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Notes and Comments

Evidence for a Time-Integrated Species-Area Effect on the Latitudinal Gradient in Tree Diversity

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ABSTRACT: The greater area of tropical forest biomes has been proposed as a factor that drives the latitudinal gradient in species diversity by modulating speciation and extinction rates. But speciation and extinction are processes that operate over millions of years, so an adequate test of area's contribution to diversity patterns must take into consideration that biome areas have changed through time in response to climate. Here we correlate estimates of current tree species diversity with a composite parameter integrating area over geological time for each continent's tropical, temperate, and boreal biomes. We find significant positive correlations between current tree diversity and area-time for periods since the Eocene, Oligocene, and Miocene, which we take as evidence for a time-integrated species-area effect on current patterns of species richness across biomes. These results contribute to explanations for why most lineages have tropical origins and why tropical forests are more diverse than extratropical forests.

Keywords: age, geographic area, tropical rain forest, tropical conservatism hypothesis.

Disparities in species richness among tropical, temperate, and boreal biomes cause the well-known latitudinal gradient in species diversity and result from the historical outcome of speciation, extinction, and dispersal in all resident lineages inhabiting them (Dobzhansky 1950; Ricklefs 1987; Wiens and Donoghue 2004). It stands to reason, then, that insight into the causes of this global pattern may be gained by studying key geographic factors affecting the diversification process. Here we propose that time and area have major importance in explaining present-day levels of species richness across biomes and provide supporting evidence from global estimates of tree diversity and paleoclimatic reconstructions of biome areas.

The importance of time in accumulating regional diversity through speciation is well known (Wallace 1876; Willis 1922; Stebbins 1974; Stephens and Wiens 2003). Populations within a newly colonized region require a minimum period (the "time-for-speciation effect"; Stephens and Wiens 2003) to become subject to forces that cause reproductive isolation, for example, the cessation of gene flow across a geographic barrier. Estimates for most modern species ages are on the order of millions of years (Avise 2000; Magallón and Sanderson 2001). Area is also positively correlated with species richness, notably in ecological models of species turnover in islands via immigration and extinction (MacArthur and Wilson 1967) as well as in evolutionary models of lineage diversification. Theory predicts that, all else being equal, lineages inhabiting larger areas should experience higher speciation rates. This can be due to greater opportunity for isolation in allopatry (Rosenzweig 1995), peripheral isolate speciation (Mayr 1954), and centrifugal speciation (Brown 1957). Larger areas should also experience lower extinction rates (see many references in Chown and Gaston 2000), leading to the prediction that larger areas should contain more species than smaller areas (Rosenzweig 1995; Chown and Gaston 2000). Thus, just as there should be a time-for-speciation effect in lineages, there should also be an "area-for-speciation effect" (Losos and Schluter 2000).

Both the greater geographic extent (Terborgh 1973; Rosenzweig 1995) and the greater longevity (Wallace 1876; Wiens and Donoghue 2004) of tropical rain forest biomes compared to extratropical biomes have been invoked to explain the latitudinal gradient in species diversity. While historical and biogeographical hypotheses involving area

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and age were the dominant explanations for the latitudinal gradient for decades, they have lost favor, in large part because they were deemed untestable (Wiens and Donoghue 2004). Here, we combine two ideas to test a "time-integrated species-area effect" in global tree diversity patterns. We argue that because of the time-for-speciation effect, an adequate test of the role that area plays in species richness must include information about the time over which evolutionary diversification must have occurred.

Using recent data on paleogeographic reconstruction of the world's biomes, we correlate an integrated measure of biome size and age with estimates of tree species richness of biomes to investigate the signal of the time-integrated species-area effect in worldwide diversity patterns. Our analysis here focuses on the intrinsic properties of biomes (age and area) that influence in situ diversification rates of resident species. We do not focus on specific clades, which may be idiosyncratic in their individual responses to forces generating the latitudinal gradient. Instead, we focus on trees, a functional plant group that is phylogenetically dispersed, reasoning that patterns in tree diversity across biomes and latitudes should represent the outcome of processes affecting clades generally. In addition, trees are an ecologically critical component of most terrestrial biomes because of their role in providing habitat, food, and shelter for so many other organisms.

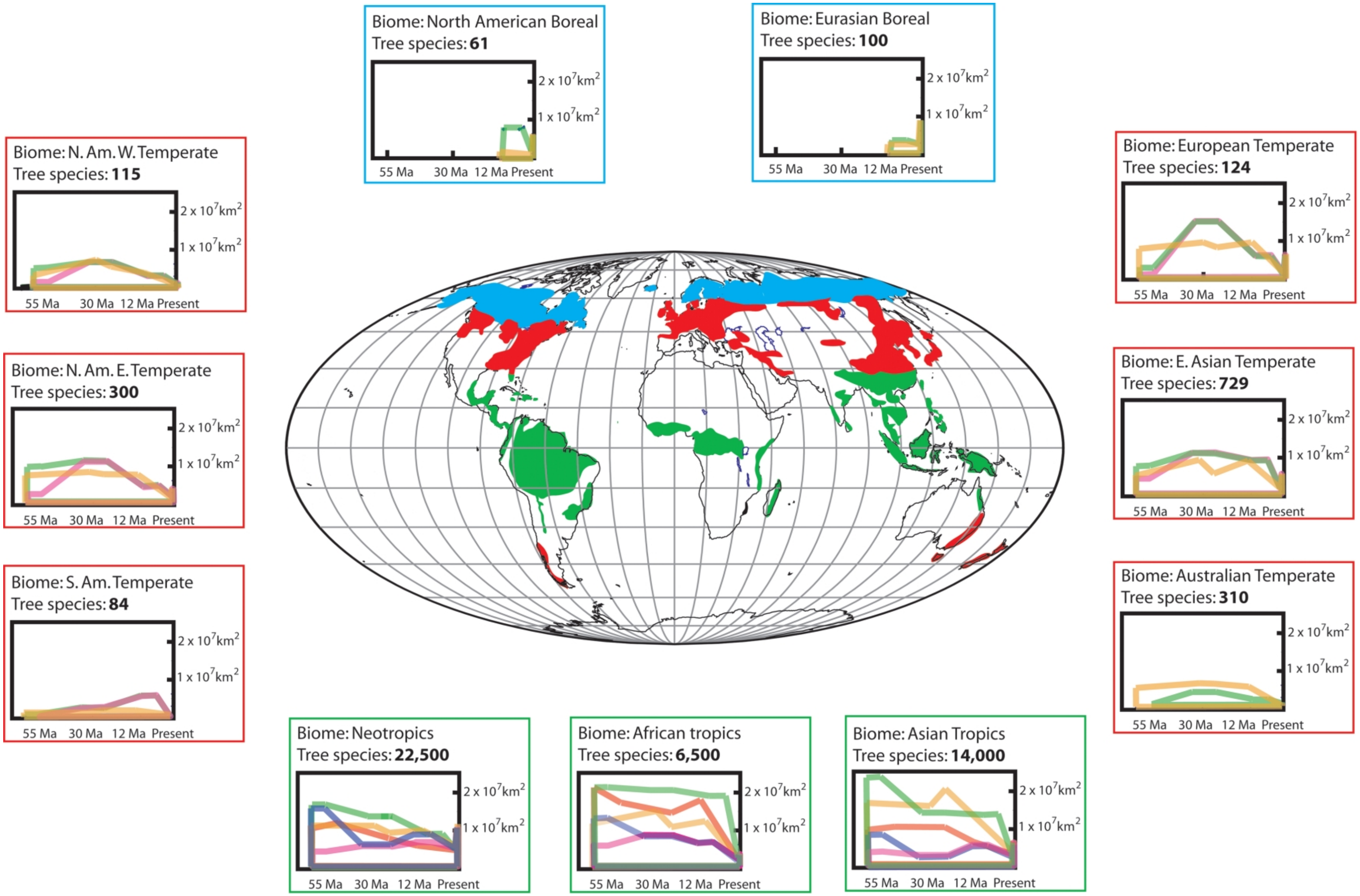
Methods

We delimited biome boundaries by temperature and precipitation thresholds that impose significant physiological trade-offs in trees. These boundaries correspond to the natural breaks where turnover in species composition occurs in the latitudinal distribution of diversity (Fine 2001). We define as boreal biomes areas that experience −40°C temperatures in winter. This is the threshold of spontaneous nucleation of supercooled water, which requires a specific adaptation in trees to avoid death by xylem cavitation (Woodward 1987). We define as temperate biomes those delimited by the −40°C isoclines on the high-latitude border and by infrequent to annual frost on the low-latitude border. Frost tolerance is a physiological barrier that has been shown to limit tropical trees from expanding into temperate areas (Sakai and Weiser 1973; Woodward 1987; Latham and Ricklefs 1993; Fine 2001). Finally, tropical biomes are defined as areas that never experience 0°C temperatures. Extratropical trees are likely limited from crossing into tropical areas by the trade-off in growth that accompanies frost tolerance, giving temperate trees a competitive disadvantage in tropical areas (MacArthur 1972; Loehle 1998; Fine 2001). "Subtropical " biomes often refer to two distinct types: areas that never experience frost but are outside of the geographic tropics or low- to midlatitude forests that do not always experience annual frost but do experience periodic frosts. For our analyses, the former type is defined as tropical, and the latter is defined as temperate (see Fine 2001).

We divided each continent into boreal, temperate, and tropical moist and dry forests using the World Wildlife Fund ecoregion map and data tables (Olson et al. 2001; also see http://www.worldwildlife.org/science). This map's ecoregions closely conform to where the frost line and occurrence of the −40°C isoclines delimit the boundaries that divide tropical, temperate, and boreal biomes for North America (Fine 2001), and it is assumed that the analogous forest biomes in the other continents would behave similarly. We were not able to obtain estimates for the world's tropical dry forest and temperate Mediterranean tree floras, so we present only moist/wet forest data. All of the boreal- and temperate-biome tree species lists were reviewed to verify that no significant overlap in species composition existed that would violate the assumption that each of our 11 biomes constitute an independent data point. No such comprehensive lists exist for the tropical biomes, but we assume that at most a small fraction of 1% of tropical forest species have distributions that span more than one of the three tropical biomes. In addition, Eurasia and North America each include two separate temperate moist forest biomes (European temperate and East Asian temperate, North American eastern temperate and North American western temperate) that are geographically separated today by more than 1,000 km and have almost no overlap in species composition (Petrides and Petrides 1992; Latham and Ricklefs 1993; Petrides 1998), and so each of these biomes is treated here as an independent data point.

We were able to produce estimates for current tree species richness for 11 biome areas: two boreal areas (North America and Eurasia), six continental temperate areas (Europe, East Asia, eastern North America, western North America, South America, and Australia), and three tropical areas (Neotropics, African tropics, and Asian tropics, the latter including India, the Malayan Peninsula, and Borneo). The Australian tropics and Papua New Guinea (PNG) were not included because we could not find reliable estimates on the species richness of the tree flora of PNG or the amount of overlap between PNG and Asia and/or Australia (to decide whether Australia/PNG warranted a separate designation from the Asian tropics). Estimates for tree diversity per biome area are admittedly speculative (see table 1 for sources), especially for tropical forests. The significance of the relationships between biome area and species richness was tested by pairwise correlation of the log-transformed variables.

Magallón and Sanderson (2001) estimated average speciation rates for angiosperms and found an average overall


Biome: North American Boreal
Tree species: **61**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: Eurasian Boreal
Tree species: **100**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: N. Am. W. Temperate
Tree species: **115**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: European Temperate
Tree species: **124**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: N. Am. E. Temperate
Tree species: **300**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: E. Asian Temperate
Tree species: **729**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: S. Am. Temperate
Tree species: **84**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: Australian Temperate
Tree species: **310**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: Neotropics
Tree species: **22,500**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: African tropics
Tree species: **6,500**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present
Biome: Asian Tropics
Tree species: **14,000**
2 x 10^{7}km^2
1 x 10^{7}km^2
55 Ma
30 Ma
12 Ma
Present

rate of 0.0893 net speciation events per million years, with a maximum rate of 0.32 events per million years in the Asteraceae. From these values, we surmised that the cumulative history of biome size on the order of tens of millions of years would be a reasonable window in which fluctuations in biome area could be expected to have an effect on extant diversity levels. Therefore, we chose three slices of time within this range to test the relationship of area-time composites with current tree diversity: from the mid-Miocene (11 million years ago [Ma]) to the present, the mid-Oligocene (30 Ma) to the present, and the early Eocene (55 Ma) to the present.

To estimate the size of biome areas through time, we used paleoclimatic and paleovegetation maps that estimated moist/wet tropical, temperate, and boreal forests from five recent sources: Morley (2000), Beerling and Woodward (2001), Willis and McElwain (2002), Scotese (2003; the PALEOMAP Project), and Ziegler et al. (2003). The authors of these five sources based their reconstructions of the history of tropical, temperate, and boreal biomes on different kinds of evidence, ranging from general circulation models (GCMs) to palynological records, plant and animal macrofossils, and geological formations (see the appendix in the online edition of the *American Naturalist* for detailed information on the sources and assumptions in our five interpretations of the history of past biomes in figs. 1 and 2). Not all sources provided maps for tropical, temperate, and boreal biomes for every time period. Moreover, sources presented very different maps with respect to historical biome areas, particularly for tropical forests in the Eocene (see fig. 2). For this reason, we made five distinct interpretations of historical biome areas that are derived from combinations of the five sources. These five interpretations are intended to cover the range of inferences that exist regarding past biome extents and provide a basic sensitivity analysis for our study (fig. 1; see appendix for detailed information).

For each source, we digitized the maps for each time period and scaled all of the equal-area maps to a uniform size. Beerling and Woodward (2001) was the only source with maps that were not equal-area projections, so we traced the biomes by eye from Beerling and Woodward (2001) onto equal-area maps of the continental configurations of the Eocene (from Smith et al. 1994) and onto maps of current continental configurations for the last glacial maximum (21,000 years ago) and mid-Holocene (6,000 years ago) reconstructions. We used ImageJ to estimate the area of each of the 11 biome areas at each time period from the digitized maps.

For each biome area, area size was plotted against time. From each of these graphs, a composite area-time parameter was calculated by estimating the area under the curve using ImageJ. This parameter was log transformed and tested by pairwise correlation with the log-transformed data on current tree diversity. This analysis was performed for time periods since the Miocene, the Oligocene, and the Eocene for each of the five interpretations in figure 1.

These methods for estimating biome area through time are crude and approximate, given the coarse temporal resolution of the underlying maps, the method used to calculate areas over time, and the many uncertainties associated with paleoclimatic reconstruction. Nevertheless, we do not expect the methods to yield systematically biased results. Moreover, given that we are using log-transformed data, the correlations are likely to be robust to substantial error in both area and tree diversity estimates.

Results and Discussion

There is no significant correlation between current biome area and tree species richness ($R^2 = 0.13$, $P = .3$; table 2). By contrast, some correlations of time-integrated area with tree species richness were found to be significant for cumulative time periods since the Miocene (two of five interpretations), the Oligocene (three of five interpretations), and the Eocene (four of five interpretations; table 2).

Our five interpretations show large variation in the amount of area that these moist tropical biomes are thought to have covered since the Eocene (fig. 1). The only interpretation that did not yield a significant correlation of area-time measures with current tree diversity is the one that assumes a dry Eocene with a relatively small tropical evergreen forest biome (Beerling and Woodward 2001). It is important to note that the disagreements among the interpretations are almost entirely based on the

Figure 1: At center is a map showing the modern extent of the 11 biomes included in the analysis. Surrounding the globe are the estimates for extant tree species richness and composite area-time measures for each biome, based on the five interpretations. Pink lines trace paleoreconstructions of interpretation 1 (tropical Eocene, based on Beerling and Woodward 2001), blue lines represent interpretation 2 (tropical Eocene, based on Morley 2000), red lines represent interpretation 3 (tropical Eocene, based on Ziegler et al. 2003), orange lines represent interpretation 4 (C. R. Scotese's [2003] PALEOMAP reconstructions, and green lines represent interpretation 5 (Willis and McElwain 2002). See figure 2 for depictions of the five interpretations at different times and the appendix in the online edition of the *American Naturalist* for detailed methods of how the five interpretations were made, including the raw data. The area of each area-time plot from each interpretation was quantified, log transformed, and then correlated with log (tree diversity) to test for the time-integrated species-area effect.

Table 1: Size and number of tree species for the 11 biomes included in this study

Biome	Area (1,000 km^2)	Estimated no. tree species	Sources
North American boreal	5,117	61	Petrides and Petrides 1992; Petrides 1998
Eurasian boreal	10,010	100	Hytteborn et al. 2005; A. Shvidenko, personal communication
North American eastern temperate	3,396	300	Petrides 1998
North American western temperate	1,698	115	Petrides and Petrides 1992
European temperate	6,374	124	Latham and Ricklefs 1993
East Asian temperate	4,249	729	Latham and Ricklefs 1993
South American temperate	413	84	Rodriguez et al. 1983
Australian temperate	735	310	Francis 1981
Neotropics	9,220	22,500	R. Condit, personal communication; R. Foster, personal communication
Asian tropics	5,903	14,000	R. Condit, personal communication; J. LaFrankie, personal communication
African tropics	3,471	6,500	R. Condit, personal communication

Note: Current biome area is estimated pre–human impact and comes from the Word Wildlife Fund (see map of biomes in Olson et al. 2001). Sources for estimated tree diversity per biome are listed.

amount of evapotranspiration thought to have been present at the lower latitudes during the Eocene (which would shrink the area of moist/wet forest of tropical biomes) rather than on where past frost lines were located (Ziegler et al. 2003). Much of the debate over the relative size of Eocene and Oligocene tropical areas centers on whether there were large "paratropical" forests (moist/wet forests in frost-free areas that were in the midlatitude Eocene and Oligocene) or whether those areas were too dry to support a well-developed moist/wet forest and were instead dry forests (composed of "tropical" elements, i.e., families that are now known as not occurring in temperate areas) or savannahs (Morley 2000; Beerling and Woodward 2001; Ziegler et al. 2003). Thus, our conclusions about the importance of the time-integrated species-area effect must include the caveat that the most conservative interpretation for tropical forest extent in the Eocene (fig. 1, interpretation 1) did not yield significant correlations between area-time and tree species diversity. But plant macrofossils interpreted as being members of a tropical moist/wet forest community (e.g., Wilf et al. 2003; see also many citations in Willis and McElwain 2002) have been found in areas that are modeled by the general circulation model (GCM) approach (Beerling and Woodward 2001) as dry forest or savannah. These observations suggest that the GCMs from the Eocene may be modeling an overly conservative extent for tropical forests (Beerling and Woodward 2001).

The results from four of five interpretations (table 2) suggest that both the size and the age of a biome are important factors in explaining its current species richness, but only when an integrated measure of both factors is included. Considered in this way, our findings corroborate earlier claims by Wallace (1876), Willis (1922), and others that the extraordinarily high diversity of tropical rain forests is due to their greater age. Other large-scale studies have noted that area and species diversity are positively related. Tiffney and Niklas (1990) found that fossil plant species richness correlated with the overall land area of the Northern Hemisphere at 12 slices in time between 410 and ∼10 Ma. In addition, a recent study of palynological data found that Neotropical tree diversity peaked in the Eocene when tropical forests covered the largest amount of area (Jaramillo et al. 2006). Nevertheless, to our knowledge, this is the first time that age and area have been combined in an empirical test of their relationship with current diversity patterns.

The time-integrated species-area effect that we test here is conceptually related to the tropical conservatism hypothesis (TCH) recently summarized by Wiens and Donoghue (2004). The TCH is based on three basic ideas. First, if a clade originated in the tropics, it is expected to include more tropical species because of the greater age of the tropics and the time-for-speciation effect. Second, if tropical areas have been larger overall than extratropical areas, a correspondingly higher proportion of extant lineages should have originated in the tropics. Third, if adaptations to survive freezing temperatures are necessary to colonize extratropical regions and these adaptations are rarely acquired, then niche conservatism within tropical lineages will maintain the disparity in species richness over time

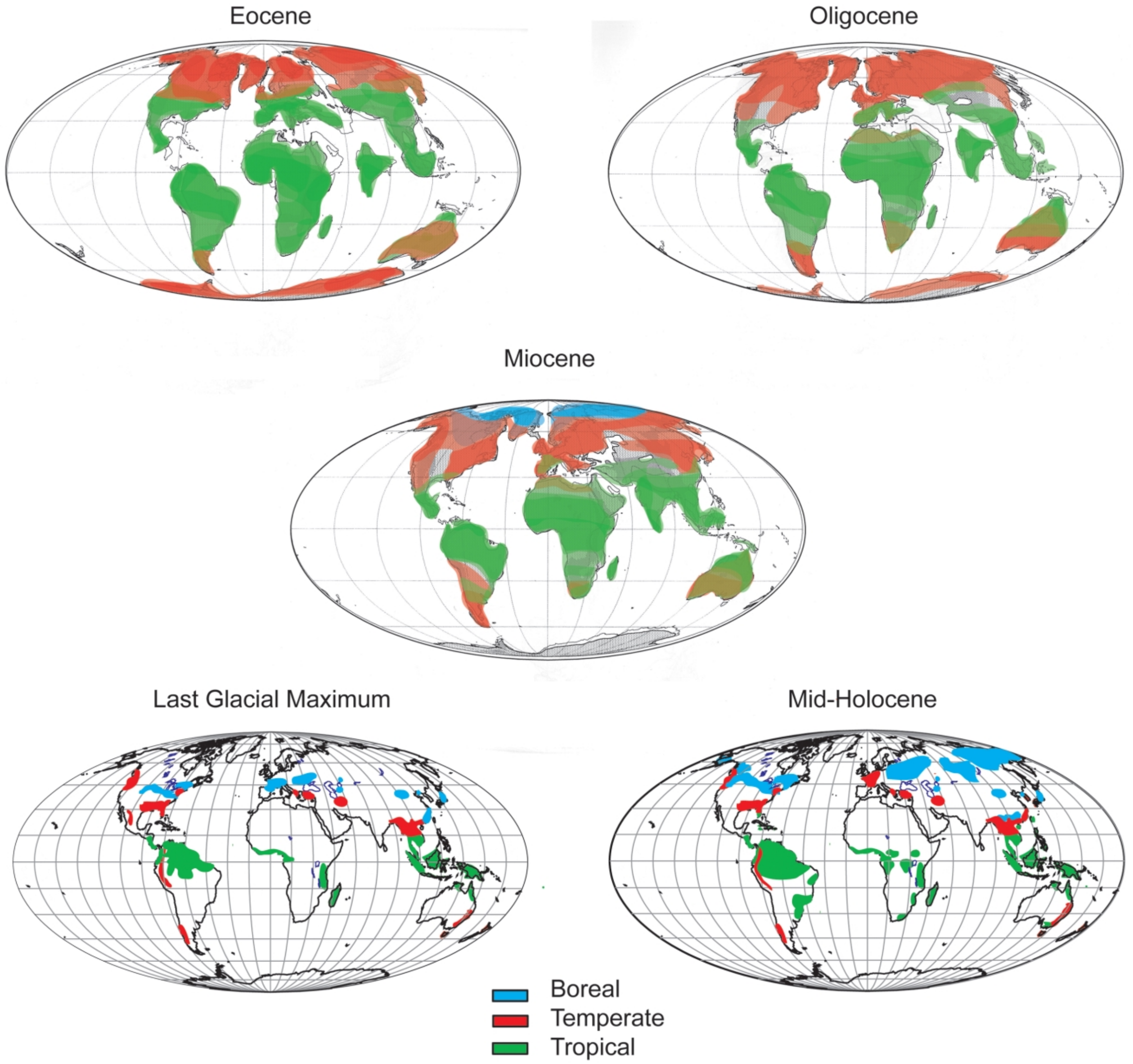


Figure 2: Five interpretations of past biomes (see fig. 1), drawn on top of one another onto paleocoastlines from Smith et al. (1994) for the Eocene, Oligocene, and Miocene. The darker colors represent agreement among the sources; shades that are neither green, red, nor blue represent disagreement. Last glacial maximum and mid-Holocene reconstructions are adapted from Beerling and Woodward (2001).

(Latham and Ricklefs 1993; Ricklefs and Schluter 1993; Brown and Lomolino 1998; Futuyma 1998; Wiens and Donoghue 2004).

While the time-integrated species-effect focuses on the intrinsic properties of biomes (area through time) that influence in situ diversification of all resident species in a functional group (trees), the TCH emphasizes clade diversification in the context of historical biogeography—namely, the frequency, timing, and directionality of cross-biome colonization events. The evolutionary mechanisms underlying the first and second ideas of the TCH are conceptually unified and empirically supported by the time-integrated species-area effect demonstrated here. In that regard, the time-integrated species-area effect is an integral part of the TCH and in fact is necessary for it to be true.

Current disparities in species diversity across biomes surely contain the historical signatures of both tropical-conservatism effects and time-integrated-area effects. For

Table 2: Results of the correlations between log (tree diversity) and log (time-integrated area) for the five interpretations shown in figure 1

Interpretation (source), cumulative time since	R^2	P
Modern (Olson et al. 2001):		
Present	.13	.283
1 (Beerling and Woodward 2001):		
Eocene	.21	.151
Oligocene	.17	.211
Miocene	.01	.730
2 (Morley 2000):		
Eocene	.37	**.046**
Oligocene	.17	.211
Miocene	.01	.730
3 (Ziegler et al. 2003):		
Eocene	.47	**.021**
Oligocene	.39	**.041**
Miocene	.07	.426
4 (Scotese 2003):		
Eocene	.51	**.014**
Oligocene	.59	**.006**
Miocene	.61	**.005**
5 (Willis and McElwain 2002):		
Eocene	.57	**.007**
Oligocene	.53	**.012**
Miocene	.42	**.030**

Note: Each interpretation's area-time composite from the Eocene (55 million years ago [Ma]), the Oligocene (30 Ma), and Miocene (11 Ma) was calculated for each of the 11 biome areas and correlated with current log (tree diversity). Significant relationships are in boldface.

example, frost tolerance is a difficult physiological barrier for angiosperms to overcome, and phylogenetic niche conservatism explains why relatively few lineages became established in the temperate zone. But temperate biomes (although often reduced in size) have been in existence throughout the entire history of the angiosperms (Willis and McElwain 2002; Ziegler et al. 2003). We speculate that if temperate areas had been consistently large and stable through the past 55 million years, they would have developed a diverse flora comparable to that of the tropics. In reality, Quaternary and Tertiary changes in climate, with glaciation at higher latitudes, resulted in much smaller effective time-integrated areas for temperate and boreal biomes. Because tropical biomes overall have been larger than temperate biomes throughout the past 55 million years (fig. 1), higher speciation rates and lower extinction rates should have contributed significantly to their high diversity.

Boreal lineages should tend to be phylogenetically nested within temperate lineages and temperate lineages within tropical lineages if the assembly of forest communities has been characterized by evolutionary responses to physiological thresholds that separate biomes (e.g., −40°C tolerance and frost tolerance; Wiens and Donoghue 2004). The data currently available support this prediction, although a large-scale quantitative analysis is lacking (Crane and Lidgard 1990; Ricklefs and Schluter 1993; Judd et al. 1994; Hoffmann 1999; Scheen et al. 2004). If diversification within a lineage could be dated and integrated with reconstructions of past biomes (similar to fig. 1), it would allow for a powerful test of how the area of a biome over time affects diversification rates (Ricklefs 2004). We caution, however, that a large number of independent lineages would need to be studied to avoid sampling bias in detecting any general relationship.

Many proponents of the species-energy hypothesis have linked global diversity patterns to productivity (or correlates of productivity; Currie and Paquin 1987; Adams and Woodward 1989; Wright et al. 1993). Although productivity (or energy) may be important at the local level, regional processes and historical events also contribute to species richness patterns and can override local effects (Ricklefs 1987, 1999; Hillebrand 2005). For example, most estimates place the origin of boreal biomes at 4–10 Ma (Graham 1999; Willis and McElwain 2002). Because trees require specific adaptations to survive boreal climates (Woodward 1987), it would require a radiation several orders of magnitude faster than the fastest known plant radiation (Hawaiian silverswords; Baldwin and Sanderson 1998) for boreal biomes to have floras as rich as tropical biomes. In other words, while productivity may mediate the effect of area (by influencing the number of individuals that can share space in a biome), the effect of productivity on current regional tree species richness patterns is likely to be small compared to the effect of historical events (including change in the size of a biome through time; McGlone 1996). As a thought experiment (see ter Steege et al. 2000), let us imagine a world where moist tropical areas were small and periodically reduced in size, perhaps by extreme aridification events, while large extratropical areas with climates similar to today's boreal biomes were just as ancient as moist tropical biomes and stayed constant in size for tens of millions of years. In such a world, would we find highly diverse tropical rain forests and low-diversity boreal forests, or vice versa? Our results suggest the latter.

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