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Trends over time in tree and seedling phylogenetic diversity indicate regional differences in forest biodiversity change

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Abstract. Changing climate conditions may impact the short-term ability of forest tree species to regenerate in many locations. In the longer term, tree species may be unable to persist in some locations while they become established in new places. Over both time frames, forest tree biodiversity may change in unexpected ways. Using repeated inventory measurements five years apart from more than 7000 forested plots in the eastern United States, we tested three hypotheses: phylogenetic diversity is substantially different from species richness as a measure of biodiversity; forest communities have undergone recent changes in phylogenetic diversity that differ by size class, region, and seed dispersal strategy; and these patterns are consistent with expected early effects of climate change. Specifically, the magnitude of diversity change across broad regions should be greater among seedlings than in trees, should be associated with latitude and elevation, and should be greater among species with high dispersal capacity. Our analyses demonstrated that phylogenetic diversity and species richness are decoupled at small and medium scales and are imperfectly associated at large scales. This suggests that it is appropriate to apply indicators of biodiversity change based on phylogenetic diversity, which account for evolutionary relationships among species and may better represent community functional diversity. Our results also detected broadscale patterns of forest biodiversity change that are consistent with expected early effects of climate change. First, the statistically significant increase over time in seedling diversity in the South suggests that conditions there have become more favorable for the reproduction and dispersal of a wider variety of species, whereas the significant decrease in northern seedling diversity indicates that northern conditions have become less favorable. Second, we found weak correlations between seedling diversity change and latitude in both zones, with stronger relationships apparent in some ecoregions. Finally, we detected broadscale seedling diversity increases among species with longer-distance dispersal capacity, even in the northern zone, where overall seedling diversity declined. The statistical power and geographic extent of such analyses will increase as data become available over larger areas and as plot measurements are repeated at regular intervals over a longer period of time.

Key words: biodiversity; climate change; conservation biology; dispersal; ecosystem function; forest health; indicator; landscape ecology; monitoring; North America; phylogenetic diversity; regional scale.

INTRODUCTION

The world's climate is forecasted to change significantly over the next century, resulting in an increase in mean surface temperatures of 2–4.5°C, more episodic precipitation events, and longer growing seasons (International Panel on Climate Change 2007), all of which, in turn, may drive changes in forest ecosystem functions and attributes (Stenseth et al. 2002). Plant species are expected to respond in one of three ways to the numerous climate change effects that could push their current habitat out of their tolerance limits: (1) on-site tolerance or adaptation, (2) range shift, or (3) extinction (Davis et al. 2005). As species are eliminated from existing areas and disperse successful propagules into new areas, the latter two of these responses could each affect forest tree biodiversity and the wide variety of ecological benefits associated with biodiversity (Knops et al. 1999, Balvanera et al. 2006, Cardinale et al. 2007, Zavaleta et al. 2010). Although climate change is expected to have large impacts on the area and location of suitable tree species habitat in the eastern United States (Iverson and Prasad 1998, Schwartz et al. 2001, Iverson et al. 2008), the composition of future forest communities remains largely unpredictable. Within this context, the development of novel indicators of forest community response to rapid climate change (e.g., loss of biodiversity or genetic diversity) will enable robust monitoring of forest ecosystems across short time frames

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and large spatial scales. These indicators have particular relevance, given the importance of considering biodiversity in policy and management decisions, especially when making decisions involving large temporal and spatial scales (Hooper et al. 2005).

Traditional measures of biodiversity, such as species richness, usually treat all species as equally important, and therefore may have more limited value than measures that account for phylogenetic relationships among species (Vane-Wright et al. 1991). Taxonomically distinct species are expected to contribute more to the diversity of features, including functional traits, present within a given community (Faith 1992), so measurements of evolutionary history within a set of co-occurring species are assumed to represent the diversity of traits present within that community (Faith 2002). Studies have determined that plant phylogenetic diversity explains more variation in community productivity than other measures of biodiversity (Cadotte et al. 2008, 2009). Community phylogenetic diversity has been linked at some phylogenetic scales to nutrient cycling, resistance to invasion, soil carbon accumulation and other ecosystem processes, and goods and services, supporting the argument that phylogenetic diversity is more useful than species richness as a conservation criterion for management decisions (Cavender-Bares et al. 2009).

Several studies (e.g., Proches et al. 2006, Coca and Pausas 2009, Vamosi and Queenborough 2010) have quantified the cumulative evolutionary history represented within plant communities using measures based on Faith's phylogenetic diversity index (Faith 1992, 1994), which sums the length of the phylogenetic tree branches representing the minimum tree-spanning path among a group of species. A comparison of phylogenetic diversity and species richness demonstrated that phylogenetic diversity is a more appropriate measure of biodiversity because species richness is more sensitive to taxonomic inflation associated with sampling effort (Pillon et al. 2006). Additionally, Forest et al. (2007) concluded that maximizing phylogenetic diversity would be the best bet-hedging strategy during a future of climatic change because doing so would maximize community feature diversity and, therefore, preserve more options for future evolutionary diversification. Similarly, Cavender-Bares et al. (2009) predicted that high phylogenetic diversity could increase ecosystem stability by ensuring that sufficient ecological strategies are represented in a community to ensure its persistence in the face of changing conditions.

Although the disciplines of phylogenetics and global change ecology overlap (Edwards et al. 2007), only a few studies have thus far focused on the relationship between evolutionary diversity and climate change (e.g., Edwards and Still 2008, Willis et al. 2008). Quantifying change over time in the phylogenetic diversity of different size classes of forest trees is a potentially valuable approach for detecting broadscale biodiversity changes associated with climate change. Specifically, at least three patterns of change in phylogenetic diversity would suggest that the composition of forested ecosystems is responding to changing climate conditions. First, seedlings should be more sensitive than adult demographic cohorts to changing environmental conditions (Watkinson 1997), so the magnitude of phylogenetic diversity change across broad regions should be greater among seedlings than in trees in response to consistent, broadscale climate change. Such change over time in seedling phylogenetic diversity may represent the early stages of potential long-term shifts in forest biodiversity associated with climate change. This is because seedling establishment in sufficient numbers is necessary to perpetuate populations (Hamrick 2004), and because the successful movement of tree species into new areas begins with the establishment of tree seeds from elsewhere. Second, change in the phylogenetic diversity of seedlings should be associated with latitude and elevation, as recent research has demonstrated that tree species distributions may be shifting northward (Parmesan and Yohe 2003, Woodall et al. 2009) and to higher elevations (Goldblum and Rigg 2002, Landhausser et al. 2010). Species dispersing seed to the north and to higher elevations should increase the diversity of these areas if species already existing there continue to reproduce successfully. The association between increased diversity and higher latitudes should be particularly apparent in regions where immigration from the south is limited by ecological barriers, such as the Gulf of Mexico in the southeastern United States and the largely nonforested prairie for the northern Midwest. Finally, the phylogenetic diversity of seedlings of species with high dispersal capacity should increase over broad areas, as these species may be best adapted to take advantage of changing environmental conditions to establish themselves in newly suitable habitats (Clark 1998, Cain et al. 2000), whereas species with lower dispersal capacity may have a lessened likelihood of reaching distant habitats to colonize (Walther et al. 2002). In all three cases, it would be useful to assess whether the direction and magnitude of change in seedling biodiversity is comparable to change in adult tree biodiversity, because change in seedling diversity across broad scales should reflect, to some degree, the change in tree diversity when, over time, forest succession proceeds in a relatively consistent manner and when approximately the same proportion of forest exists in early vs. later successional stages.

The goal of this study was to use a region-wide permanent forest inventory in the eastern United States to assess change over time in forest tree (diameter at breast height > 2.54 cm) and seedling (diameter at breast height < 2.54 cm) phylogenetic diversity at two scales: within two latitudinal zones and within broad ecoregions inside each zone. Repeated measurement data from nearly 7000 forest inventory plots were analyzed to test the following hypotheses: (1) phylogenetic diversity is a measure of biodiversity that, for forest trees across broad regions in the eastern United States, is substantially different than species richness; (2) forest communities have undergone recent phylogenetic diversity changes that differ by size class, region, and seed dispersal strategy; and (3) these patterns of phylogenetic diversity change are consistent with expected early effects of climate change, including greater change in seedling than in mature tree diversity, greater seedling diversity change at more northerly latitudes and at higher elevations, and increased seedling diversity among species with high dispersal capacity.

Materials and Methods

Data

The Forest Inventory and Analysis (FIA) program of the United States Department of Agriculture (USDA) Forest Service is the primary source for information about the extent, condition, status, and trends of forest resources across all ownerships in the United States (Smith 2002). FIA applies a nationally consistent sampling protocol using a systematic design to conduct a multiphase inventory of all ownerships in the entire nation (Bechtold and Patterson 2005). In Phase 1, land area is stratified by land cover using aerial photography or classified satellite imagery to increase the precision of estimates with stratified estimation. Remotely sensed data also may be used to determine if plot locations have forest land cover; forest land is defined as areas at least 10% stocked with tree species, at least 0.4 ha in size, and at least 36.6 m wide (Bechtold and Patterson 2005). In Phase 2, permanent fixed-area plots (~0.067 ha in size) are installed when field crews visit plot locations that have accessible forest land. Field crews collect data on more than 300 variables, including land ownership, forest type, tree species, tree size, tree condition, and other site attributes, such as slope, aspect, disturbance, and land use (Smith 2002, USDA Forest Service 2008*a*). Plot intensity for Phase 2 measurements is approximately one plot for every 2428 ha of land (~125 000 plots across the 48 conterminous United States and southeastern Alaska). The FIA system is designed so that field crews revisit plots in the eastern United States every five years, with 20% of all plots being remeasured every year on a 5-year rotating basis thereafter. Initial annual inventory plots were established between 1999 and 2005.

Each FIA inventory plot consists of four 7.2-m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center. All trees with a diameter at breast height (dbh) of at least 12.7 cm are inventoried on forested subplots. Trees are defined as woody plants usually having one or more erect perennial stems, a stem diameter at maturity of at least 7.62 cm, a more or less definitely formed crown of foliage, and a height of at least 4.75 m at maturity. Within each subplot, a microplot (radius 2.07 m) is established, offset 3.66 m from the subplot center, in which all trees with a dbh between 2.54 and 12.7 cm are inventoried. Within each microplot, all live tree seedlings are tallied according to species. Conifer seedlings must be at least 15.2 cm in height with dbh < 2.54 cm. Hardwood seedlings must be at least 30.5 cm in height with a dbh < 2.54 cm. Therefore, in this study, seedlings are defined as trees with dbh < 2.54 cm, including those that cross the conifer or hardwood height threshold but are not tall enough to measure diameter at breast height, whereas trees are defined as having dbh ≥ 2.54 cm.

All inventory data are managed in an FIA database (FIADB) and are publicly available. Data for this study were taken entirely from the FIADB from plots using the most recent annual inventory in eight eastern states, divided into northern and southern latitudinal zones to investigate differences in phylogenetic diversity across a climatic gradient. The first measurement for each plot included in the study was taken between 2001 and 2003, with the subsequent remeasurement five years later, between 2006 and 2008.

To evaluate changes in biodiversity at different latitudes, we selected four northern and four southern states, based on spatial contiguity and adequate remeasurement data. States were chosen in which FIA inventories had been remeasured sufficiently to allow for statistical testing of change over time, and where contiguity allowed for representation of spatially extensive forested ecosystems. Tree inventory data were assembled from 6970 FIA plots, each with two observations five years apart, from the two latitudinal zones. The zones were each ~6.5° in latitudinal width and are separated by ~5.8° latitude (Fig. 1). The southern zone encompassed 2394 plots from four contiguous southern states (north of 30.18° N, which is the southernmost extent of Alabama, and south of 36.68° N, which is the northernmost extent of Tennessee). Of these, 2365 contained trees and 2232 contained seedlings. The northern zone encompassed 4576 plots from four contiguous northern states (north of 42.5° N, which is the southern border of Wisconsin, and south of 49.38° N, which is the northernmost point of Minnesota). Of these, 4524 contained trees and 4233 had seedlings. Unequal regional sample intensities are due to the ongoing implementation of a fully annual forest inventory. Because the FIA inventory is systematic, with sample plots distributed across the geographic extent of each state, varying sample intensities will not bias assessment of tree species locations; it will only affect the precision of the estimates. To eliminate the potential effects of management activities and to reduce the relative influence of forest succession compared to climate change on seedling biodiversity, plots were not included in the analysis if any management activity had occurred on them.

Analysis

We calculated Faith's (1992) index of phylogenetic diversity (PD) for each plot using Phylocom version 3.41 (Webb et al. 2008). PD is the minimum spanning

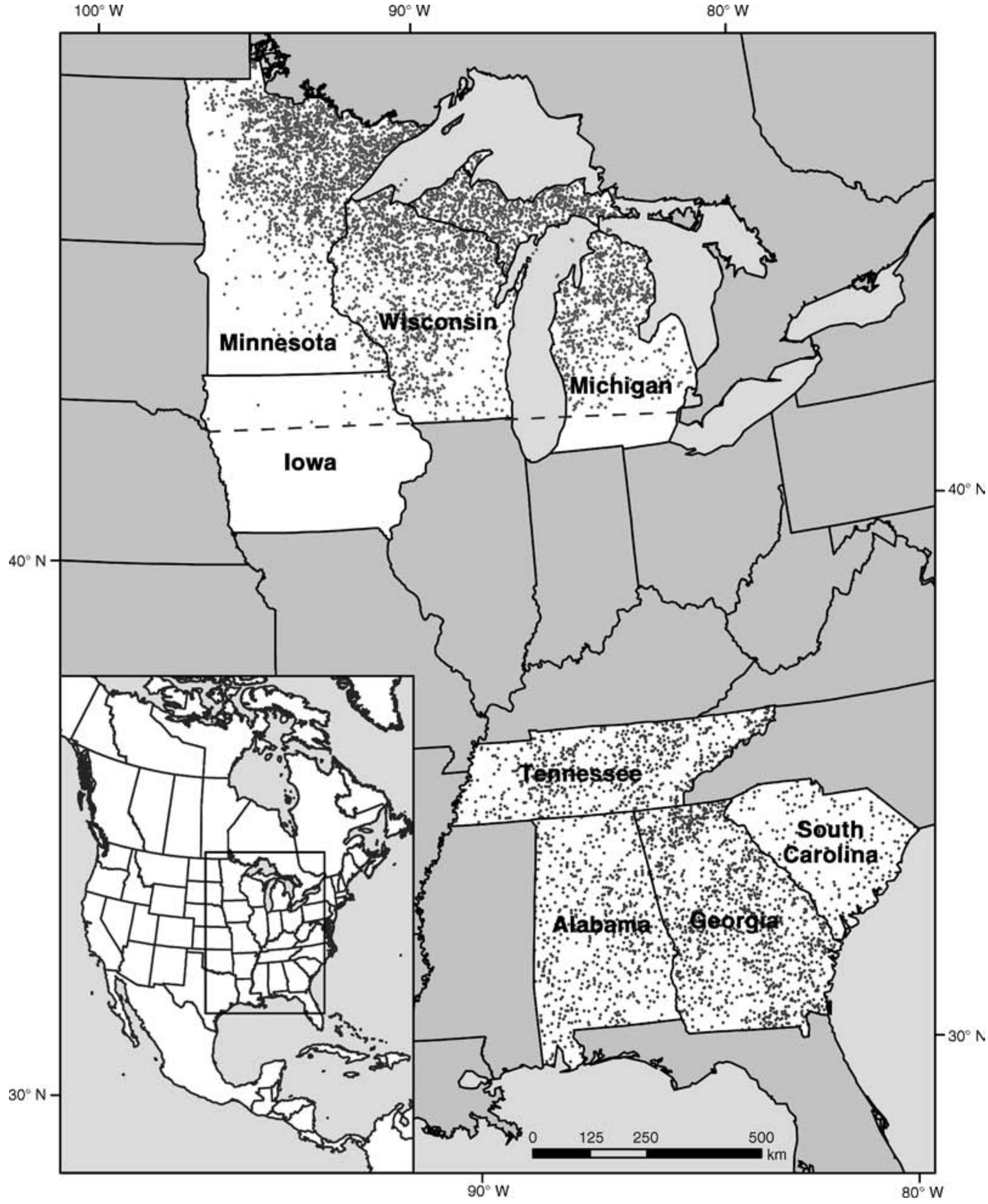

FIG. 1. The Forest Inventory and Analysis (FIA) plots ($N = 6970$) included in the study from four northern and four southern states; for each, forest trees >2.45 cm diameter at breast height (dbh) and tree seedlings <2.45 cm dbh were inventoried at two time points five years apart. The dashed line depicts the southern boundary of the northern latitudinal zone. Each plot is ~0.067 ha in size; locations are approximate.

distance (sum of all branch lengths) of a phylogenetic tree including all the species from a given plot. It was chosen from among many metrics of phylogenetic diversity because it is conceptually simple, relatively easy to calculate, widely used, and among the first such metrics to be developed. Determining plot-level PD required construction of a hypothesized phylogenetic supertree of all 311 North American tree species included in the FIA database (Fig. 2). We first used the online phylogenetic database and toolkit Phylomatic (Webb and Donoghue 2005), reference megatree R20040402, to generate a backbone phylogenetic supertree topology based on the Angiosperm Phylogeny Group (APG) II classification of flowering plant families (Angiosperm Phylogeny Group 2003). We then used the BLADJ (Branch Length ADJustment) module in Phylocom 3.41 (Webb et al. 2008) to assign ages to nodes in this supertree based on the fossil and molecular

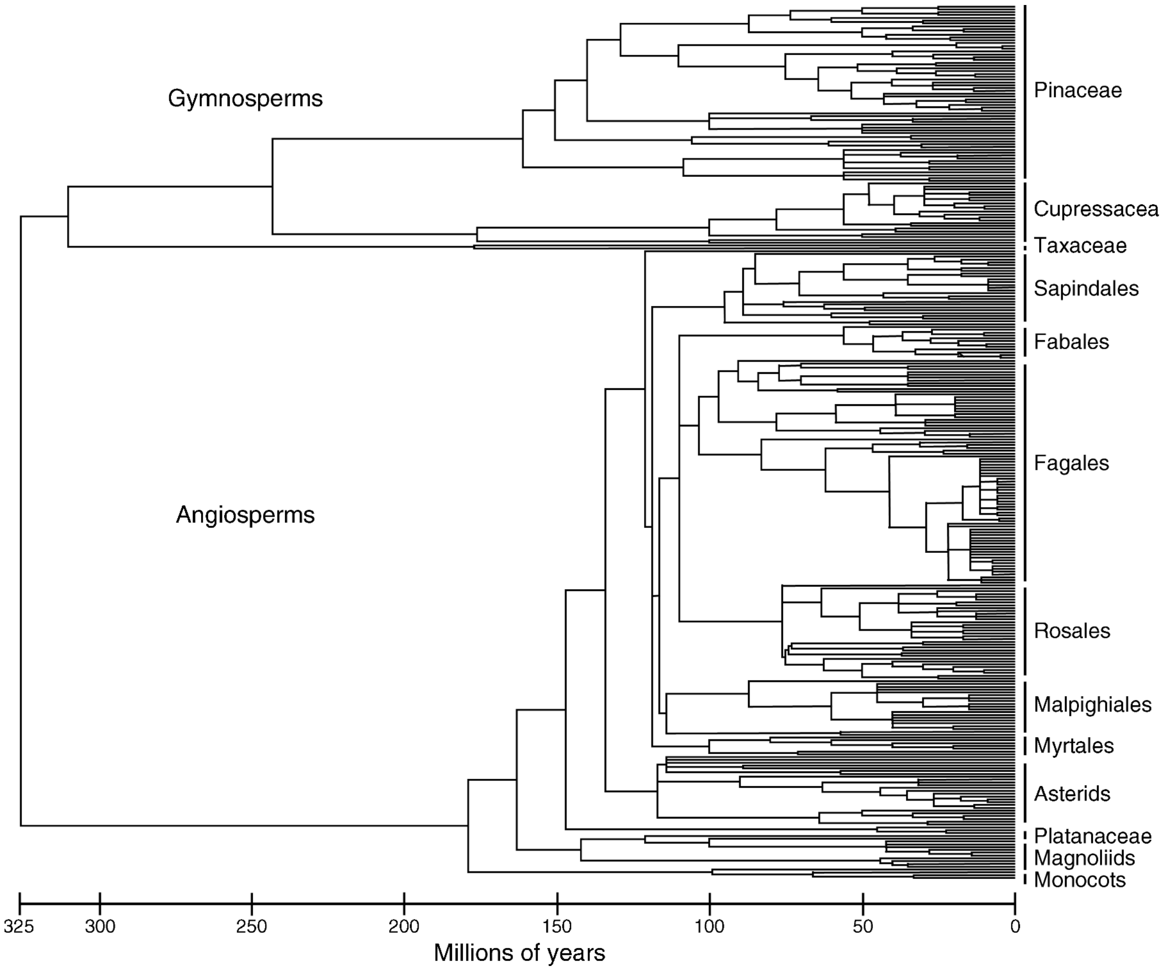

FIG. 2. The phylogenetic supertree of the 311 North American forest tree species included in the Forest Inventory and Analysis database, with branch lengths measured in millions of years.

estimates reported by Wikström et al. (2001), with undated nodes spaced evenly between dated nodes to minimize variance in branch lengths. We are aware of more recent backbone supertree topologies from the APG (e.g., R20100701) and updated node ages that are likely to be more accurate (Bell et al. 2010), but the differences should be minimal for the taxa included in our study. The resulting "pseudo-chronogram" can be used to estimate phylogenetic distance, in units of time, between taxa (Webb et al. 2008). This process, however, does not generate well-supported node ages below the family level, and includes only flowering plants. To improve the resolution of the phylogenetic supertree to the species level, and to incorporate gymnosperms, we surveyed recent molecular systematic and paleobotanical studies of the families and genera that encompass North American tree species, and of the higher-level gymnosperm groups (see Appendix A). We added dated node constraints to the supertree topology where possible, and then re-ran the BLADJ algorithm in Phylocom to again set the ages of undated nodes evenly between dated nodes for the supertree used in this study (Appendix B). Such supertree phylogenies approximate the actual evolutionary relationships among species, and can be improved with additional molecular systematic research and with enhanced understanding of the fossil record.

We used this supertree to calculate plot-level phylogenetic diversity, measured in millions of years, separately for trees and seedlings for all species present on each plot. We conducted linear regression analyses using PROC REG in SAS 9.2 (SAS Institute 2008) to quantify relationships between plot-level tree phylogenetic diversity and species richness, and between seedling phylogenetic diversity and species richness. This was done at time 2 (T2), and for change over time in phylogenetic diversity, for trees and seedlings separately for the northern and southern zones. Additionally, we conducted these same regressions, separately for seedlings and trees, for each ecoregion section contained within the northern and southern zones, using the most recent geographic information system (GIS) mapping of ecoregions by the USDA Forest Service (Cleland et al. 2007). Ecoregion sections encompass areas similar in their geology, climate, soils, potential natural vegetation, and potential natural communities (Cleland et al. 1997); ecoregions containing fewer than 15 plots were not included in the analysis. We additionally conducted loess regressions (Cleveland 1979, Cleveland and Devlin 1988) of phylogenetic diversity on species richness, during the second measurement time, using PROC LOESS in SAS 9.2 (SAS Institute 2008) as a robust nonparametric curve-fitting method to compare the two diversity indices (Forest et al. 2007). We selected smoothing parameters using bias-corrected Akaike information criteria (Hurvich et al. 1998); the selected smoothing parameters were 0.4 for northern zone trees and seedlings and for southern zone seedlings, and 0.1 for southern zone trees. We then interpolated the plot-level loess regression residuals using inverse distance-weighting in ArcMap 9.2 (ESRI 2006), at a resolution of 1 km^2 with a 100-km search radius. A forest cover map (1-km^2 resolution), derived from Moderate Resolution Imaging Spectroradiometer (MODIS) imagery by the USDA Forest Service Remote Sensing Applications Center (USDA Forest Service 2008*b*) was used as a mask for the interpolation results.

To aid in the selection of taxonomic groups for future monitoring of climate change, we quantified PD at four taxonomic scales: (1) for all species, (2) separately for angiosperms and gymnosperms, (3) separately for four families that are species-rich and widespread in both the north and south (Betulaceae, Juglandaceae, Pinaceae, and Rosaceae), and (4) separately for three genera that are species-rich and widespread in both the north and south (*Acer*, *Pinus*, and *Quercus*). To test whether species' ability to disperse their seed at longer distances would affect patterns of PD, we separated species into groups based on seed dispersal strategy. Seeds for each species were categorized as (1) small fruits dispersed by birds and water, (2) fruits and seeds dispersed by wind, or (3) large fruits dispersed by mammals and gravity. These assignments were based on species and genera descriptions in *Silvics of North America* (Burns and Honkala 1990), the *Woody Seed Plant Manual* (Bonner and Karrfalt 2008), and *Flora of North America North of Mexico* (Flora of North America Editorial Committee 1993+). To eliminate the possibility that the results would be skewed by the presence or establishment of nonnative tree species on FIA plots, all tree and seedling species not native to North America were removed from the analyses (<1% of the total number of stems in both latitudinal zones during both measurements).

Because the plot-level PD results were not normally distributed, we used a Wilcoxon signed rank test (Conover 1971) to determine whether change over time in tree and seedling phylogenetic diversity was significant for each species group. To approximate the spatial patterns of PD across the study zones, we conducted inverse distance-weighting interpolation of the plot-level results in ArcMap 9.2 (ESRI 2006), at a resolution of 1 km^2 with a 100-km search radius.

Finally, to examine finer-scale patterns of phylogenetic diversity change, we computed mean plot-level PD values for trees and seedlings within ecoregion sections. We dropped ecoregions containing fewer than 15 FIA plots from this analysis, and used a Wilcoxon signed rank test to determine whether the mean percentage change values across each ecoregion were significant (Conover 1971). Finally, we used PROC CORR in SAS (SAS Institute 2008) to test for correlations between plot-level change in seedling diversity and latitude, and between plot-level change in seedling diversity and elevation, both within latitudinal zones and within ecoregion sections.

RESULTS

Significant linear relationships existed between phylogenetic diversity and species richness in both trees ($R^2 = 0.704$ in the north; $R^2 = 0.796$ in the south) and seedlings ($R^2 = 0.746$ in the north; $R^2 = 0.855$ in the south). Similarly, change in species diversity and change in phylogenetic diversity were also related in both the northern zone ($R^2 = 0.667$ for trees; $R^2 = 0.795$ for seedlings) and the southern zone ($R^2 = 0.601$ for trees; $R^2 = 0.793$ for seedlings). The interpolation of the loess regression residuals from the comparison of phylogenetic diversity with species richness, however, showed important geographic patterns in the degree to which the two biodiversity metrics were related. For example, a gradient of higher-than-expected to lower-than-expected values of tree PD existed in the northern zone from northeast to southwest (Fig. 3a). Meanwhile, higher-than-expected values of PD tended to cluster in the central and southeastern parts of the southern latitudinal zone, whereas lower-than-expected values generally clustered in the northwestern parts of the zone (Fig. 3a). Similar patterns existed among seedlings, except that in the southern zone, patches with lower-than-expected PD tended to be smaller and more widely distributed (Fig. 3b). Linear regressions within each ecoregion section provide further evidence of considerable geographic variation in the strength of the relationship between phylogenetic diversity and species richness (Appendix C). For example, from the regression of tree PD during the second measurement on species richness during the same measurement, R^2 values were as low as 0.483 and 0.510 and as high as 0.877 and 0.873. Similarly, section-level R^2 values from regressions of tree PD change over time on species richness change over time ranged from 0.404 and 0.471 to 0.948.

Although the phylogenetic diversity of trees increased slightly both in the north and in the south (Table 1a), seedling diversity declined in the north and increased in the south (Table 2a). The phylogenetic diversity for trees in the northern latitudinal zone during their first measurement had a mean of 837.97 million years per plot (hereafter, myp), with SD of 302.55 myp, and a

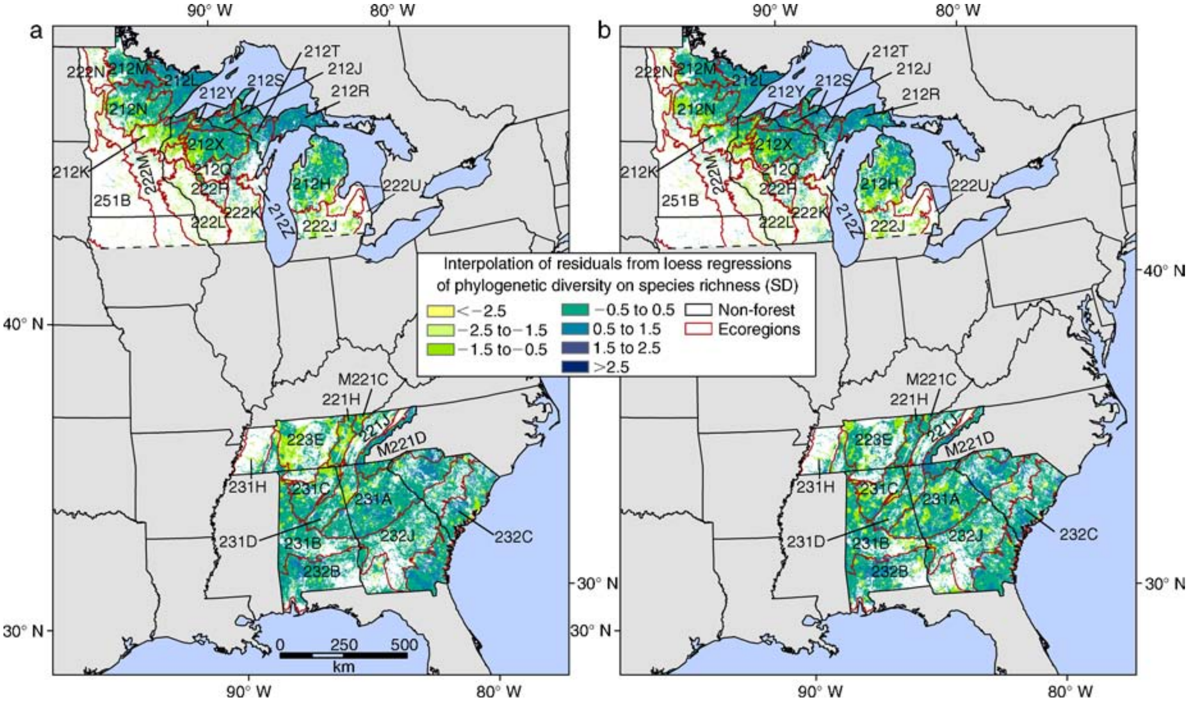

FIG. 3. Interpolation of plot-level residuals from regression of phylogenetic diversity on species richness for (a) forest trees (dbh > 2.54 cm) and (b) seedlings (dbh < 2.54 cm) at measurement time 2, displayed by standard deviation. Negative values denote smaller-than-expected phylogenetic diversity, whereas positive values are larger than expected. Regressions were conducted separately for trees and seedlings in the northern and southern latitudinal zones. For ecoregion section names, see Table 3.

range from 325 million years on single-species plots to 1927.43 million years on one plot containing 12 species. After five years (i.e., during the plot remeasurement), the mean plot-level PD for trees increased slightly to 841.21 ± 303.6 myp (mean ± SD). This increasing trend over time was consistent with the results from the south, where mean plot phylogenetic diversity was 986.6 ± 357.79 myp in the first measurement and 991.29 ± 359.52 myp in the second measurement. The mean plot-level increase in tree PD for both regions was small but significant, as determined by a Wilcoxon signed rank test (Conover 1971). The direction of change over time in seedling PD, meanwhile, was not consistent between the two regions (Table 2a). Seedling diversity in the north decreased significantly from the first measurement to the second. Seedling diversity in the south, however, increased significantly over time.

Slight increases in tree diversity, coupled with decreases in seedling diversity, occurred consistently across several taxonomic groups in the north: flowering plants and conifers, Pinaceae species, and *Acer* and *Quercus* species (Appendices D and E). In the south, only gymnosperm, Pinaceae, and *Pinus* species demonstrated this pattern; seedling diversity increased for all other species groups.

Significant changes in seedling PD also differed by seed dispersal strategy and by region, as determined by a Wilcoxon signed rank test (Conover 1971); see Table 2b. Specifically, mean plot PD for seedlings of species that are bird-dispersed increased significantly in both the north (38.18 ± 213.91 myp [mean ± SD] for Time 2

TABLE 1. Measures of mean phylogenetic diversity (PD) and PD change over time (T1, T2) for forest trees >2.54 cm dbh on Forest Inventory and Analysis plots in the northern and southern zones of the eastern United States.

	Northern trees					Southern trees				
Categories of tree species	*N*	PD, T2	PD, T1	PD, T2 − T1	*P*	*N*	PD, T2	PD, T1	PD, T2 − T1	*P*
a) All species	4524	841.21	837.97	**3.24**	**<0.001**	2365	991.29	986.60	**4.70**	**<0.001**
b) Dispersal strategy										
Bird-dispersed	1821	367.34	357.36	**9.98**	**<0.001**	1992	541.95	538.10	**3.85**	**<0.001**
Wind-dispersed	4428	726.64	724.90	**1.73**	**<0.001**	2266	582.46	581.21	**1.26**	**0.01**
Gravity-dispersed	1790	379.00	379.93	−0.94	0.975	1456	470.72	469.21	1.51	0.145

Notes: PD is measured in millions of years per plot. Significant measures of mean plot-level change over time, based on a Wilcoxon signed rank test, are in bold.

TABLE 2. Measures of mean phylogenetic diversity (PD) and PD change over time (T1, T2) for forest tree seedlings <2.54 cm dbh on Forest Inventory and Analysis plots in the northern and southern zones of the eastern United States.

	Northern seedlings					Southern seedlings				
Categories of tree species	*N*	PD, T2	PD, T1	PD, T2 − T1	*P*	*N*	PD, T2	PD, T1	PD, T2 − T1	*P*
a) All species	4233	712.30	722.56	**−10.26**	**<0.001**	2232	923.26	887.41	**35.85**	**<0.001**
b) Dispersal strategy										
Bird-dispersed	2731	330.14	291.96	**38.18**	**<0.001**	2177	564.56	530.33	**34.23**	**<0.001**
Wind-dispersed	4113	575.05	597.69	**−22.64**	**<0.001**	2027	464.84	466.56	−1.72	0.519
Gravity-dispersed	1659	270.99	304.23	**−33.23**	**<0.001**	1504	373.80	352.63	**21.17**	**<0.001**

Notes: PD is measured in millions of years per plot. Significant measures of mean plot-level change over time, based on a Wilcoxon signed rank test, are in bold.

minus Time 1) and the south (34.23 ± 240.53 myp), but seedling diversity for heavy-seeded species increased significantly in the south (21.17 ± 207.78 myp) and decreased significantly in the north (−33.23 ± 213.14 myp). The diversity of wind-dispersed species also decreased significantly in the north (−22.64 ± 206.3 myp), but did not undergo a significant change in the south.

The interpolations of plot-level percentage change in tree diversity and seedling diversity showed a widespread but small increase in tree diversity in both the north and the south (Fig. 4a), but indicated strong clustering of both increases and decreases in seedling diversity for both latitudinal zones (Fig. 4b). In the south, decreased seedling diversity was clustered mainly in South Carolina and western Alabama, whereas increased diversity was clustered in Tennessee, central Georgia, and central to south-central Alabama. Increased seedling diversity in the north tended to be clustered in northern Minnesota and the northern part of the lower peninsula of Michigan, whereas decreased diversity was widespread across Wisconsin and far western and southern Michigan.

Mean plot-level percentage change in tree PD in the northern and southern zones was significantly positive but small, ~0.5% (Table 3). Mean plot-level percentage change in seedling diversity was 9.45% in the southern zone, but not significantly different from 0% in the northern zone. Mean seedling percentage PD change was significantly positive in three northern ecoregions and significantly negative in five other ecoregions (Table 3a). The three northern ecoregions with a significantly positive percentage increase in seedling diversity (>15%) were located in the northwestern part of the region (Fig. 5). The five ecoregions with significantly negative seedling diversity were located in north-central Wisconsin and the far western edge of the upper peninsula of Michigan (Fig. 5). In the south, percentage change in seedling PD was significantly positive in seven ecoregions and negative in none (Table 3b). All seven southern ecoregions with increases in seedling PD were located in the northern half of this latitudinal zone (Fig. 5).

Mean plot percentage change in seedling PD was weakly, but significantly, correlated with latitude in the northern and southern zones (Table 3). Elevation was weakly correlated with percentage seedling change in the south, but not in the north. Within most ecoregions, the relationships of seedling change with latitude and elevation were weak or not significant, with some exceptions. A moderately strong positive relationship existed between seedling diversity change and latitude in three southern-zone ecoregions (Northern Cumberland Plateau [221H], Coastal Plains-Middle [231B], and Coastal Plains-Loess [231H]). Increased seedling diversity was positively and strongly correlated with elevation in one southern ecoregion (Southern Cumberland Plateau [231C]) and negatively correlated in another (Central Ridge and Valley [221J]) (Table 3b).

DISCUSSION

Comparison of biodiversity metrics

Our analyses demonstrate that although phylogenetic diversity and species richness have similar distributions when quantifying forest biodiversity, important differences exist between the two. Specifically, the linear relationship between the two indices varies both between latitudinal zones and among ecoregions within each latitudinal zone (Appendix C). Considerable variation exists, as well, in the degree to which phylogenetic diversity is greater or less than expected based on the species richness of a plot, as revealed in the interpolation of the residuals from the loess regression of PD on species richness. This variation occurs at small scales, but with clear geographic trends among ecoregions (Fig. 3), which are defined by geology, climate, soils, and potential plant communities (Cleland et al. 1997).

Applying indicators of biodiversity change using phylogenetic diversity rather than species richness seems appropriate, given the decoupling of the two indices at small to medium scales, and the imperfect relationship even at large scales, and given the ability of evolutionary history measurements to better represent community trait variation in at least some cases (Faith 2002, Forest et al. 2007, Cadotte et al. 2008, 2009). We analyzed change in the plot-level phylogenetic diversity of forest communities across two widely separated latitudinal zones to test the applicability of these biodiversity indicators to areas encompassing widely differing forest ecosystems in the eastern United States. Our results

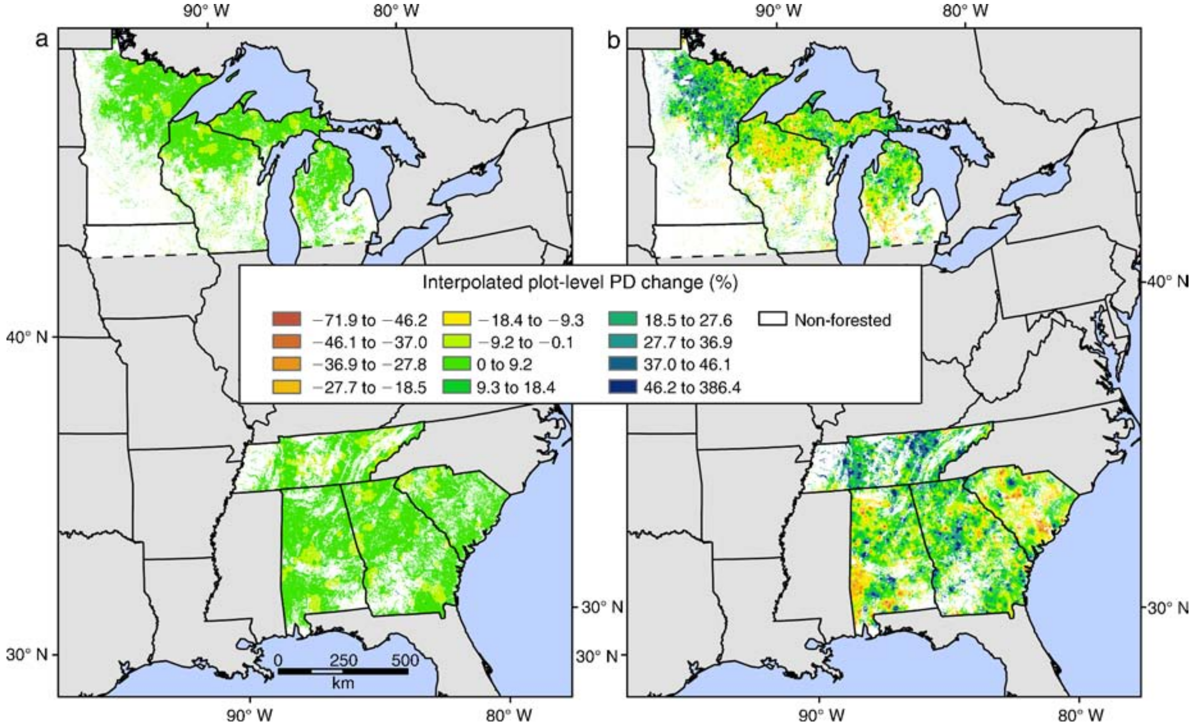

FIG. 4. Interpolation of plot-level percentage change in (a) forest tree (dbh > 2.54 cm) and (b) seedling (dbh < 2.54 cm) phylogenetic diversity across four northern and four southern states. Forest cover is from USDA Forest Service (2008*b*).

detected significant regional change in forest phylogenetic diversity, suggesting that the quantification of differences in this metric over time within forest tree size classes, particularly seedling phylogenetic diversity, represents a sensitive indicator of regional biodiversity change that may prove useful for tracking climate-change-related impacts on forest community structure, ecology, and function.

Phylogenetic diversity change and climate change expectations

Three patterns of change over time in forest phylogenetic diversity would be consistent with the expected effects of climate change on the biodiversity of forested ecosystems at broad scales: (1) strong regional changes in the phylogenetic diversity of seedlings relative to changes in mature trees, (2) correlations within regions between seedling phylogenetic diversity change and latitude and elevation, and (3) greater regional increases in the phylogenetic diversity of taxa with long-distance dispersal capacity.

The results of this study confirm that the first of these patterns exists. The statistically significant increase over time in seedling diversity in the south (Table 2) suggests that conditions there became more favorable for the reproduction and dispersal of a wider variety of existing tree species, whereas the significant decrease in northern seedling diversity indicates that conditions in the north may have become generally less favorable. Little change in tree diversity occurred in either latitudinal zone, however (Table 1), underscoring the expectation that increases or decreases in seedling diversity may serve as a better short-term indicator of biodiversity response to the rapidly evolving conditions expected to be associated with global climate change. The survival of established plants may not ensure the long-term survival of a species in the face of climate change, because trees must germinate, grow, compete, and reproduce effectively under the new environmental regime (Hamrick 2004). Trees that are maladapted to the new conditions at a given site may not produce successful propagules, but may still be able to tolerate short-term climatic changes while gradually senescing. The presence of seedlings, however, is direct evidence of a species' ability to regenerate. Even if seedlings do not reach maturity at a specific location, their presence holds open the possibility that a species might be able to adapt to local environmental conditions as a result of natural selection favoring potentially novel or atypical seedling phenotypes.

The directional difference in seedling diversity change between the northern and southern zones may appear contrary to the findings of Woodall et al. (2009) that the mean latitude of seedlings of northern tree species was significantly farther north compared to the mean latitude of tree biomass for those species, whereas southern species had no shift and more widespread species demonstrated a southern expansion. It is

TABLE 3. Mean plot-level percentage change in phylogenetic diversity (PD) over time in trees and seedlings, by region and ecoregion section, and correlation coefficients from linear regressions of percentage seedling change with plot latitude and elevation.

		Mean percentage change		Correlation with percentage seedling change	
Region	No. plots	Trees	Seedlings	Latitude	Elevation
a) North	4576	**0.44*****	4.78	**0.100*****	0.01
Northern Lower Peninsula (212H)	538	**0.47****	3.61	**0.101****	0.008
Southern Superior Uplands (212J)	153	−0.06	**−5.34****	0.006	−0.061
Western Superior Uplands (212K)	242	**0.83*****	5.90	0.076	−0.072
Northern Superior Uplands (212L)	520	**0.38****	4.08	**−0.100†**	0.013
Northern Minnesota and Ontario (212M)	398	**0.72*****	**15.20*****	**−0.086†**	0.042
Northern Minnesota Drift and Lake Plains (212N)	514	**0.70*****	**16.14*****	**0.097†**	0.014
North Central Wisconsin Uplands (212Q)	99	**0.68†**	**−4.57****	−0.128	0.005
Eastern Upper Peninsula (212R)	293	0.13	4.45	**−0.146†**	0.004
Northern Upper Peninsula (212S)	207	**0.40†**	3.52	**0.175†**	**−0.178†**
Northern Green Bay Lobe (212T)	278	0.04	6.59	0.089	−0.023
Northern Highlands (212X)	474	0.10	**−4.59*****	**0.089†**	0.066
Southwest Lake Superior Clay Plain (212Y)	80	**0.22†**	**−4.42†**	−0.019	0.058
Green Bay-Manitowac Upland (212Z)	22	0.23	−5.66	−0.078	0.202
South Central Great Lakes (222J)	94	**1.06†**	−2.29	0.075	−0.16
Southwestern Great Lakes Morainal (222K)	84	0.20	−0.46	−0.015	0.053
North Central U.S. Driftless and Escarpment (222L)	270	0.53	3.95	−0.085	−0.013
Minnesota and Northeast Iowa Morainal-Oak Savannah (222M)	90	**1.08†**	9.36	0.145	0.149
Lake Agassiz-Aspen Parklands (222N)	36	0.57	**20.49****	0.022	−0.039
Wisconsin Central Sands (222R)	98	0.01	**−5.24†**	0.14	0.136
Lake Whittlesey Glaciolacustrine Plain (222U)	22	−0.24	−3.14	−0.016	−0.032
North Central Glaciated Plains (251B)	16	2.23	−2.04	0.062	0.000
b) South	2394	**0.50*****	**9.45*****	**0.129*****	**0.061****
Northern Cumberland Mountains (M221C)	28	−0.32	**21.58****	−0.132	0.044
Blue Ridge Mountains (M221D)	166	0.24	**15.56*****	−0.024	0.031
Northern Cumberland Plateau (221H)	87	0.30	**30.47*****	**0.221†**	−0.174
Central Ridge and Valley (221J)	71	0.01	7.98	0.036	**−0.291†**
Interior Low Plateau-Highland Rim (223E)	239	0.19	**18.59*****	**0.117†**	−0.105
Southern Appalachian Piedmont (231A)	406	**0.34†**	**7.60†**	−0.032	−0.078
Coastal Plains-Middle (231B)	197	**0.72****	7.68	**0.283*****	0.112
Southern Cumberland Plateau (231C)	97	**0.67†**	3.77	0.139	**0.275****
Southern Ridge and Valley (231D)	132	**0.61†**	**7.88†**	0.047	0.087
Coastal Plains-Loess (231H)	54	0.35	**22.44****	**0.267†**	−0.053
Gulf Coastal Plains and Flatwoods (232B)	237	**0.69†**	5.14	0.103	0.052
Atlantic Coastal Flatwoods (232C)	277	**0.47****	3.24	−0.125	**0.107†**
Southern Atlantic Coastal Plains and Flatwoods (232J)	365	**0.95*****	6.05	−0.047	0.024

† $P < 0.1$; ** $P < 0.01$; *** $P < 0.001$; significant values are in bold.

important to note that Woodall et al. (2009) compared the mean latitudes of seedlings and tree biomass of individual species at one point in time, rather than analyzing change over time in a biodiversity metric encompassing multiple species. The responses of dozens of species, as reported here, would together affect both the tree biodiversity on a given plot and the distribution of tree biodiversity across broad regions. Changes in the distributions of individual tree species, meanwhile, can be quantified using a variety of approaches, including the measurement of range-margin contraction and of latitudinal differences between seedlings and adult trees, metrics that may not account for relatively fine-scale patterns of tree occurrence. In other words, species with seedlings found at higher latitudes than expected, given existing tree distributions, may be unable to successfully reproduce across large portions of their existing range, with the potential to affect broadscale forest biodiversity.

Our study offers evidence of the second broadscale pattern of biodiversity change expected in response to climate change: associations of seedling phylogenetic diversity change with latitude and elevation. In both latitudinal zones, we found a weak but significant correlation between the percentage change in seedling diversity and latitude, in addition to a very weak correlation in the southern zone between elevation and seedling diversity change (Table 3). While significant at the broad scale of a latitudinal zone, these relationships are sometimes stronger at the more localized ecoregion scale, especially in the southern zone. The strongest correlations between plot-level percentage change in seedling diversity and latitude occur in two coastal plain ecoregions (Coastal Plains-Middle [231B] and Coastal Plains-Loess [231H]), each with relatively low elevation and little topographic variation, potentially allowing for easier northward shift of tree species. A moderately strong relationship between diversity change and lati-

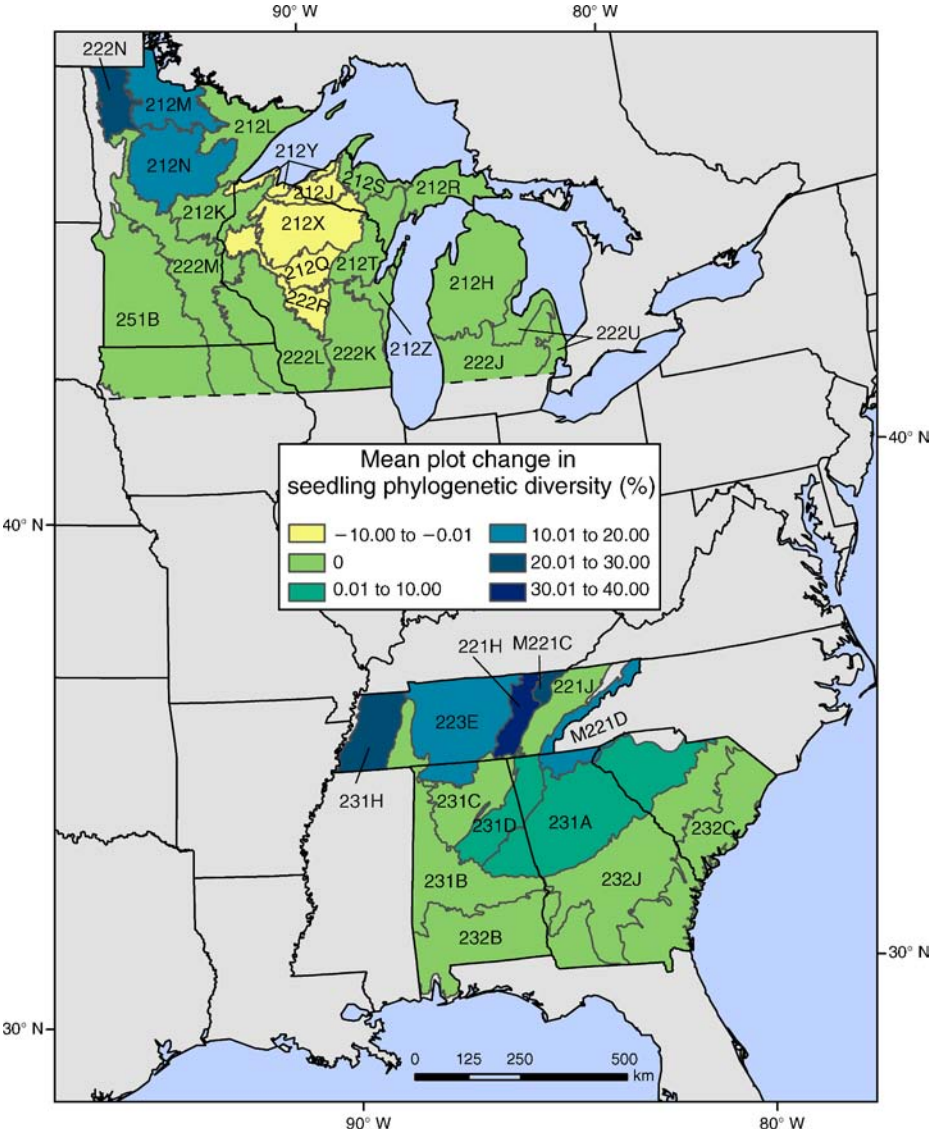

FIG. 5. Mean plot-level percentage change over time in seedling phylogenetic diversity across ecoregion sections, using the most recent mapping of these regions by the USDA Forest Service. For ecoregion section names, see Table 3.

tude also exists in the North Cumberland Plateau (221H), a region that, like the Coastal Plains-Loess ecoregion, is narrow and oriented generally south-to-north. Three ecoregions with considerable topographic variation had a fairly strong relationship between seedling diversity change and elevation; in one, the Southern Cumberland Plateau (231C), higher-elevation plots are becoming more diverse, while lower-elevation plots are becoming more diverse in two others (the Central Ridge and Valley [221J] and the Northern Upper Peninsula [212S]). These findings suggest that community responses to climate change may vary considerably based on local conditions, including topography, and species composition.

Patterns of phylogenetic diversity change in both latitudinal zones may be affected by the fact that each zone contains several species at the southern edges of their ranges, and that the immigration into both zones of new species from the south is likely to be limited by ecological barriers: the Gulf of Mexico for the southern zone and the largely nonforested midwestern prairie for the northern zone. It was not surprising, then, that ecoregions with the greatest percentage increase in seedling diversity are located near the northern edges of both the southern and northern latitudinal zones (Fig. 5). One possible explanation is that tree species distributions within the latitudinal zones may already be shifting northward via regeneration, consistent with other studies (Parmesan and Yohe 2003, Woodall et al. 2009), and that less successful regeneration is occurring for some species in the southern parts of both zones. Such a decrease in regeneration would be expected, given that adaptation to changing climate might be the most restricted among populations at the southern edge of species' distributions, because these populations would be deprived of gene flow from "preadapted" populations farther south (Davis and Shaw 2001). Already, a disproportionate number of population extinctions has been documented along southern and low-elevation range edges in response to recent climate warming (Parmesan 2006).

Finally, this study found broadscale seedling diversity increases among species with longer-distance seed dispersal capacity, even in the northern zone, where overall seedling diversity declined. These results have important climate change implications because the ability of plants to disperse seeds is expected to be critical for their survival under the current constraints of landscape fragmentation and climate change (Cain et al. 2000), with seed dispersal mechanism likely to play a key role in the ability of species to shift their distributions (Vittoz and Engler 2007).

Predictions of relatively high forest tree migration rates in the face of changing climate conditions have been based on fossil pollen records from the Quaternary (Davis and Shaw 2001). Although current tree distribution data suggest that some species may be able to shift their ranges at relatively high rates (Woodall et al. 2009), recent molecular evidence also suggests that the existence of low-density refugia near the Laurentide Ice Sheet may dramatically lower estimates of historical migration rates for some species (McLachlan et al. 2005). If, as expected, climate conditions evolve more rapidly in the near future compared to the speed of the Pleistocene changes, at least some tree species may not be able to shift locations quickly enough to match suitable climate conditions (Davis and Shaw 2001). This could result in an overall reduction in biodiversity through a selection for highly mobile and opportunistic species (Malcolm et al. 2002). This may be particularly likely in the northern zone, where our study shows an increase in the seedling diversity of bird-dispersed species (including species in the Rosaceae), but decreases in the diversity of shorter-distance wind-dispersed species (including in Betulaceae and *Acer*) and gravity-dispersed species (including in *Quercus*). This scenario appears to be less of a concern in the southern zone, however, where the seedling diversity increased for both bird-dispersed and gravity-dispersed species (such as *Quercus* and Juglandaceae), as well as predominantly wind-dispersed taxa (*Acer* and Betulaceae).

Processes other than changing climate conditions are likely to have affected the three patterns of forest seedling biodiversity change highlighted here. Patterns of seedling diversity change, for example, may be associated with differences in historical land use (Motzkin et al. 1999, Lafon et al. 2000), successional dynamics following widespread forest harvesting or agricultural abandonment (Friedman and Reich 2005, Hart and Grissino-Mayer 2008), fire suppression (Abrams 2005, Friedman and Reich 2005), and deer herbivory (Inouye et al. 1994, Liang and Seagle 2002). At the same time, it is probably not possible to separate the seedling biodiversity impacts from forest successional processes from those of climate change, in part because climate change is expected to lead to an overall increase in the frequency and intensity of extreme disturbances (Milad et al. 2011), which are in turn expected to favor early-successional species (Aitken et al. 2008, Moser et al. 2010). Another potential cause of seedling diversity change, seed masting (Kelly 1994, Koenig and Knops 2000), is directly influenced by variability in rainfall and temperature (Kelly and Sork 2002). Therefore, seed masting patterns could be affected by changing climatic conditions, leading to negative consequences for tree recruitment (Perez-Ramos et al. 2010) indirectly associated with climate change.

Although small-scale patterns of biodiversity change have many causes, the quantifiable and significant biodiversity changes identified here across broad geographic scales support, but do not confirm, the hypothesis that changing climate conditions may be affecting the structure, function, and ecology of forests. Actual changes in seedling phylogenetic diversity have occurred across broad regions, and they are consistent with recent studies demonstrating that tree seedlings are becoming established at higher latitudes and higher elevations (Goldblum and Rigg 2002, Gamache and Payette 2005, Landhausser et al. 2010), that some tree species' seedlings in the eastern United States may already be demonstrating an ability to shift their range northward by up to 100 km per century (Woodall et al. 2009), and that 80% of species with changes in their range distributions are shifting in the direction expected with increased temperatures, based on their known physiological constraints (Root et al. 2003). Additional Forest Inventory and Analysis remeasurement data will help to detect long-term trends in forest biodiversity change, and may help in attributing causes to these trends, as plots are remeasured at regular intervals over a longer period and across the conterminous United States.

Conclusions

To detect broadscale shifts in forest biodiversity over time in the eastern United States, we quantified change in forest community phylogenetic diversity on ~7000 standardized forest inventory plots. We found that our measures of forest phylogenetic diversity are substantially different from measures of tree species richness, and are perhaps preferable, given that phylogenetic diversity may better represent the diversity of traits present within a community (Faith 2002) and may be linked to a range of ecosystem services in certain circumstances (Cavender-Bares et al. 2009). In the face of climate change, maximizing phylogenetic diversity may represent the best strategy for preserving the diversity of features present in plant communities, therefore allowing more options for future evolutionary diversification (Forest et al. 2007). We detected broad-scale patterns of phylogenetic diversity change over time that are consistent with shifts in community biodiversity expected under climate change: greater change in seedling diversity than in tree diversity, greater change in seedling diversity at higher latitudes and elevations, and greater change in seedling diversity among species with higher dispersal capacity. These results demonstrate that indicators of phylogenetic diversity change in forest communities are able to detect relatively subtle biodiversity differences over time across broad regions. The importance, statistical power, and geographic extent of such indicators will increase in the coming decades as repeated remeasurements occur on all of the ~125 000 Forest Inventory and Analysis plots across the conterminous United States and southeast Alaska.

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Supplemental Material

Appendix A

Published sources used in construction of phylogenetic supertree for Forest Inventory and Analysis (FIA) tree species (*Ecological Archives* A022-033-A1).

Appendix B

Phylogenetic supertree encompassing all species in the USDA Forest Service Forest Inventory and Analysis (FIA) tree species database, in Newick format (*Ecological Archives* A022-033-A2).

Appendix C

A table showing coefficients of determination (R^2) from linear regressions of phylogenetic diversity on species richness for trees and seedlings at time 2, and from linear regressions of change in phylogenetic diversity on change in species richness over time, for northern and southern latitudinal zones, and for ecoregion sections within each zone (*Ecological Archives* A022-033-A3).

Appendix D

A table showing measures of phylogenetic diversity (PD), and PD change over time, at three taxonomic scales for forest trees >2.54 cm dbh on Forest Inventory and Analysis plots in the northern and southern zones (*Ecological Archives* A022-033-A4).

Appendix E

A table showing measures of phylogenetic diversity (PD), and PD change over time, at three taxonomic scales for forest tree seedlings <2.54 cm dbh on Forest Inventory and Analysis plots in the northern and southern zones (*Ecological Archives* A022-033-A5).