpopulations in the northwestern quadrant had the highest rate of poleward and westward shifts (median, 6.9 and 15.7 km per decade, respectively) compared to subpopulations in other quadrants (Fig. 3, A and B). Moreover, the northwestern sub-

populations within each species range had the highest increase in stem density (median, 24%), whereas other subpopulations had low increases (5.6 and 8.1% in the northeastern and southwestern quadrants, respectively) or were nearly flat (0.6% in the southeastern quadrant) (Fig. 3C).

We also observed regional differences in species abundance shifts (Fig. 4). The majority of species (85%) centered in the warm continental Northern Hardwood region shifted their abundance poleward at a median rate of 20.1 km per decade. Species centered in the hot continental Central Hardwood region shifted primarily westward (83%) at a median rate of 18.9 km per decade. Similarly, species centered in the subtropical Southern Pine-Hardwood region also had a primarily westward shift (77%) at a median rate of 24.7 km per decade. Species centered in the Forest-Prairie Transition region had a westward shift at a median rate of 30.0 km per decade.

Sapling-sized trees had a slightly higher proportion but longer distance in westward and poleward shifts than adults (Fig. 2, B and C, and table S1A). About 71% of tree species shifted their sapling abundance westward versus 70% for adult trees (61 and 65% were significant, respectively, at *P* < 0.05). Similarly, 59% of species shifted their sapling
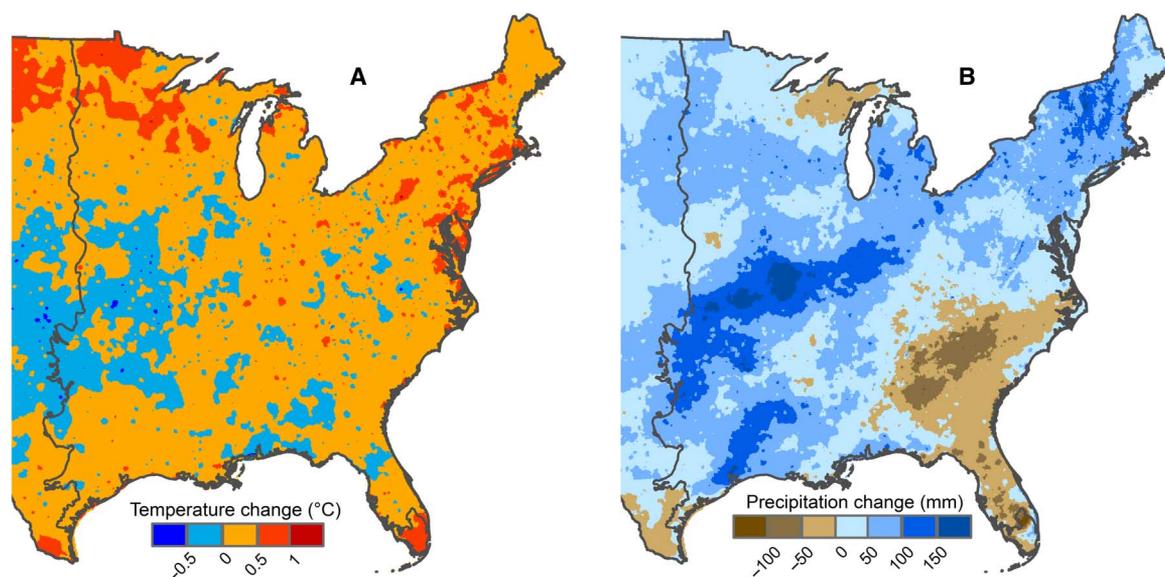
Fig. 1. Changes in temperature and precipitation across the eastern United States. (**A**) Changes in MAT and (**B**) TAP between the recent past (1951–1980) and the study period (1981–2014).
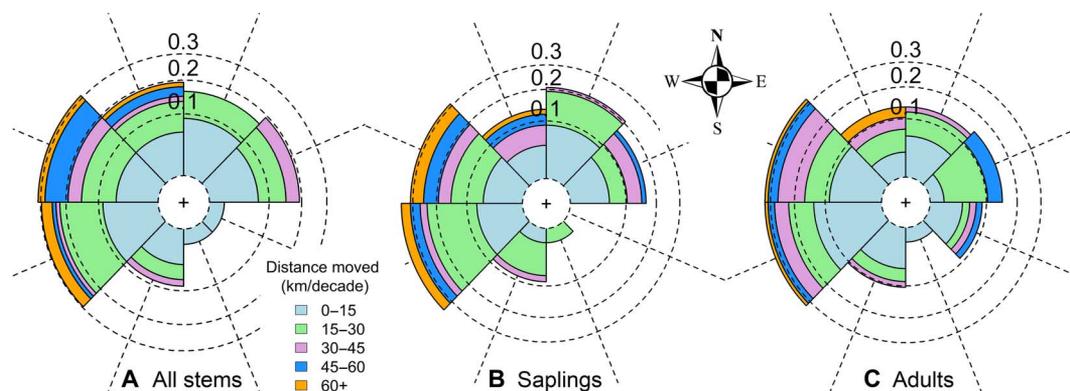

Fig. 2. Rose diagrams depicting the direction and distance of abundance shifts for 86 species. Spatial shift of species abundance for (**A**) all stems, (**B**) saplings, and (**C**) adult trees between two inventory periods (1980s and 2010s). Color represents the different distance categories, and wedge width represents the proportion of species in each direction-distance category.

abundance poleward versus 56% for adults (57 and 58% were significant, respectively, at $P < 0.05$). The median westward and poleward shift distances for saplings (20.7 and 13.1 km per decade, respectively) were longer than those for adults (15.6 and 12.5 km per decade, respectively; table S1A). A paired Wilcoxon signed-rank test demonstrated that the westward shift distances for sapling and adult tree abundance were statistically different ($P = 0.063$).

Associations with climate variables and forest succession

Changes in species abundance during the study period are related to climatic conditions (Fig. 5). With some exceptions, species located in higher temperature and precipitation climatic space experienced reductions in abundance, as indicated by the species' density change. On the other hand, species located in the lower temperature and precipitation climatic space experienced increases (Fig. 5A). Among 38 species associated with mean temperature and precipitation less than the median values (the lower left part of Fig. 5A), 84% experienced an increase in their total stem density.

Changes in species abundance had a stronger association with moisture (precipitation and drought index) than with temperature (Fig. 5B and fig. S2). Changes in TAP were positively associated with changes in species abundance, explaining about 19% of the variability in abundance change (Fig. 5B). The majority of species (80%) that experienced an increase in TAP over 40 mm in their distribution ranges underwent an increase in abundance, and all species increased in abundance when precipitation increased over 60 mm. Not surprisingly, changes in drought condition (PDSI) were also positively associated with species abundance changes ($r^2 = 0.19$; fig. S2A), because of the highly correlated nature between TAP and PDSI. The association between changes in temperature (MAT) and species abundance was significant but weak ($r^2 = 0.05$; fig. S2B).

Forest successional processes, as approximated by stem density and basal area of all overstory trees, also had influences on the observed species abundance shift. Changes in species abundance were positively related to the changes in overall stem density but negatively related to the changes in total basal area (Fig. 5C and fig. S2C), indicating that forests in relatively early successional stages (that is, rapid increases in density

but low accumulations in basal area) had more gains in abundance of the studied species than forests in late successional stages. A multiple regression analysis further confirmed that changes in TAP and total stem density were positively associated with changes in species abundance (table S2).

Trait-specific shifts

The observed spatial shifts in species abundance are associated with certain functional traits that are related to physiological tolerance and dispersal ability. In general, species that shifted westward had a larger seed size ($P = 0.012$) and higher wood density ($P = 0.039$) than species that shifted eastward. For species that shifted significantly eastward and westward, the median value for seed weight is 0.007 and 0.069 g per seed, and the median value for wood density is 0.47 and 0.51 g/cm^3, respectively (fig. S3). In addition, species with different degrees of drought tolerance had different westward shift rates, where species with low drought tolerance had the lowest westward shift rate (median rate, 2.6 km per decade) compared to the medium and high drought tolerance groups (median rate, 14.3 and 11.6 km per decade, respectively) (fig. S4).

On the other hand, species that shifted northward had a lower maximum annual precipitation ($P < 0.01$) and lower wood density ($P = 0.055$) than species that shifted southward (primarily southwest). The median maximum annual precipitation is 1524 and 2032 mm/year, and the median wood density is 0.49 and 0.56 g/cm^3, respectively, for species that shifted significantly northward and southward (fig. S5). In addition, wind-pollinated species primarily shifted northward, whereas animal-pollinated species shifted southward (fig. S6). All other investigated traits (see details in table S3) are not significantly associated with the observed shifts ($P > 0.1$), except for maximum elevation of species distribution, which is marginally significant ($P = 0.085$).

We also detected a small but statistically significant phylogenetic signal of longitudinal shifts in species abundance ($K = 0.023$, $P = 0.004$), but no such signal for latitudinal shifts ($K = 0.007$, $P = 0.760$). In other words, members of some evolutionary groups exhibit relatively consistent westward or eastward shifts (Fig. 6). Fifty-three of the 65 angiosperm species (81.5%) shifted westward, 34 (52.3%) of which significantly shifted,
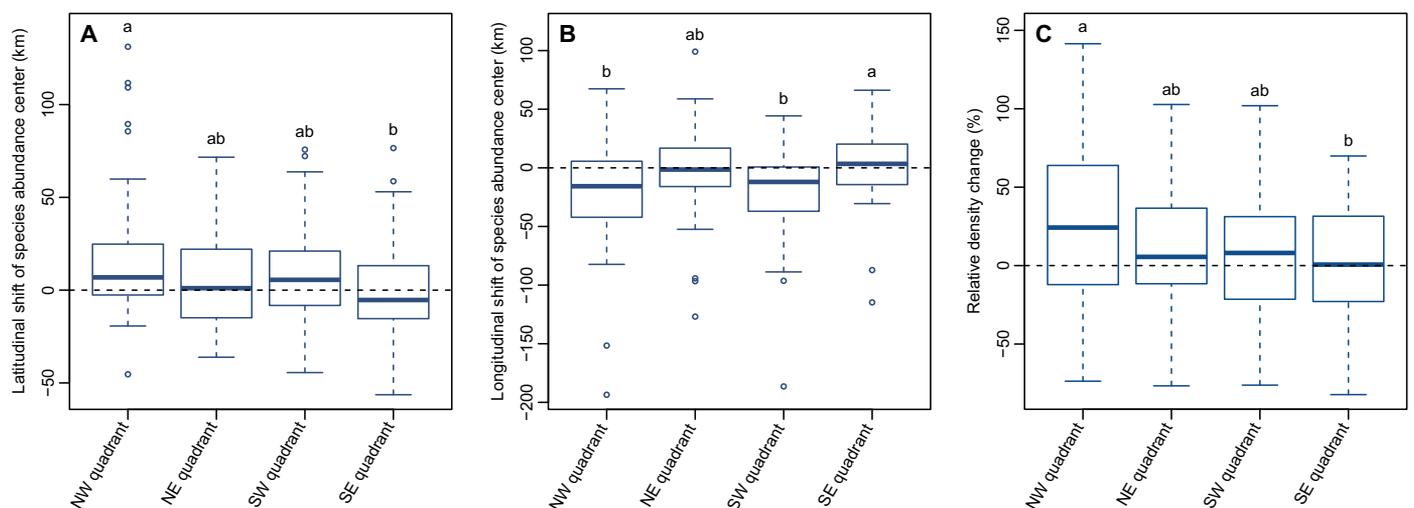
Fig. 3. Spatial shift of species abundance by subpopulations. (**A**) Latitudinal shift and (**B**) longitudinal shift of species abundance center and (**C**) relativity stem density change by subpopulations (four quadrants that are defined by species density center at T1). Positive values indicate northward or eastward shift, and negative values indicate southward or westward shift in (A) and (B). Different letters represent significant differences according to the Tukey post hoc test using *glht* in R. NW, northwestern; NE, northeastern; SW, southwestern; SE, southeastern.
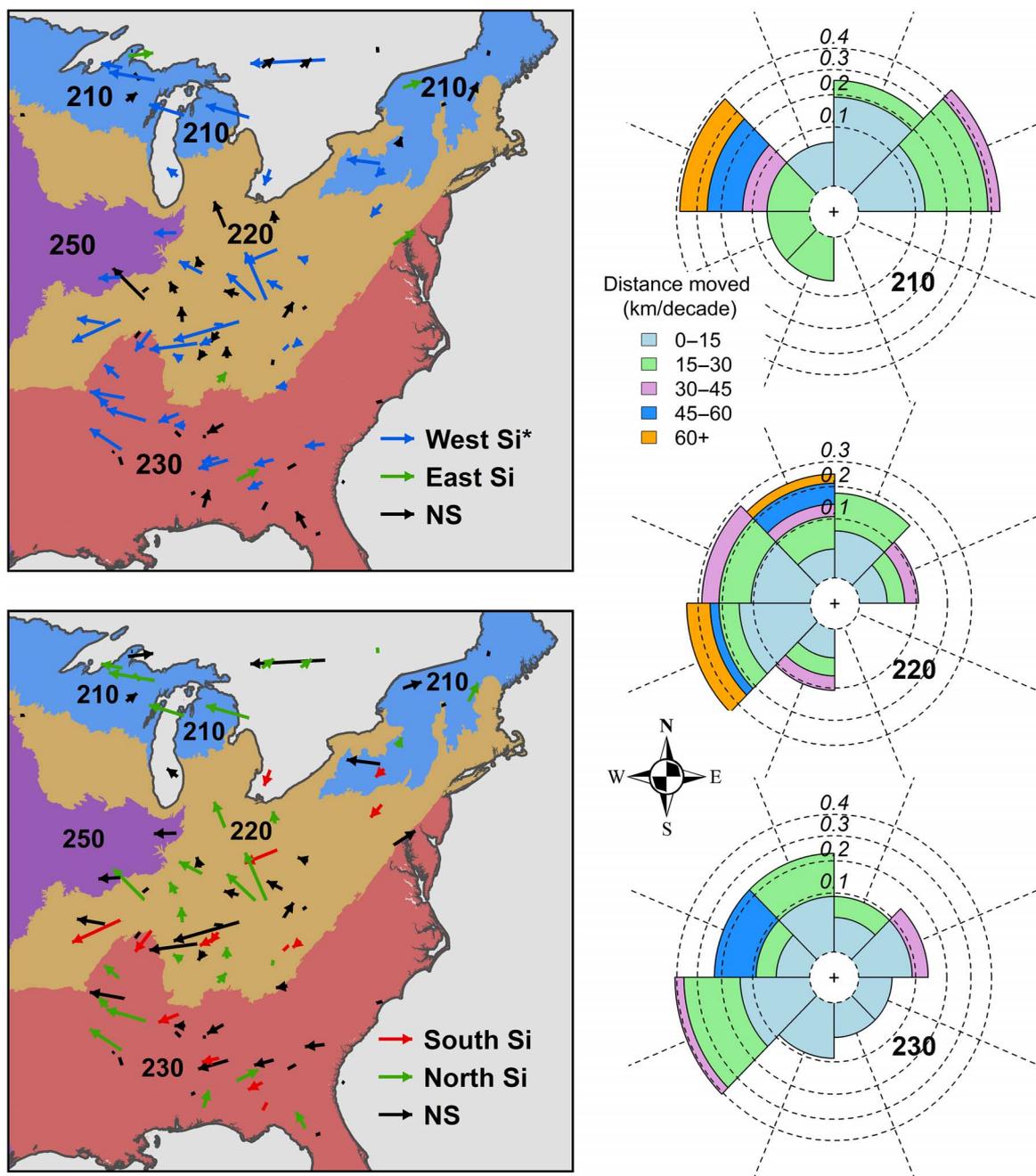
Fig. 4. Shift of species mean abundance center by ecoprovinces in the eastern United States during the last three decades. 210, Northern Hardwood region; 220, Central Hardwood region; 230, Southern Pine-Hardwood region; 250, Forest-Prairie Transition region (*44, 51*). All three species centered in ecoprovince 250 shifted westward (rose diagram not shown). "Si*" indicates that the shift is statistically significant (*P* < 0.05). NS, nonsignificant.

whereas 10 of the 21 gymnosperm species shifted westward. At a finer evolutionary resolution, all 13 red oak species (section *Lobatae*) had westward movement, with 53.8% (7 species) being statistically significant, whereas 3 of the 9 white oaks (section *Quercus*) moved east. Meanwhile, all the members of the Fabaceae, Juglandaceae, and Lauraceae, and most members of the Sapindaceae, moved westward. At the same time, three of the four *Betula* species moved eastward. No clear patterns were observed for the latitudinal shifts among the angiosperms (38 species shifted poleward and 27 shifted southward), whereas the majority of gymnosperms (15 species, or 71.4%) shifted poleward (fig. S7).

DISCUSSION

Our results revealed prominent range-wide westward shifts during a short 30-year period, especially for species in low latitudes. The westward shifts are partially associated with the increased moisture availability in the western regions of the study area, coupled with decreased moisture availability in the southeastern regions. Although plants are unlikely to experience precipitation as a direct impact on physiology, they can track changes in water availability through multiple mechanisms, such as their ability to deal with drought, as shown in previous observational studies (*3, 22*) and modeling simulations (*30, 31*). The
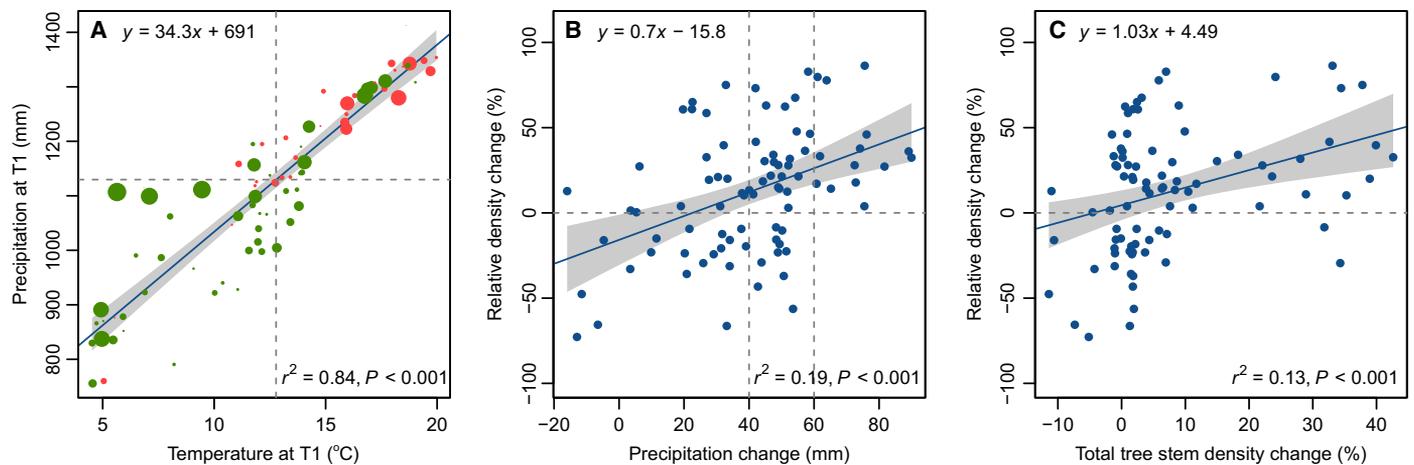
Fig. 5. Relationships between climate variables and species abundance change (shaded area indicates 95% confidence interval). (**A**) Relative changes in species density [(Density_T2 − Density_T1)/Density_T1 × 100)] in association with species MAT and TAP at T1 within the overlapped species distribution range at T1 and T2. Dot size is proportional to the relative density change. Red and green represent negative and positive change in the relative density, respectively. (**B**) Positive association between relative changes in species density and changes in species' respective TAP. (**C**) Positive association between relative changes in species density and changes in total tree stem density.

correlation between changes in drought index and species abundance further confirms the importance of moisture availability and/or tolerance, which is also underscored by the fact that the species that shifted significantly westward are those with relatively high drought tolerance. Although the western portion of the study area has increased in moisture availability during the study period, it is still considerably drier compared to the eastern part (fig. S1). However, species with medium and high drought tolerance can take the advantage of the increased moisture availability in the relatively dry region. Future studies using finer measures of physiological traits such as embolism resistance could better address moisture-related mechanisms on species response to climate change.

As expected, we also found evidence of poleward shifts in abundance, which is more prominent in high latitudes where substantial warming has occurred during the study period. Our abundance-based poleward shift rate (11.0 km per decade) is similar to a previous estimated rate (10 km per decade) that is based on leading/trailing edges for forests in the eastern United States (*23*). The fact that the longitudinal shift was 1.4 times faster than latitudinal shift suggests that vegetation dynamics are more sensitive to precipitation than to temperature, at least in a near-term time frame, because moisture availability is considered a critical factor in forest dynamics of eastern North America (*32*). When considering the predominantly westward and northward shifts of tree species, it is important to understand the geographical settings of the study area, because it has hard boundaries to the east and south (that is, ocean) but soft boundaries to the west and north (that is, climate limitations). Nevertheless, abundance shifts could still be observed even if species ranges are limited by the ocean.

It is not surprising that saplings have experienced a higher proportion and faster rate in poleward and westward shifts than adult trees, because new recruitments (that is, young trees) are expected to respond to climate change more quickly (*23, 24*). The observed differential shift rates could also be due to the fact that saplings are more sensitive to droughts in terms of survival than adult trees (*25*), as substantial drought was observed in the southeastern region of the study area during the study period. The differential shift rates among subpopulations in the four cardinal quadrants further confirmed that the observed range shift is primarily due to the changes in the leading edges of species distribution ranges,

which agreed with early findings by Woodall *et al.* (*23*) of significant poleward shifts of seedlings for most of the northern species in the eastern United States.

The observed trait- and phylogenetic-specific spatial shift in species' abundance is fascinating (most angiosperms shifted westward whereas most gymnosperms shifted poleward). There are several mechanisms that could explain these traits and phylogenetic-specific responses. The lack of westward shift in gymnosperms might be partially explained by the fact that gymnosperms have lower maximum growth rates than angiosperms as a result of their less efficient water transport systems (*19*), making them less competitive in the western portion of the study area, which is drier than the eastern portion (fig. S1). The association between seed size and directional movement of certain species is also interesting and is potentially related to the different colonization, tolerance, and competitive strategies used by different species (*33, 34*). However, there are large variabilities in seed size among species, and seed size is embedded in a complex of many other traits that together define the life history of a tree species (*35*). The association between the observed spatial shift and wood density is also an interesting one. Low wood density is often associated with fast growth, whereas high wood density is often associated with high survival (*36*), which can partially explain the observed southward and westward shift of high wood density species. Because the southern region of the study area experienced droughts and the western part was relatively dry, species with high wood density might have a better chance to survive.

The predominantly northward shift of gymnosperm trees, along with all *Populus* species and most *Betula* species, is intriguing. The mechanism for the northward shift could potentially be linked to species pollination methods because we found that most wind-pollinated species (most gymnosperms and some angiosperms) shifted northward while animal-pollinated species (most angiosperms) shifted southward. Similar northward shifts of clades were observed in the New England area during the early Holocene (between 10,000 and 8000 years ago), where *Picea* was replaced by *Pinus*, followed by *Betula* and then *Quercus* species (*37*). However, the historical process took place over several thousand years, whereas the observed shift in this study happened in a few decades, suggesting the impacts of recent climate
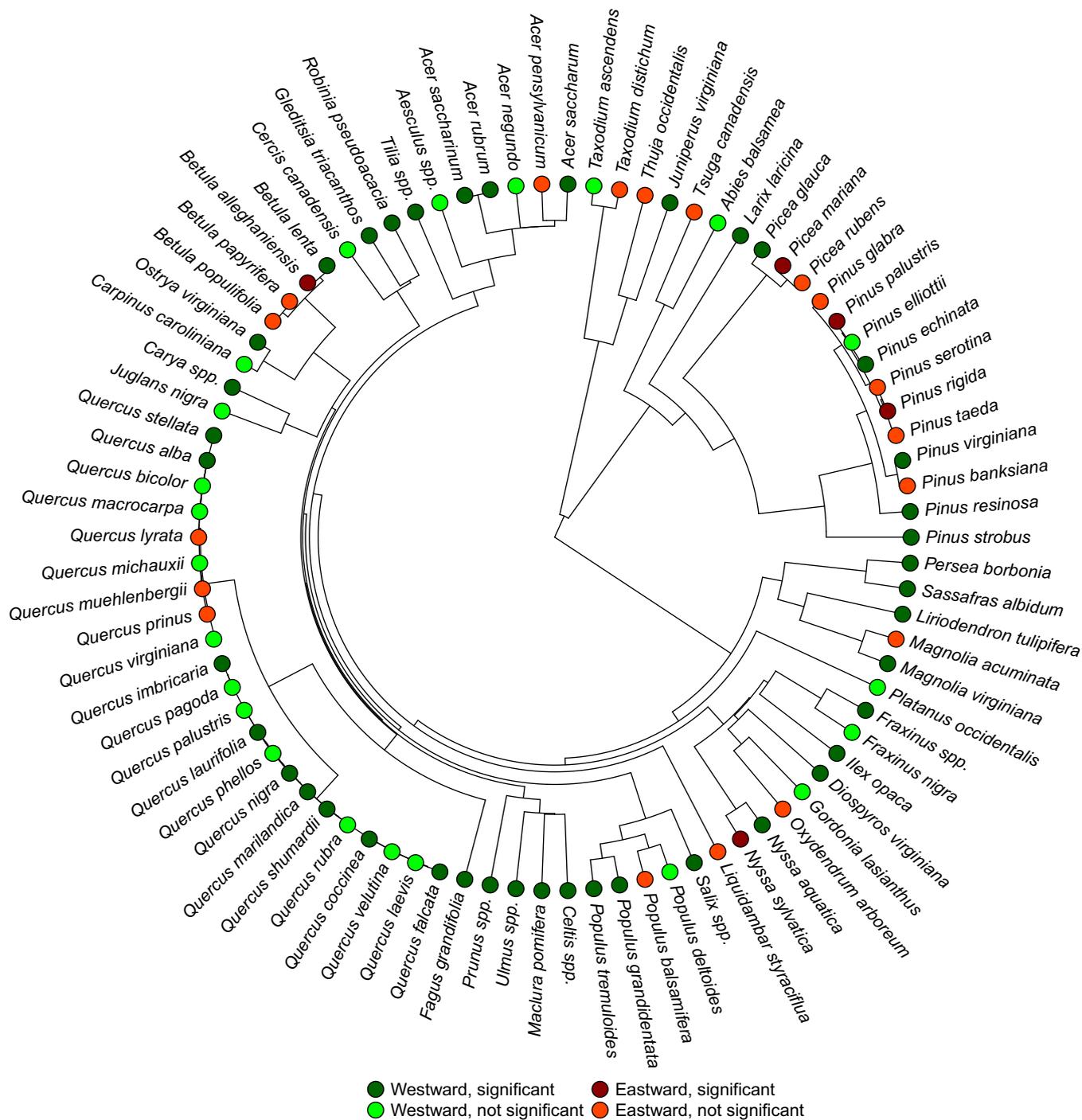
Fig. 6. Longitudinal species abundance shift mapped on a phylogram representing evolutionary relationships among the 86 study species.

change, along with other nonclimatic factors (for example, land use change and forest management), on vegetation dynamics.

These trait- and phylogenetic-specific shifts can have profound implications for the resilience and sustainability of the studied forest ecosystems, because phylogenetic relatedness among species can have strong influences on community assemblage and composition (38). Because some closely related species groups (both in functional traits and in evolutionary history) have different responses to the changing climate com-

pared to other groups, the resultant differing spatial shifts among various groups can lead to the possible marked reduction of some evolutionary lineages. The reduction or replacement of certain species in a community can be consequential, because species can have substantially different effects on ecosystem structure, function, and services, and the impacts can cascade through a broad range of ecosystem processes (39, 40).

Given the broad scale at which our analysis was conducted, a variety of indirect and nonclimatic factors (for example, fire regimes, invasive

species, forest management, conservation efforts, and land use change) could also have influenced the directional trends observed. The fact that the observed abundance change is positively correlated with the densification of forests, which is often attributed to diminishing fire frequency and severity (*26*), confirms that nonclimatic factors are also responsible for the observed spatial shift of species abundance. Heavy infestations of invasive insects, plants, and pathogens could contribute to species shifts in other directions (*41, 42*). In addition, forest conservation and plantation efforts in the study area such as those by the U.S. Department of Agriculture (USDA) Conservation Reserve Program could also influence the observed spatial shift. Nevertheless, we observed clear broad-scale evidence of the impact of climate change on forest tree spatial dynamics, where changes in mean annual precipitation alone explained about 19% of the variability in species abundance change and spatial shift. It could be beneficial for future studies to investigate the impacts of inter- and intra-annual variability of moisture availability at finer spatial and temporal resolutions (for example, for droughts and floods) on vegetation dynamics, given the high likelihood of more variable precipitation patterns in the future (*43*). In addition, because more repeated plot-level measures are becoming available across the regional scale, we can better study the degree to which climate change induces new community assemblages owing to the varying mortality and recruitment and/or competitive release of different trait- and phylogenetic-specific groups. These repeated measures may eventually enable the analysis of more tree species in the eastern U.S. forests, rather than the selected ones in this study, allowing the detection of phylogenetic- and trait-specific patterns that might be undetected in the current analysis.

In summary, trees in the eastern United States have experienced prominent westward and northward shifts in response to climate change and successional processes. These spatial shifts are more sensitive to the changes in moisture availability than to changes in temperature. The observed spatial shifts are associated with species that have similar functional traits and evolutionary histories. The resultant divergent spatial shifts among various groups can have significant ecological consequences and possible extinction of certain evolutionary lineages in some forest communities. Management actions to increase forest ecosystems' resilience to climate change should consider the changes in both temperature and precipitation.

MATERIALS AND METHODS

We obtained tree abundance data from the U.S. Forest Inventory and Analysis (FIA) program from two different inventory periods (Supplementary Text). FIA provides a long-term data set of forest conditions across all forest land in the United States, which has been used to study regional spatial and temporal forest dynamics (*23, 24, 44, 45*). The first inventory (T1) included in this study was between 1980 and 1995 and varied by state. The second inventory (T2) was the latest completed inventory, which was finished in 2015 for most states. The time period between the two intervals ranged from 20 to 35 years, with an average of 29.5 years (table S4).

Across the study area, a total of 201 species/groups were recorded during T1, and 240 were recorded during T2. To account for the variations of sampling protocols between the two inventory periods, we first applied a set of selection criteria (Supplementary Text), which resulted in a total of 86 species/groups in our analysis (table S5). Because a significant portion of the plots were measured during only one of the two inventory periods, we aggregated plot-level abundance data to the hexagon level (a spatial tessellation design used by FIA). A total of 2747

hexagons of 1452 km^2 in area, approximately the mean size of eastern counties, were used as the unit of analysis in our study. Total number of stems in a hexagon (stems/ha × total forested area) was used to measure species abundance within each hexagon for saplings [defined as <12.7 cm in diameter at breast height (dbh)] (*24*), for adult trees (>12.7 cm in dbh), and for all trees by species.

To investigate how species abundances shifted between the two inventories, we used the shift distance and direction of the geographic center weighted by species abundance (Supplementary Text). We conducted a total of 10,000 random permutations per species to test whether the observed shift was statistically significant (Supplementary Text). Rose diagrams were generated in the R circular package (*46*) to illustrate the overall pattern of abundance shift of both direction and distance for all species studied. To understand whether the observed spatial shift is due to the changes in leading or trailing edges, we first subdivided each species distribution range into four cardinal quadrants on the basis of its abundance center at T1. We then calculated and compared the shift distances and density changes for subpopulations within each quadrant. To avoid sampling biases, only species with sufficient sample sizes (≥30 hexagons and ≥300 plots) at either T1 or T2 for each subpopulation were included in this analysis. A Tukey post hoc test was applied to test whether the shifts among subpopulations in each quadrant were statistically different.

We then analyzed the relationship between the observed species shifts in relation to climate variables and forest succession status. For climate variables, we first calculated MAT, TAP, and mean PDSI in the recent past (1951–1980) and during the study period (1981–2015). MAT and TAP were calculated using the 4-km spatial resolution climate data from the PRISM Climate Group (http://prism.oregonstate.edu/), and PDSI data were obtained from the WestWide Drought Tracker (www.wrcc.dri.edu/wwdt/), which also had a spatial resolution of 4 km. These climate variables were then aggregated at the hexagon level for each period. We used stem density and basal area for all trees regardless of species as indicators of successional status at T1 and T2 for each hexagon. In general, overall stem density decreases whereas basal area increases as forest progresses from early to late successional stages. Next, we calculated relative changes in mean stem density between the two inventories by species, and we calculated relative changes between T1 and T2 in total stem density and basal area for all trees and changes over time in mean MAT, TAP, and PDSI within each species' overlapped distribution range at T1 and T2 (that is, only with hexagons that contain the target species at both T1 and T2). A multiple linear regression with a mixed-effects model was performed to test the association among changes in species-level mean stem density and changes in MAT, TAP, PDSI, total stem density, and total basal area.

To test whether the observed spatial shifts are trait-specific, we first constructed a database with two functional trait groups (table S3). The first group encompassed traits associated with trees' ability to migrate, including seed weight, dispersal mechanism, and rate of spread. The second group encompassed traits associated with trees' physiological tolerances, including temperature, precipitation, fire, shade, and drought tolerances. Because of the lack of actual precipitation and temperature tolerance data, we used minimum temperature, minimum precipitation, and maximum precipitation from species-specific realized climatic niche as surrogates in our study (see table S3 for variable definition and data sources). We compared species traits among four classes: significant westward or northward shift, nonsignificant westward or northward shift, nonsignificant east or southward shift, and significant eastward or southward shift. A Kruskal-Wallis test was used for traits with continuous variables, and a χ^2 test was used for traits with categorical variables due

to the non-normality of the data. Additionally, a Kruskal-Wallis test for differences in latitudinal and longitudinal shift rates was used for categorical plant traits.

We investigated the degree to which longitudinal and latitudinal shifts were associated with the evolutionary relatedness of tree species by displaying these shifts on a phylogenetic supertree encompassing the 86 species in the study and by testing for phylogenetic signal in these shifts. The phylogenetic supertree was pruned from one generated for 397 native tree species occurring throughout the forests of the contiguous 48 states and inventoried by FIA, as described by Potter and Woodall (47). We used the R package phytools (48) to display each species' longitudinal and latitudinal shifts (across all life stages) on the phylogenetic tree, with trees in the aforementioned four classes. We then used the R package picante (49) to test the degree to which the tree species phylogeny predicts the ecological similarity of the species with respect to these shifts. Specifically, we generated the K statistic, which compares the observed phylogenetic signal in a trait (in this case, the longitudinal or latitudinal shift) to the signal under a Brownian motion model of trait evolution on a phylogeny (50), and then assessed the statistical significance of the phylogenetic signal by comparing observed patterns of the variance of independent contrasts of each trait to a null model of shuffled taxon labels across the tips of the phylogeny.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/5/e1603055/DC1

Supplementary Text

fig. S1. Average environmental conditions during the study period.

fig. S2. Relationships between changes in species abundance, PDSI, temperature, and total tree basal area.

fig. S3. Box plots of functional trait values for species that experienced different longitudinal shifts (E0, nonsignificantly eastward; E1, significantly eastward; W0, nonsignificantly westward; W1, significantly westward).

fig. S4. Box plots of latitudinal and longitudinal stem density shifts by physiological trait groups.

fig. S5. Box plots of functional trait values for species that experienced different latitudinal shifts (N0, nonsignificantly northward; N1, significantly northward; S0, nonsignificantly southward; S1, significantly southward).

fig. S6. Box plots of latitudinal and longitudinal stem density shifts by dispersal trait groups.

fig. S7. Latitudinal species abundance shift mapped on a phylogram representing evolutionary relationships among the 86 study species.

table S1A. Summary of shift percentage and distance by directions.

table S1B. Shift of species abundance for all trees during the last three decades.

table S1C. Shift of species abundance for sapling-sized trees during the last three decades.

table S1D. Shift of species abundance for adult trees during the last three decades.

table S2. Linear mixed-effect model parameter estimates and significance for the relationships between species shift and changes in environmental variables and successional processes.

table S3. Description of functional traits used in the analysis.

table S4. Years during which the first inventory (T1) and second inventory (T2) were completed for each state.

table S5. Species used in the study and their sample sizes and their mean density at the first and second inventories.

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