Introduction

The facilitation of evolutionary processes is a necessary biological criterion for judging the sustainability of forests because these processes allow for the adaptation of species and resilience of communities to changes in environmental conditions. Levels and patterns of genetic diversity within species are the result of evolutionary and ecological processes, and therefore reflect the integrity and functioning of these processes (Brown and others 1997). The fundamental importance of genetic variation is recognized by its incorporation into criteria and indicators of forest sustainability, including the Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests (Montréal Process Working Group 2007).

The Montréal Process, as amended in 2007, incorporates three indicators of genetic diversity under criterion 1 (conservation of biological diversity): (1) number and geographic distribution of forest-associated species at risk of losing genetic variation and locally adapted genotypes, (2) population levels of selected representative forest associated species to describe genetic diversity, and (3) status of onsite and offsite efforts focused on conservation of genetic diversity (Montréal Process Working Group 2007). While these indicators address population characteristics that affect the maintenance of genetic variability within individual species, they are necessarily limited to a handful of indicator species inhabiting forest ecosystems, rather than to entire communities of flora and fauna.

Community phylogenetic analysis (Webb and others 2002) is a new approach that quantifies genetic diversity for communities of species and can easily be used to describe the spatial distribution of such genetic variation across landscapes. This synthesis of evolutionary biology and landscape ecology has potential as a tool for assessing the health of forest communities, both in terms of biodiversity and community resistance to stress (Potter 2009). Specifically, it should shed light on the effects of ongoing environmental changes on the evolutionary potential and biological distinctiveness of biotic communities at a range of temporal and spatial scales.

Community phylogenetics has been made possible by the recently improved ability to create well-supported phylogenies of plant species. These hypothesized phylogenetic "family trees" of species are generated following surveys of existing molecular systematic studies that use gene sequencing to determine the relationships among species and to estimate the amount of time since their common ancestors diverged. Fossil evidence from paleobotanical studies is further used to calibrate the age of the nodes at which species or species groups diverged. The lengths of all the branches within these phylogenetic trees are calculated in millions of years, with the branch lengths used to compute

Chapter 2. Evolutionary Diversity and Phylogenetic Community Structure of Forest Trees Across the Conterminous United States

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a variety of statistics. No new gene sequencing work is required to construct these phylogenetic trees because, in recent years, molecular systematic studies have been published for a wide variety of plant groups, including those of most North American tree species.

Phylogenetic diversity (PD) statistics (Faith 1992, Webb and others 2006), which rely on such phylogenetic trees, may be more meaningful measures of biodiversity than traditional metrics such as species richness, abundance, and evenness because they measure the cumulative evolutionary age and evolutionary potential of all the species in the community of interest, rather than weighting all species equally regardless of their relatedness. This is of particular interest in the context of conservation because existing evolutionary lineages will generate future biodiversity, and as such are the cornerstone of natural environmental health (Erwin 1991). Therefore, conserving the evolutionary potential of individual lineages, species, and groups of species, as measured by PD statistics, has become an increasingly important goal (Rodrigues and Gaston 2002, Sechrest and others 2002, Soltis and Gitzendanner 1999).

Additionally, it is possible to use species phylogenies to determine whether the species within a specific community are more clustered or dispersed across the overall phylogenetic tree (of all the tree species in North America, for example) than expected by chance (Webb 2000). These measures of phylogenetic clustering or

dispersion may serve as useful community-level measures of potential genetic resilience to pests, pathogens, climate change, and other stressors. This is because communities of species that are more evenly dispersed on the phylogenetic tree—that is, less closely related than expected by random chance—possess greater-than-expected evolutionary diversity, and may, therefore, encompass a higher proportion of species unaffected by a given stressor or able to adapt to it. Phylogenetically clustered communities, in contrast, contain less evolutionary diversity and are more closely related than a random set of species, and may therefore be more vulnerable to stressors such as pests, pathogens, and climate change.

Methods

I used the software package Phylocom 3.41 (Webb and others 2008) to examine forest tree community phylogenetics across the 48 conterminous United States, quantifying forest tree PD and phylogenetic community structure for each of 102,304 one-sixth-acre Forest Inventory and Analysis (FIA) plots. These plots represented the latest available FIA phase 2 tree and sapling inventory data (trees ≥ 1 inch d.b.h.) as of November 2007 (Forest Inventory and Analysis Program 2007). They encompassed the latest annualized data available or periodic data when a full cycle of annualized data was unavailable.

This analysis required the construction of a phylogenetic reference supertree (fig. 2.1) encompassing the 311 forest tree species

Gymnosperms

Angiosperms

Pinaceae
Cupressaceae
Taxaceae
Sapindales
Fabales
Fagales
Rosales
Malpighiales
Myrtales
Asterids
Platanaceae
Magnoliids
Monocots

325   300   250   200   150   100   50   0
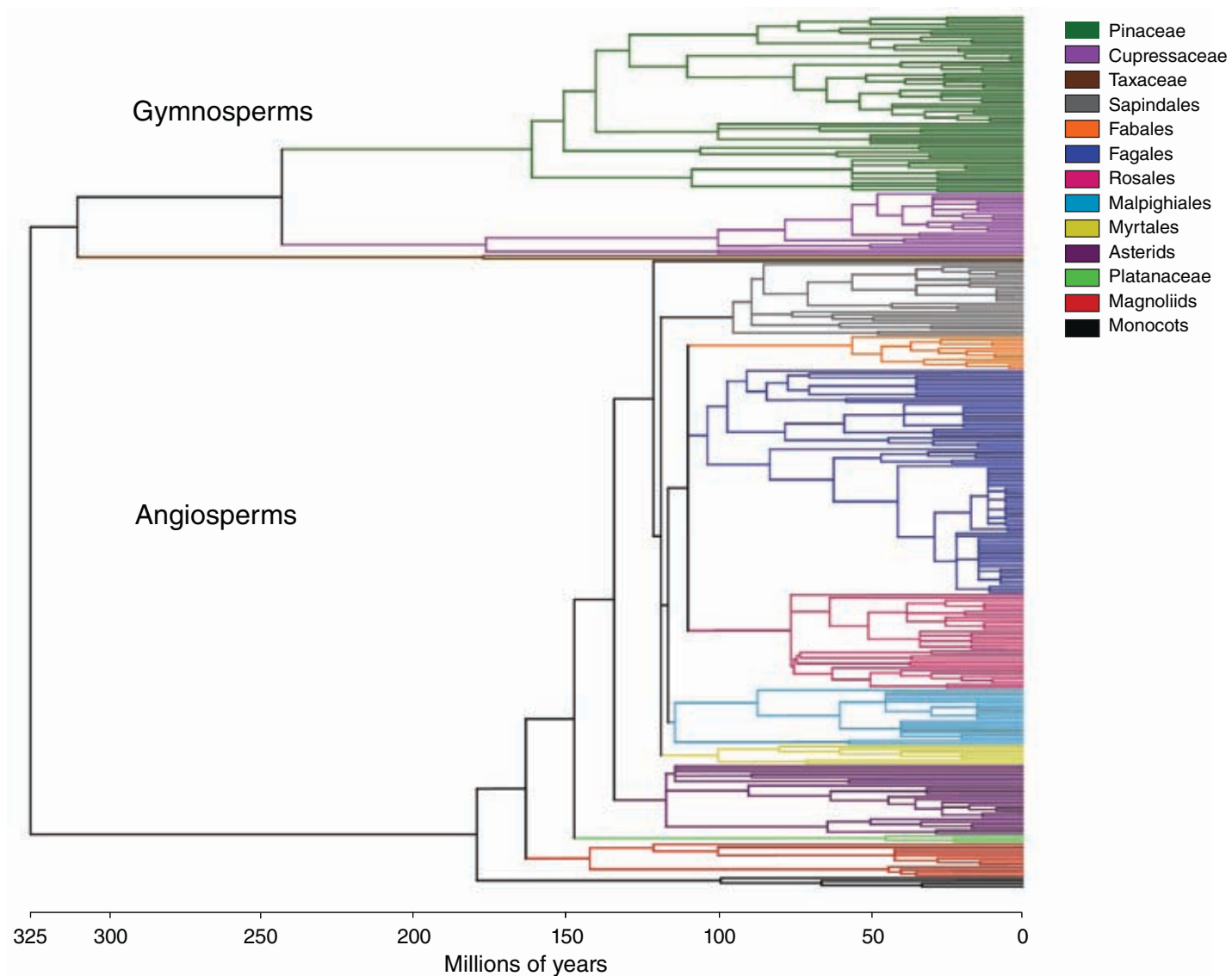
Millions of years

Figure 2.1—The phylogenetic supertree of the 311 forest tree species of the conterminous United States inventoried by FIA, with branch lengths measured in millions of years (Potter and Woodall 2012). Evolutionary relationships and branch lengths were based on a survey of recent molecular systematic and paleobotanical studies, except for basal angiosperm relationships, which were from Wikström and others (2001).

inventoried by FIA (Potter and Woodall 2012). This reference phylogeny, which can be used to estimate phylogenetic distance among species in units of millions of years, approximates the actual evolutionary relationships among species. (See appendix A for additional details about the construction of the reference phylogeny.)

Three sets of analyses were conducted for differing groups of species: all species, angiosperm (flowering) species, and gymnosperm (cone-bearing) species. In addition to plot-level species richness (the number of species present on a plot), I calculated three measures of PD:

1. Faith's (1992) index of PD measures the total evolutionary history represented by the species on a plot. This is done by generating a phylogenetic tree encompassing the species on the plot [taken from the phylogenetic reference tree (fig. 2.1)] and then summing the branch lengths of that plot-level phylogenetic tree, measured in millions of years of evolutionary time (Potter 2009). I calculated mean PD and species richness values for ecoregion sections, after excluding sections containing fewer than 25 plots.

2. The Nearest Taxon Index (NTI) is a standardized measure of the branch-tip phylogenetic structure of species in a community (Webb and others 2006). This statistic measures whether evolutionary diversity among the species on a plot is greater (dispersed) or less (clustered) than

expected by chance, as compared to the pool of species present in the ecoregion section in which the plot is located.

3. The Net Relatedness Index (NRI) is a standardized measurement of basal phylogenetic structure of species in a community (Webb and others 2006). This statistic measures whether evolutionary diversity among the deeper phylogenetic ranks (families, orders, classes, and divisions) on a plot is greater (dispersed) or less (clustered) than expected by chance, again as compared to the pool of species present in the ecoregion section.

NTI and NRI values are positive when species occur with other closely related species (clustered), and are negative when species do not occur together with closely related species (dispersed) (Kembel and Hubbell 2006). These statistics measure different evolutionary characteristics of communities, so it is, therefore, possible for a community to be considered clustered by one metric and overdispersed by the other (table 2.1). Because the data were not normally distributed, I used a Wilcoxon signed rank test to determine whether section-level median NTI and NRI scores were significantly different from zero, with positive values significantly clustered and negative values significantly overdispersed. Sections with fewer than 25 plots were not included in the analysis. (See appendix A for additional details about the calculation of these statistics.)

Table 2.1—Interpretation of the evolutionary characteristics of forest communities based on their phylogenetic structure as measured by the Net Related Index and Nearest Taxon Index

		Clustered	Neither	Dispersed
		Net Related Index—Treewide Phylogenetic Structure		
Nearest Taxon Index—Branch-Tip Phylogenetic Structure	Clustered	Low overall diversity/evenness, including higher order groups (angiosperms vs. gymnosperms, etc.) Low diversity/evenness across lower order groups (families, genera, etc.)	Moderate overall diversity/evenness including higher order groups Low diversity/evenness across lower order groups	High overall diversity/evenness, including higher order groups (angiosperms vs. gymnosperms, etc.) Low diversity/evenness across lower order groups (families, genera, etc.)
	Neither	Low overall diversity/evenness, including higher order groups Moderate diversity/evenness across lower order groups	Moderate overall diversity/evenness including higher order groups Moderate diversity/evenness across lower order groups	High overall diversity, including higher order groups Moderate diversity/evenness across lower order groups
	Dispersed	Low overall diversity/evenness, including higher order groups (angiosperms vs. gymnosperms, etc.) High diversity/evenness across lower order groups (families, genera, etc.)	Moderate overall diversity/evenness including higher order groups High diversity/evenness across lower order groups	High overall diversity/evenness, including higher order groups (angiosperms vs. gymnosperms, etc.) High diversity/evenness across lower order groups (families, genera, etc.)

Results and Discussion

The two metrics of biodiversity, species richness and PD (a measure of evolutionary history), were highly correlated at the plot level ($r = 0.89$). As expected, a similar general pattern appeared between the metrics at the ecoregion section scale (fig. 2.2). For each, mean plot species richness and PD are higher in the Eastern United States than in the West, with the lowest values located in the interior West. At the same time, some important differences existed between these measures of biodiversity. For
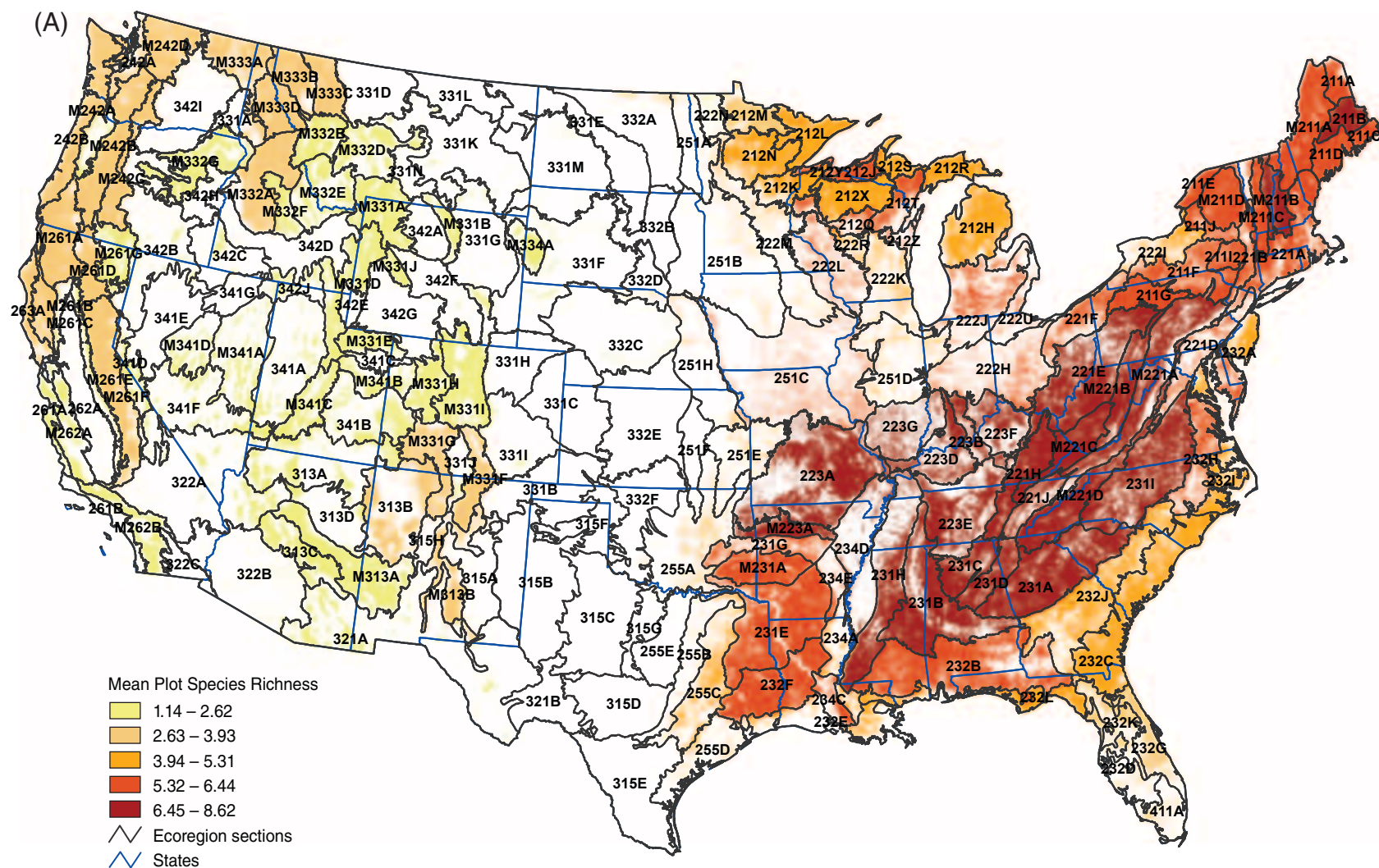
Figure 2.2—Mean forest tree (A) species richness and (B) Faith's index of phylogenetic diversity for FIA plots across ecoregion sections (Cleland and others 2007). The two statistics were divided into five equal interval classes for comparison purposes. Forest cover is derived from MODIS imagery by the Forest Service, Remote Sensing Applications Center. (Data source: Forest Service, Forest Inventory and Analysis Program) (continued on next page)
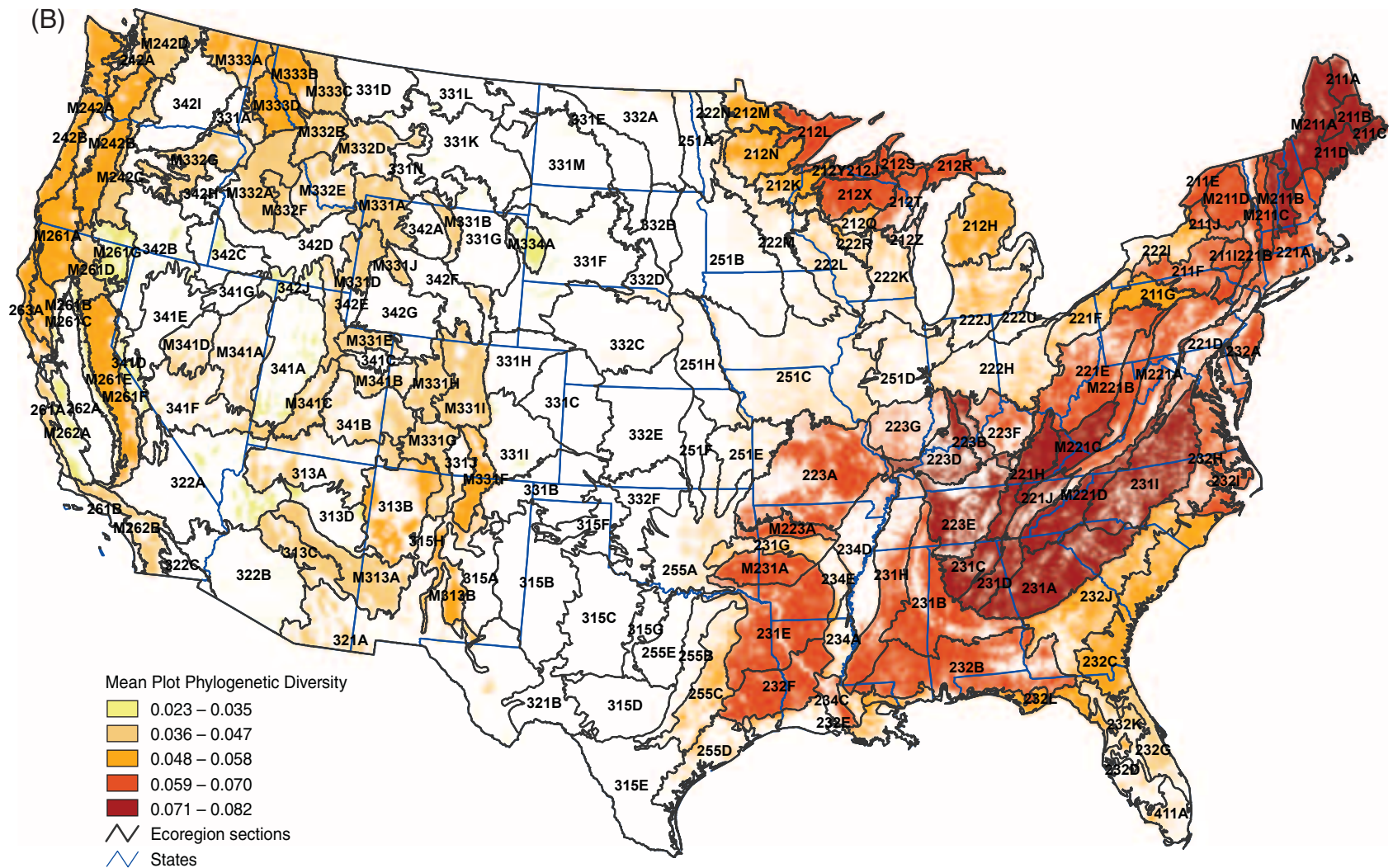
Figure 2.2 (continued)—Mean forest tree (B) Faith's index of phylogenetic diversity for FIA plots across ecoregion sections (Cleland and others 2007). The two statistics were divided into five equal interval classes for comparison purposes. Forest cover is derived from MODIS imagery by the Forest Service, Remote Sensing Applications Center. (Data source: Forest Service, Forest Inventory and Analysis Program)

example, the 10 sections with the highest species richness were all located in the Southeast, while four of the sections with the highest PD were in the Northeast, in addition to six from the Southeast (table 2.2). Additionally, PD was higher relative to species richness in several sections along the Pacific coast and in the northern and southern Rocky Mountains.

Interestingly, some of the regions with higher PD values relative to species richness are regions that contain a combination of relatively high angiosperm (flowering) and gymnosperm (cone-bearing) forest tree PD, particularly in the Lake States and New England (fig. 2.3). In general, angiosperm PD is high in the East and very low in the West (fig. 2.3A). Gymnosperm PD was highest in the West and in parts of the Upper Midwest and Northeast (fig. 2.3B). The Southeast generally had low gymnosperm PD, except for three ecoregion sections with moderate PD [the Central Ridge and Valley (221J), the Central Appalachian Piedmont (231I), and the Blue Ridge Mountains (M221D)].

Meanwhile, the analysis of phylogenetic structure (fig. 2.4) found strong regional differences in phylogenetic dispersion and clustering. Because the two calculations of phylogenetic structure measure different evolutionary characteristics of communities

Table 2.2—Ecoregion sections with the highest species richness and phylogenetic diversity

Section	Species richness
M221C—Northern Cumberland Mountains	8.62
M221D—Blue Ridge Mountains	8.36
221H—Northern Cumberland Plateau	8.33
223E—Interior Low Plateau-Highland Rim	8.20
221J—Central Ridge and Valley	8.15
231I—Central Appalachian Piedmont	8.08
231C—Southern Cumberland Plateau	8.03
223D—Interior Low Plateau-Shawnee Hills	7.79
223B – Interior Low Plateau – Transition Hills	7.75
M223A—Boston Mountains	7.46

Section	Phylogenetic diversity
231I—Central Appalachian Piedmont	0.0816
211B—Maine-New Brunswick Foothills and Lowlands	0.0812
M221D—Blue Ridge Mountains	0.0799
221J—Central Ridge and Valley	0.0768
211D—Central Maine Coastal and Embayment	0.0757
M221C—Northern Cumberland Mountains	0.0749
221H—Northern Cumberland Plateau	0.0748
231C—Southern Cumberland Plateau	0.0743
M211B—New England Piedmont	0.0737
211A—Aroostook Hills and Lowlands	0.0731

(table 2.1), they may lead to different predictions about the susceptibility of forest communities to threats. A community consisting of species evenly dispersed across the phylogenetic tree (e.g., consisting of both flowering trees and conifers), but clustered toward the branch tips (e.g., consisting of mostly pines and oaks), may contain more species adapted or simply not susceptible to a given threat, but may be more likely to lose important ecological functions provided by the species eliminated by that agent. Meanwhile, a community of species clustered across the phylogenetic tree (e.g., dominated by only conifers), but evenly dispersed at the tips (e.g., consisting of several conifer genera, such as spruces, firs, and pines), may better retain its ecological functionality in that situation, but might encompass more species at risk of elimination.

The two measures of phylogenetic structure showed similar general patterns, with moderate to high phylogenetic clustering in the Upper Midwest and Northeast, slight to moderate clustering near the Pacific coast and along the Appalachian Mountains, and slight to moderate dispersion in the Interior West. However, some differences were apparent between the two measures. Using the NTI, which quantifies clustering at the tips of the phylogenetic tree, portions of the Southeast were slightly or moderately dispersed (fig. 2.4A). With the NRI, however, these same areas were slightly to moderately clustered (fig. 2.4B). This may be the result of low gymnosperm diversity in

the region (fig. 2.3B), resulting in tree-wide phylogenetic clustering, combined with moderate angiosperm diversity (fig. 2.3A).

Also interesting is the patchwork of dispersion and clustering in ecoregion sections across the Interior West. In this region of low angiosperm diversity (fig. 2.3A), section-level differences in phylogenetic structure are likely the result of the interaction between differences in conifer richness (the number of different conifer species) and differences in the degree of relatedness among the conifer species present (how phylogenetically related the species are).

The phylogenetic structure of a community or region reveals something about the ecological processes that predominate there. For example, when the species present are more closely related than chance would dictate (phylogenetic clustering), this suggests a pattern of environmental filtering. Environmental filtering occurs when closely related species share similar tolerances to the abiotic environment, and where, as a result, habitat use is a conserved trait among the species in the community (Cavender-Bares and others 2004, Tofts and Silvertown 2000). Because such plant communities share a great deal of evolutionary history as well as an affinity for similar environmental conditions, they may be particularly susceptible to a variety of threats, such as generalist insects and diseases and shifting conditions associated with global climate change.

Figure 2.3—Mean forest tree phylogenetic diversity for (A) angiosperm (flowering) tree species and (B) gymnosperm (cone-bearing) tree species from FIA plots across ecoregion sections (Cleland and others 2007). The results were divided into five equal interval classes for comparison purposes. Forest cover is derived from MODIS imagery by the Forest Service, Remote Sensing Applications Center. (Data source: Forest Service, Forest Inventory and Analysis Program) (continued on next page)

Figure 2.3 (continued)—Mean forest tree phylogenetic diversity for (B) gymnosperm (cone-bearing) tree species from FIA plots across ecoregion sections (Cleland and others 2007). The results were divided into five equal interval classes for comparison purposes. Forest cover is derived from MODIS imagery by the Forest Service, Remote Sensing Applications Center. (Data source: Forest Service, Forest Inventory and Analysis Program)
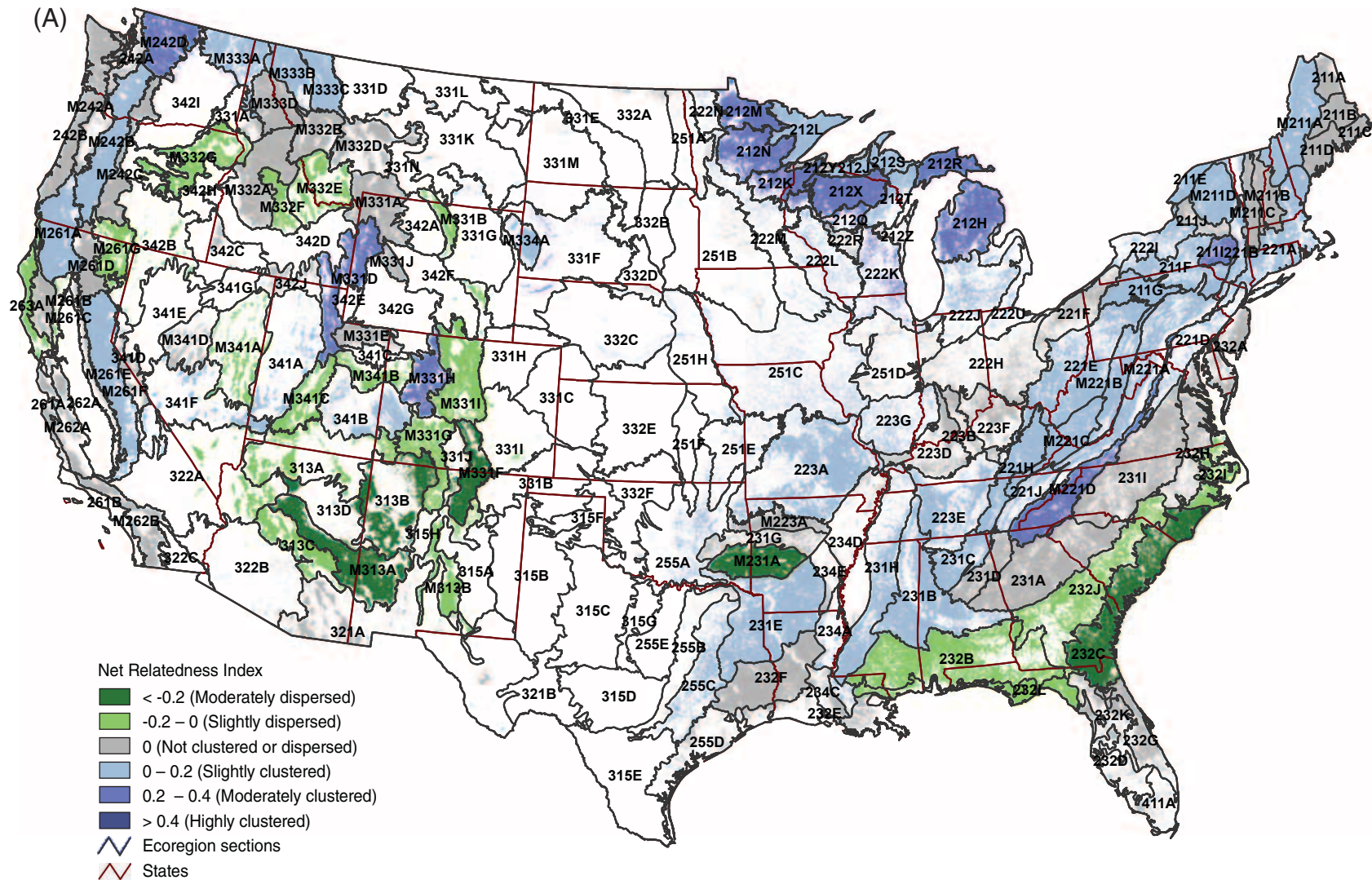
Figure 2.4—Mean FIA plot-level measures of phylogenetic clustering across ecoregion sections (Cleland and others 2007) using (A) the Nearest Taxon Index, a measure of clustering at the branch tips of the phylogenetic tree, and (B) the Net Relatedness Index, a measure of clustering throughout the phylogenetic tree. A Wilcoxon signed rank test was used to determine whether index values were significantly different from zero, with negative index values dispersed and positive values clustered compared to random. Forest cover is derived from MODIS imagery by the Forest Service, Remote Sensing Applications Center. (Data source: Forest Service, Forest Inventory and Analysis Program) (continued on next page)

Figure 2.4 (continued)—Mean FIA plot-level measures of phylogenetic clustering across ecoregion sections (Cleland and others 2007) using (B) the Net Relatedness Index, a measure of clustering throughout the phylogenetic tree. A Wilcoxon signed rank test was used to determine whether index values were significantly different from zero, with negative index values dispersed and positive values clustered compared to random. Forest cover is derived from MODIS imagery by the Forest Service, Remote Sensing Applications Center. (Data source: Forest Service, Forest Inventory and Analysis Program)

On the other hand, a pattern of phylogenetic dispersion, where the species in a community are less closely related than chance, may indicate the existence of competitive exclusion among closely related species. This occurs when closely related species are competing for similar environmental niches within the community, and are excluding each other when they share limiting resources (Cavender-Bares and others 2004, Tofts and Silvertown 2000). The ecological integrity of such communities may be less at risk from changing conditions because they may encompass a wider variety of evolutionary adaptations to respond to those changes, and because these communities may encompass a wider variety of niches than communities where environmental filtering is a more dominant ecological process.

The pattern of forest tree phylogenetic structure in this study suggests that competitive exclusion for resources among related species is an important process in certain warmer and drier ecoregion sections, while niche conservativism may be a more common occurrence in moister and more temperate areas. Additionally, broad-scale historical patterns, such as the plant migrations associated with the series of ice ages occurring during the Pleistocene epoch, may also contribute to the patterns of phylogenetic clustering and dispersion. Historic

outbreaks of invasive insects or pathogens, such as the chestnut blight fungus (*Cryphonectria parasitica*), hemlock woolly adelgid (*Adelges tsugae*), and white pine blister rust (*Cronartium ribicola*), have eliminated individual species or groups of species and may also have left a phylogenetic signature—increased phylogenetic clustering when the eliminated species are relatively distinct evolutionarily and increased phylogenetic dispersion when the eliminated species are more closely related to other species in their community.

Generating PD and community structure statistics at large scales is one approach for investigating the role evolutionary biology plays in shaping the processes and patterns in the natural world. Similar approaches that consider the evolution of forest species within the community context also have the potential to improve our understanding of important forest health issues. Future analyses could include:

• Assessments of whether nonnative invasive species are more or less phylogenetically related than expected by chance, compared to nonnative species that are not invasive (Strauss and others 2006). Results could help identify evolutionary groups of species most at risk of becoming invasive.

- Incorporation of phylogenetic relationships among forest tree species in assessments of risk from imported pathogens, including mapping likely pathogen host ranges (Gilbert and Webb 2007). This approach may be useful because the likelihood that a pathogen can infect two plant species decreases continuously with phylogenetic distance, and because the phylogenetic structure of forest communities is likely to impact the rate of spread and the ecological impacts of a disease through a natural plant community (Gilbert and Webb 2007).

- Research aiming to detect the phylogenetic signal (e.g., Silvertown and others 2006) of forest tree traits relating to forest health, such as susceptibility to insect and disease infestation. This would be particularly helpful in identifying evolutionary groups of tree species at risk from insects and pathogens with multiple hosts, such as sudden oak death (*Phytophthora ramorum*), and at risk from broad environmental changes such as those associated with global climate change.

- Studies that investigate which local environmental characteristics, such as climate and soil factors; and historical elements, such as Pleistocene species migration patterns or selective mortality caused by invasive forest pests, are associated with PD and phylogenetic structure measures within forest tree communities.

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Reference Tree Construction

I built the reference phylogeny (Potter and Woodall 2012) in part by using the online phylogenetic database and toolkit Phylomatic (Webb and Donoghue 2005) to generate a backbone phylogenetic supertree topology based on the Angiosperm Phylogeny Group II classification of flowering plant families (Angiosperm Phylogeny Group 2003). I then used the Branch Length ADJustment module in Phylocom 3.41 (Webb and others 2008) to assign ages to nodes in this supertree based on the fossil and molecular estimates reported by Wikström and others (2001), with undated nodes spaced evenly between dated nodes to minimize variance in branch lengths. To extend the resolution of this supertree from the family and genus level to the species level and to include gymnosperms in addition to angiosperms, I incorporated the results of approximately 80 recent molecular systematic and paleobotanical studies.

Calculating Nearest Taxon Index and Net Relatedness Index Values

The NTI and NRI are calculated using two other statistics that measure different aspects of phylogenetic relatedness among the species in a community or plot.

Mean nearest neighbor distance is the mean minimum phylogenetic distance between each species on the plot and the most closely related species also on the plot, measured in millions of years (Webb and others 2006). This statistic quantifies how closely related, on average, each species in a community is to the most closely related species. It is used to determine the NTI, a standardized measure of the terminal (branch-tip) clustering of co-occurring taxa regardless of the clustering of the higher level groups in the phylogenetic tree:

$$NTI = -(MNND - MNND_{NULL}) \, / \, \sigma MNND_{NULL}$$

where

$MNND_{NULL}$ = mean nearest neighbor phylogenetic distance from 1,000 randomly generated null communities, drawn from the pool of species present in the plot's ecoregion section

$\sigma MNND_{NULL}$ = the standard deviation of the null community scores

To generate null communities, I used the independent swap algorithm, which randomizes patterns of species co-occurrence on the plots.

The algorithm does not introduce species from the reference phylogeny tree into the null community plots (Webb and others 2008). Rather, the null communities for each plot were drawn from species contained within plots in the same ecoregion section.

Meanwhile, mean phylogenetic distance is the mean evolutionary distance, again measured in millions of years, between each species on a plot and all of the other species on the plot (Webb and others 2006). This statistic quantifies how closely related, on average, each species in a community is to every other species in the community. It is used to ascertain the NRI, a standardized measurement of phylogenetic structure across the phylogenetic tree. It is calculated as:

$$NRI = -(MPD-MPD_{NULL}) / \sigma MPD_{NULL}$$

where

MPD_{NULL} = mean nearest neighbor phylogenetic distance from 1,000 null communities, drawn from the pool of species present in the plot's ecoregion section

σMPD_{NULL} = the standard deviation of the null community scores

Again, null communities for each plot were drawn from species across plots within the same ecoregion section.