Evolutionary Ecology Research, 2001, **3**: 413–428

An evaluation of the geographic area hypothesis using the latitudinal gradient in North American tree diversity

Paul V.A. Fine*

Department of Biology, University of Utah, 257 S. 1400 East, Room 201, Salt Lake City, UT 84112, USA

ABSTRACT

One hypothesis to explain the latitudinal gradient in species diversity is the geographic area hypothesis. This hypothesis posits that the size of a biome has considerable influence on its species diversity. Since the tropics are so much larger than any other extra-tropical biome, one would predict the latitudinal gradient to resemble a step function if area and species richness were tightly correlated. When there is a smooth latitudinal gradient in species diversity, it must be because tropical species' ranges extend into extra-tropical areas, inflating the number of species in the extra-tropical areas nearest to the tropics. Here, using data for North American tree ranges, I test whether tropical species' ranges do extend into extra-tropical areas. In a second test, I expand my definition of a tropical species to include species from genera with tropical origins (speciation spillovers). This second test searches for the effect of spillover events over evolutionary time. Only a few tropical species also live in the extra-tropics and, therefore, the latitudinal gradient in tree diversity at large scales is a step function. Thus, spillover species do not contribute to the shape of the latitudinal gradient. However, speciation spill-overs account for a quarter of subtropical areas' species richness, and past range expansion was probably important in generating today's North American tree diversity. The lack of tropical species expanding their ranges into North America may be a result of a trade-off between frost tolerance and growth rate.

Keywords: frost tolerance, geographic area hypothesis, latitudinal gradient, North American tree diversity.

INTRODUCTION

The latitudinal gradient in species diversity is one of the best-documented patterns in biology. Organisms as diverse as insects, trees, mammals and birds increase in species diversity towards the equator (Wallace, 1876; Schall and Pianka, 1978; Rosenzweig, 1995; Givnish, 1999). However, there still is no consensus explanation for this pattern. Initial hypotheses focused on the tropics' relative climatic stability, benign conditions and older

---

* e-mail: fine@biology.utah.edu

evolutionary age, whereas more recent ones look for ecological explanations regarding increases in biotic interactions, niche packing and resource specialization (for reviews, see Pianka, 1966; Begon *et al.*, 1990). John Terborgh proposed perhaps the simplest explanation of all: the tropics (defined as the portion of the earth's surface with a mean range in annual temperature of less than 10°C) have the largest area. All else being equal, large areas will support larger numbers of species because, if a large area and a small area were to have the same number of species, species in the large area would experience higher rates of speciation and lower rates of extinction than species in the small area (Terborgh, 1973, 1992; Rosenzweig, 1975, 1995). Rosenzweig explains that the species in the large area would tend to have larger populations and larger ranges than those in the small area. These differences would enhance their allopatric speciation rates and diminish their probability of extinction by random disturbances.

Terborgh (1973) connected such differences in area to the latitudinal gradient of species diversity. Rosenzweig (1992) adopted this idea, roughly divided the earth's land area into five biomes, and measured their areas worldwide. The tropics (0–26° latitude) are much larger than any other biome. In the Northern Hemisphere, each biome has about the same land area. Therefore, if the species diversity of a biome is due entirely to area, then one would expect a large number for the tropics and equal numbers for each of the more northern biomes (Rosenzweig, 1992, 1995). The relationship should be a step function with the equal-sized biomes having the same diversity, and the tropical biome having a much higher diversity.

However, all species may not be confined to their natal biomes. Some may have ranges that spill over into a neighbouring biome. If the number of range spillover events between biomes is even between equal-sized areas but uneven between differently sized areas, then one would predict that the number of range spillover events from the tropics to its smaller-sized neighbouring biomes should be much greater – and that these tropical spillover species should decrease in number the further they are from the tropics. When taxa exhibit a latitudinal gradient outside of the tropics, then it must be caused by tropical species that have extended their ranges into the extra-tropics, changing the latitudinal gradient from a step function to the familiar, gradually increasing relationship (Rosenzweig, 1992, 1995). Therefore, a natural prediction follows from the geographic area hypothesis (a phrase coined by Blackburn and Gaston, 1997): If one removes tropical species from lists of species of the extra-tropics, the extra-tropical latitudinal gradient should be affected in two ways. First, it should change its shape, becoming flat. Second, this flattening should increase the magnitude of difference in species numbers between the tropics and the extra-tropics. I evaluate this idea using tree species and equal-sized areas in the North American biomes north of the tropics. I test to see how the removal of tropical tree species affects the shape and magnitude of the latitudinal gradient.

Since biomes that abut the tropics have climates with frequent freezes, tropical spillover species should be under different selective pressures in tropical or extra-tropical parts of their range. The extra-tropical populations would be selected for freezing tolerance, whereas the tropical populations would not. This might lead to speciation. Then, even if true, the effect of the geographic area hypothesis could be masked. Therefore, in a second test, I extend my definition of a tropical species. I reason that if a non-tropical species is a member of a mainly tropical genus, then I will count the species as tropical (a 'speciation spillover') and exclude it as I would a tropical species.

Blackburn and Gaston (1997) tested the geographic area hypothesis using data for New

World birds. Grappling with the arbitrary nature of choosing a latitudinal boundary for the tropics, Blackburn and Gaston wisely limited their study to species with partly tropical ranges. Their reasoning was that, if these partly tropical species decreased in frequency away from the equator, it would be consistent with the predictions of the geographic area hypothesis. Indeed, partly tropical bird species did follow this pattern in North America (Blackburn and Gaston, 1997). However, it is unclear whether the gradient exists in extra-tropical latitudes when extra-tropical bird species are considered. If extra-tropical bird species also exhibit a latitudinal gradient, the geographic area hypothesis cannot be the sole cause of the gradient.

In this study, I consider all species of North American trees north of the tropics. 'Hard boundaries' (*sensu* Colwell and Hurtt, 1994) are of less concern as I define 'tropics' and 'extra-tropics' using climatic boundaries rather than fixed latitudes. Moreover, I evaluate each tree species' range individually to gauge whether or not it is 'tropical'. Certainly, tree diversity increases towards the equator, but whether this increase is gradual or abrupt has previously been evaluated only at the scale of 0.1 ha plots. These data portray the latitudinal gradient as a steeply sloped line, increasing towards the equator (Gentry, 1988). The shape of the latitudinal gradient may depend on the scale used for analysis (Lyons and Willig, 1999). In this study, I examine the shape of the latitudinal gradient of tree diversity in North America with large-scale sample areas. I also assess to what extent tropical trees have ranges that extend into North America. Finally, I explore whether the latitudinal gradient of North American tree diversity fits the predictions of the geographic area hypothesis.

METHODS

To generate large-scale latitudinal gradients, I counted the total number of tree species in two large, equal-area transects, from 26°N to 60°N, one in eastern North America and one in central North America (Table 1). The eastern transect was composed of eight areas of approximately 250,000 km^2; the central transect was composed of eight areas of approximately 350,000 km^2 (Fig. 1).

Using current field guides (Petrides and Petrides, 1992; Petrides, 1998), I examined the range maps for every North American tree species and counted how many of them occurred in each area of my transect. I then counted how many species within each area also range into the tropics (see below). I generated two graphs for each transect. One represented all species in each area arranged from north to south; the other represented only extra-tropical species. According to the geographic area hypothesis, the extra-tropical line should be a flat line, or at least have a more gradual slope than the all-species line. To determine whether or not the slopes of the two lines (all species and all extra-tropical species) were different, I performed an analysis of covariance (mean degree of latitude of each area *vs* number of species) and tested whether or not the interaction term 'latitude × species' was significant (Statview).

To see more clearly the shape of the diversity curves, I plotted the data for the eastern and central transects using log number of species. This is necessary because of the disparity in richness between tropical and extra-tropical areas at such a large scale. To add a tropical data point to the figure, I used an estimate for a 350,000 km^2 area in the Amazon Basin of South America (Neill and Palacios, 1989; Valencia *et al.*, 1994; R.B. Foster, personal communication). I chose the Amazon Basin to calculate the estimate so as to avoid inflating the number of species. Large areas in the tropics that include both sides of the Andes

Table 1. The quadrats used to tabulate total numbers of tree species*

Quadrat	Biome	Latitude (°)	Latitudinal range (°)	Area (km^2)	Location
Central transect					
A	Boreal	57–60	3	375,000	Northern Alberta and Saskatchewan
B	Boreal	54–57	3	375,000	Central Alberta and Saskatchewan
C	Temperate	46–49	3	373,540	North Dakota and northern half of Montana
D	Temperate	43–47	4	390,153	South Dakota and southern half of Montana
E	Temperate	39–43	4	335,146	Nebraska and northern half of Colorado
F	Temperate	37–40	3	347,893	Kansas and southern half of Colorado
G	Temperate	32–36.5	4.5	345,000	Northern half of Texas
H	Subtropical	26–32	6	345,000	Southern half of Texas
Eastern transect					
A	Polar/boreal	54–60	6	250,000	Northern Labrador
B	Boreal	50–54	4	250,000	Southern Labrador and Quebec between Labrador and St. Lawrence River
C	Temperate	45–49	4	260,000	Northern Maine, southern Quebec and Atlantic provinces
D	Temperate	41–45	4	245,000	New York, Rhode Island, Connecticut, New Hampshire, Vermont, Massachusetts and southern Maine
E	Temperate	39–42	3	240,000	Pennsylvania, New Jersey and northern two-thirds of Ohio
F	Temperate	36.5–40	3.5	270,000	Virginia, Kentucky and West Virginia (except for northernmost arm)
G	Subtropical	32–35	3	250,000	South Carolina, northern Alabama and Georgia (non-Appalachian areas)
H	Subtropical	28–32	4	220,000	Central and northern Florida, southern Alabama and Georgia

* See Fig. 1 for visual depiction.

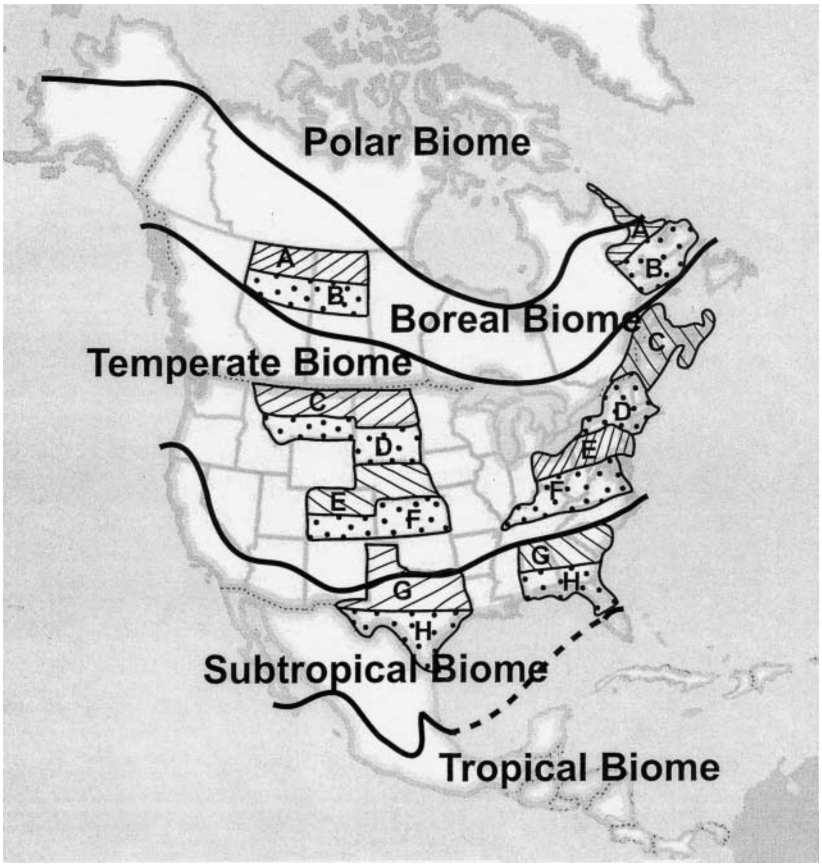

Fig. 1. Map of North America showing the biome boundaries and location of the quadrats within the transects.

or the Cordillera Central in Central America contain allopatrically separated, closely related species and, therefore, would not be topographically analogous to either of the two transects that I used for North America.

Accurately determining what is and what is not a tropical species is vital for this kind of analysis. Previous studies have used fixed latitudes to determine tropical species (Blackburn and Gaston, 1997; Rohde, 1997; Rosenzweig and Sandlin, 1997). However, in North America, areas with tropical climates exist north of the Tropic of Cancer and areas with non-tropical climates exist well south of that line. Temperature exhibits broad predictable patterns with respect to latitude and is the basis for how we classify biomes (Schultz, 1995). Problems arise when geographers (and ecologists) use latitude alone to define biomes. The following is a climatic description of the earth's biomes (adapted from Terborgh, 1973; Larcher and Bauer, 1981; Schultz, 1995):

- *Tropical*: never freezing temperatures, annual range less than 10°C.
- *Subtropical*: infrequent or occasional freezing temperatures, winter mean temperatures always above 5°C.

- *Temperate*: annual frost, winters with many consecutive sub-zero days.
- *Boreal*: common –40°C temperatures in winter, 5–6 months with mean temperatures below 0°C.
- *Polar*: temperatures severe enough, or growing season short enough, such that trees cannot survive.

From these definitions, it should be clear that subtropical and temperate zones exist within the geographic tropics (below 23.5°N). Also, in extreme South Florida, a tropical area exists within the geographic subtropics. Because I was interested in the ranges of tropical species spilling into non-tropical biomes, I excluded South Florida from the eastern transect. South Florida enjoys a tropical climate and supports almost 100 species of tropical trees that have dispersed there from the West Indies (Long and Lakela, 1971). In addition, I did not classify the few temperate trees that live in South Florida as tropical if their only tropical distribution was South Florida because they almost certainly did not originate there. To be considered a tropical species, then, a North American tree species must live anywhere south of Florida that experiences a tropical climate. For this reason, temperate trees that also lived in high-altitude areas of Mexico (but not in its lowlands) were not considered tropical.

To extend the test of the geographic area hypothesis to include speciation spillovers, I expanded my definition of a tropical species. I reasoned that, if a non-tropical species were a member of a mainly tropical genus, then I would count the species as tropical and exclude it as I would a tropical species. A genus was identified as mainly tropical if there was evidence of diversification in the tropics, or a lack thereof in the temperate zone. Although one cannot be sure that these mainly tropical genera actually originated in the tropics, this approach is a conservative estimate of tropical spillover. Many species that cross into the extra-tropics from the tropics diverge morphologically under their new selective regimes – so much so, that taxonomists may classify them as new genera, thereby obscuring their recent tropical origins. Diversification patterns of North American genera were evaluated using Mabberley's (1997) descriptions of the distribution of the world's genera of plants. For each transect, I compared the latitudinal gradient of all species to the gradient that excluded the speciation spillovers and, as above, I performed an analysis of covariance to determine if the two regression lines had significantly different slopes.

In addition to testing the geographic area hypothesis for North American trees, I was interested in whether species distributions were restricted to the boundaries of the biomes as I defined them, and whether there were patterns to the range spillovers between them. So, I counted the tree species diversity of each North American biome and, for each species, I identified whether it was endemic to its biome. If a species was not endemic, I noted where its centre of distribution was and if more than 10% of its range extended into a neighbouring biome. Species whose biomes of origin were impossible to identify were excluded from the analysis (less than 10% of total). Using this approach, I measured the number of spillover events between all neighbouring biomes.

RESULTS

At large scales, the latitudinal gradient for tree diversity (for both the eastern and central transects) appears to be a step function (Fig. 2). Plotting the latitudinal gradient against log species number, and including a very conservative estimate for a 350,000 km^2 area in the

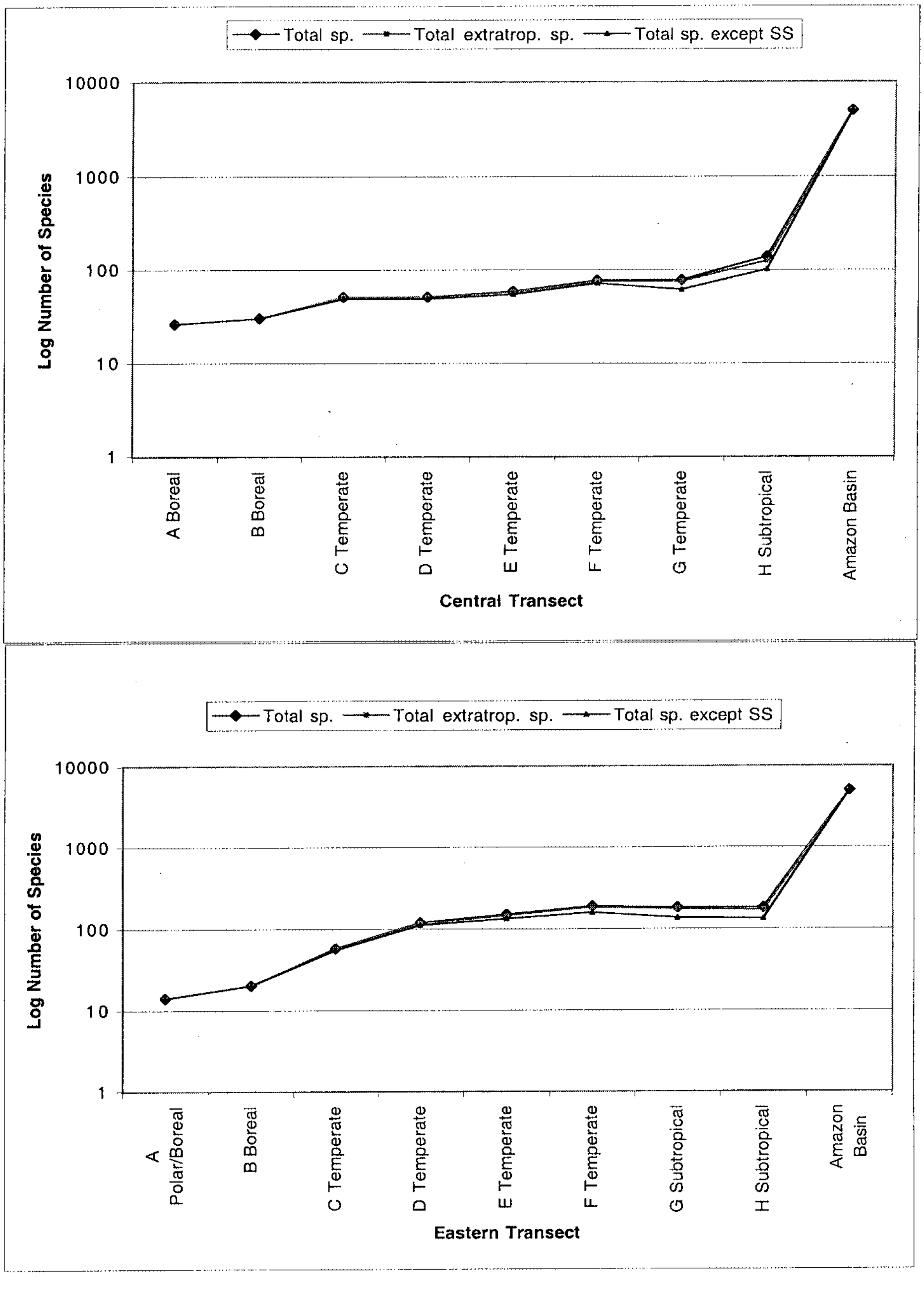

Fig. 2. Latitudinal gradient of log (species numbers) generated from counting the number of tree species in each quadrat for the central (top) and eastern (bottom) transects. The diamond series represents the total species number for each quadrat, the square series represents total extra-tropical species number, and the triangle series represents total species excluding the speciation spillovers. The specific locations and areas of the quadrats are listed in Table 1 and are shown in Fig. 1, with an added tropical quadrat.

Table 2. Total numbers of tree species for all of North America (north of Mexico)

Biome	Area (km^2)	Total species	% Endemics
Boreal	6,472,000	61	3.2
Temperate	6,814,000	286	11.9
Subtropical	3,109,000	411	40.6
Tropical (including Central and South America)	11,650,000	17,000*	99+

* Tropical species estimate from R.B. Foster (personal communication).

Table 3. Total numbers of tree species*

Quadrat	Biome	Total spp.	Total extra-tropical	Total excluding speciation spillovers
Central transect				
A	Boreal	26	26	26
B	Boreal	30	30	30
C	Temperate	51	51	49
D	Temperate	51	51	49
E	Temperate	59	58	55
F	Temperate	77	75	72
G	Temperate	78	75	62
H	Subtropical	139	126	101
Eastern transect				
A	Polar/boreal	14	14	14
B	Boreal	20	20	20
C	Temperate	57	56	55
D	Temperate	118	115	110
E	Temperate	149	145	132
F	Temperate	187	182	157
G	Subtropical	181	174	136
H	Subtropical	180	168	132

* See Table 1 and Fig. 1 for areas and locations of quadrats in the transects. See Fig. 3 for graphical representation of the data.

Amazon Basin, clearly shows a two-step relationship – low boreal diversities, medium diversities for the two temperate areas and the subtropical areas, and a very high tropical diversity.

Looking at the scale of biome, we find again the two-step relationship, with lowest diversity in the boreal biome, mid-diversities in the temperate and subtropical biomes, and very high diversity in the tropics (Table 2). The percentage of endemics (or the amount of 'zonal endemism', *sensu* Rosenzweig and Sandlin, 1997) decreases steadily towards the poles (Table 2).

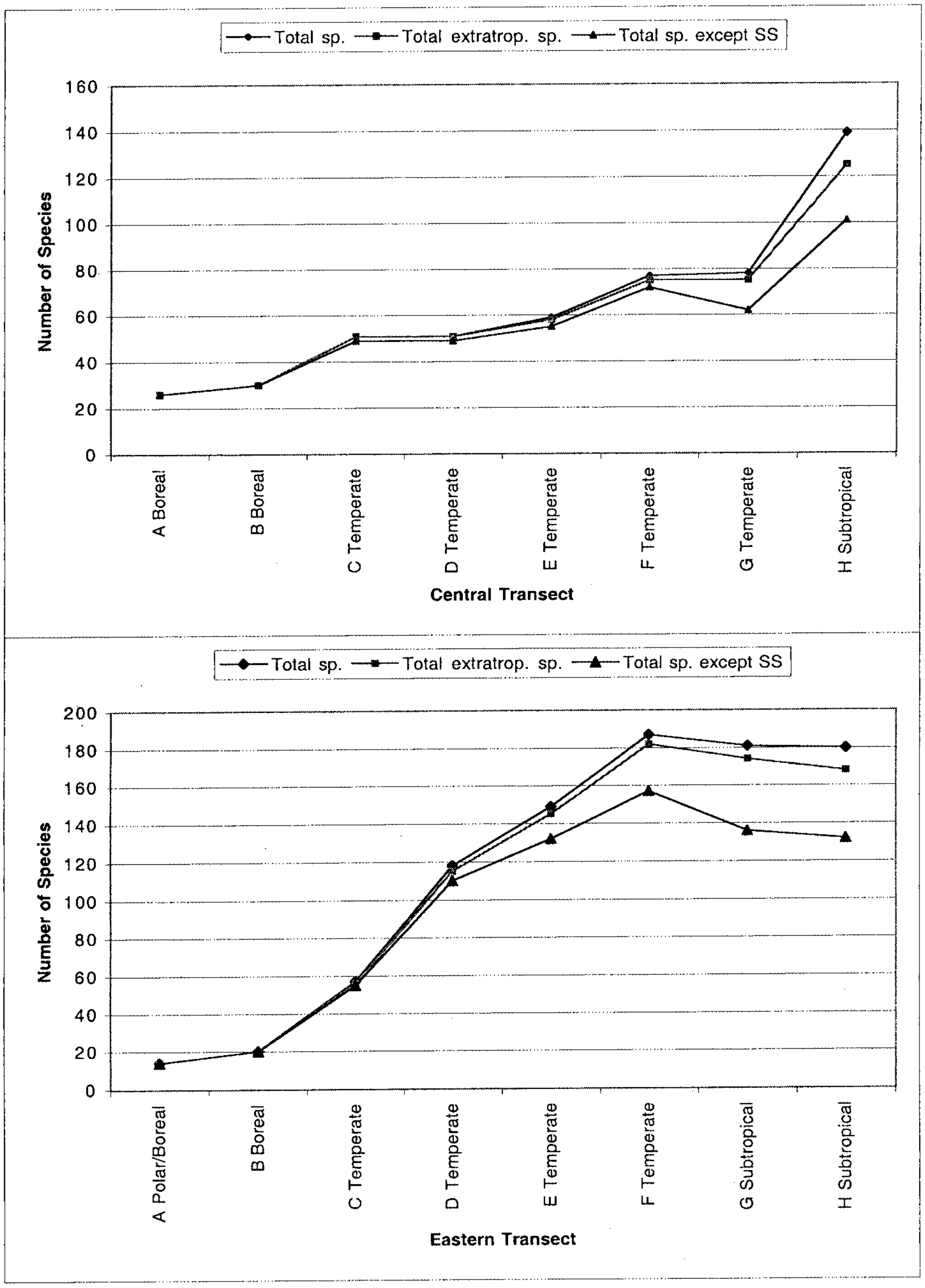

Fig. 3. Latitudinal gradients generated by counting the number of tree species in each quadrat (A–H) for the central (top) and eastern (bottom) transects. The diamond series represents the total species number for each quadrat, the square series represents total extra-tropical species number, and the triangle series represents total species excluding the speciation spillovers. The specific locations and areas of the quadrats are listed in Table 1 and are shown in Fig. 1.

The latitudinal gradients generated by the total number of species did not differ from the latitudinal gradients generated by only extra-tropical species for either of the transects (central transect: $F = 0.073$, $P < 0.7910$; eastern transect: $F = 0.203$, $P < 0.6604$). The removal of tropical species from the two transects had only a minor flattening effect on the shape of the curve (Fig. 3; Table 3). Only a very few tropical species – that is, 12 in the east (7% of total) and 13 in the central (9% of total) transects – extend their ranges north into the extra-tropics. Over half of these are restricted to marshes, salty areas, desert oases and other marginal habitats (see Appendix).

The latitudinal gradient excluding speciation spillovers was not statistically different from the gradient including all species (central transect: $F = 2.232$, $P < 0.1610$; eastern transect: $F = 1.696$, $P < 0.2173$). The removal of speciation spillovers caused only a slight difference in the shapes of the graphs (Fig. 3; Table 3). However, for the subtropical areas in both transects (‘G’ and ‘H’ in the east, ‘H’ in the central), removal of speciation spillovers increased the magnitude of difference between the subtropical and tropical areas (Fig. 2). Speciation spillovers accounted for over 25% of the total species (Table 3).

Range spillover is relatively rare between most biomes. The exception to this is the temperate/subtropical barrier, which was easy to cross (Fig. 4). There appears to be no north–south or south–north trend in range spillover, and the area of the biome had no effect on the number of range spillover events (Fig. 4).

DISCUSSION

Why does the latitudinal gradient appear like a step function?

Using large areas to investigate the latitudinal gradient in tree species diversity indicates that the gradient is not a smooth increase from the poles to the equator, but close to a step function. Previous work regarding the latitudinal gradient in tree diversity used 0.1 ha plots (Gentry, 1988). One hectare generally contains 600 individuals over 2.5 cm diameter at breast height (dbh). If an entire region’s diversity is over 5000, it is clear that even 1 ha plots are far too small to compare regional diversity patterns outside of the lowest diversity forests (Gentry and Dodson, 1987; Latham and Ricklefs, 1993).

The geographic area hypothesis predicts that the removal of tropical species spilling over into extra-tropical areas would level the latitudinal gradient of the extra-tropics, causing the entire gradient to appear like a step function. But, even including the spillover species, the diversity gradient already *is* a step function (Fig. 2). If the tropics support a much higher diversity of trees, and a factor such as freezing temperatures prevent tropical tree species from spilling over into the extra-tropics, then a step-like function is what one would expect to see. Other organisms, like birds, may not be as sensitive to occasional freezing temperatures and their gradient, therefore, may be smoother. So, although removing tropical species does not change the latitudinal gradient in the northern neighbouring biomes, this result does not disprove the geographic area hypothesis. In fact, the latitudinal gradient does not have the shape that was expected, since the expectation was based on Gentry’s (1988) data generated using 0.1 ha plots. Most studies concerning the latitudinal gradient have used smaller scale samples to investigate the relationship (Schall and Pianka, 1978; Rosenzweig, 1995; Blackburn and Gaston, 1997; Lyons and Willig, 1999). Whether

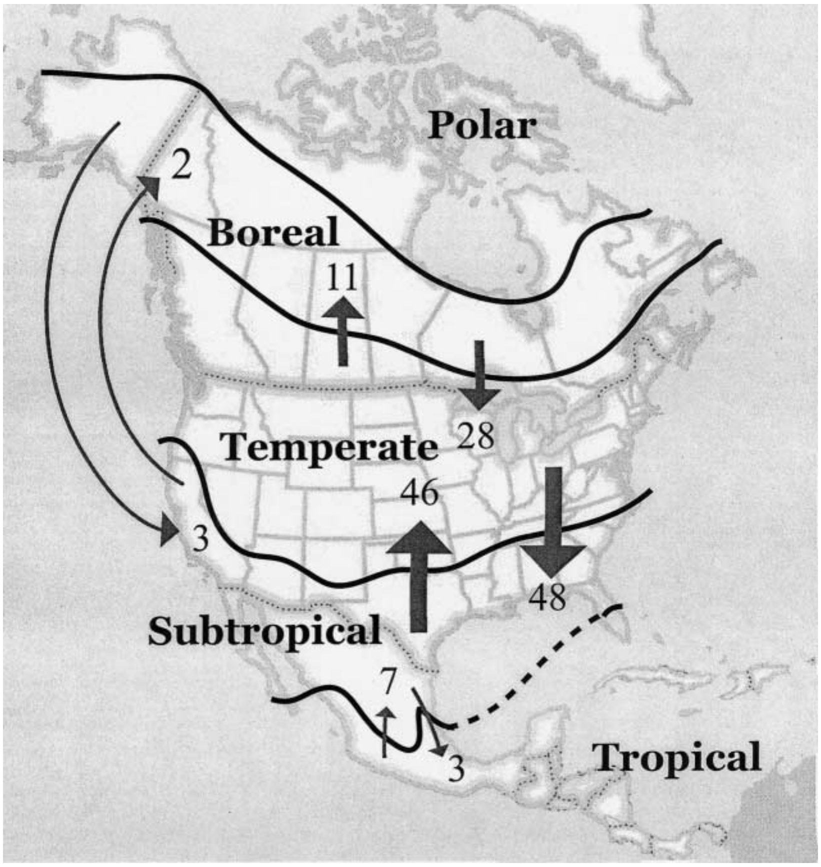

Fig. 4. Map of North American biomes showing the number of spillover species that cross each biome boundary.

measuring diversity at large scales will change interpretations of the latitudinal gradient for other taxa should be investigated.

Why don't tropical species spillover?

Only a very few tree species have ranges that span tropical and extra-tropical climates (Fig. 3; Appendix). Living north of the tropics requires frost tolerance, a trait that is an unnecessary cost for tropical trees. Frost tolerance trades off against growth rate (Sakai and Weiser, 1973; Loehle, 1998). Thus, for a tropical tree growing in a tropical climate, being frost-tolerant would put it at a competitive disadvantage. Tropical trees that disperse into extra-tropical zones are either killed by freezing temperatures or undergo selection for frost tolerance. Gene flow between frost-tolerant and frost-intolerant populations may reduce the fitnesses of both populations. If so, selection for isolating mechanisms could be rapid, and speciation the conclusion (Endler, 1977; Rice, 1989).

Only one species, *Cephalanthus occidentalis* (Rubiaceae), has an extensive range on both sides of the subtropical/tropical border. This species lives only in marshes and other flooded habitats. Perhaps species that live in such marginal habitats suffer less competitive pressure and are able to maintain populations with divergent temperature tolerances. The small number of tropical species that cross the frost line mainly live in specialized habitats such as mangroves, swamps and desert oases (Appendix). However, the overwhelming majority of tropical species do not live north of the frost line, preventing tropical species from affecting the shape of the latitudinal gradient or the magnitude of the difference between the tropics and the extra-tropics.

Speciation spillovers, however, account for 25% of the diversity in the southern subtropics (Table 3). This implies that tropical species have indeed been spilling into extra-tropical zones and speciating, thus obscuring the spillover event. While removal of the speciation spillovers does not affect the shape of the latitudinal gradient, it does affect the magnitude of the difference between subtropical and tropical diversities (Fig. 2). With this new, broader definition of a tropical spillover species, the difference between subtropical and tropical diversities becomes more pronounced, which is one of the predictions of the geographic area hypothesis.

The geographic area hypothesis, productivity and historical contingency

Rosenzweig and Sandlin's (1997, p. 174) hypothesis to explain the latitudinal gradient contains three elements: 'Large area dictates high diversities in the tropics. Very low productivities prevent the same in the Holarctic tundra. And species' ranges bleed out into the biomes into which they were not born'. The first and second elements of their hypothesis were not addressed by the present study, although the American tree diversity data do agree with both. The larger tropics have more species and diversity is correlated with productivity among North American samples (Table 2).

The third element, whether or not species 'bleed into other biomes', was examined directly in this study. My results show that, for North American trees, only 23 tropical tree species bleed into extra-tropical biomes (Appendix). Nevertheless, the fact that speciation spillovers account for 25% of the diversity in the southern subtropics gives arguable support for the idea that tropical species have spilled over into extra-tropical areas in the past. Although Rosenzweig (1995) has argued convincingly for the role of area in generating diversity, an alternative hypothesis is that the tropics are more diverse because there has been more time for species to diversify (Latham and Ricklefs, 1993; Tilman and Pacala, 1993; McGlone, 1996). Latham and Ricklefs (1993) noted that, since angiosperm trees have a tropical origin and need to be frost-tolerant to increase their distribution, and if one assumes that all lineages produce species independently of latitude, then species should accumulate in the tropics due to the larger number of existing clades. Although this hypothesis is important, it is difficult to evaluate hypotheses concerning historical contingency because data do not exist for the origination of lineages. Moreover, one cannot currently assume that speciation is a constant process, independent of latitude (Gilinsky, 1998).

The two hypotheses are not mutually exclusive. Area and history may interact to influence the latitudinal gradient. The temperate zone was subjected to glacial–interglacial climate cycles, and areas in which temperate species could survive were reduced to a much larger extent than areas in the tropics (McGlone, 1996). Therefore, the relatively depauperate temperate tree diversity may in part be due to the extremely high extinction rates and low speciation rates that temperate trees experienced when glacial periods drove them into small refuges.

Which barriers are important?

The climatic boundaries that I chose to define the biomes coincide for the most part with tree species ranges. The exception is the distinction between the subtropical and temperate biomes. For a long-lived tree, it may make little difference whether there is annual frost or frost once every decade. If age of first reproduction is longer than 10 years, then every individual must possess frost tolerance. Many species cross this barrier, indicating that annual frost (as opposed to occasional frost) is not a threshold-like barrier, at least for trees (Fig. 4).

In contrast, the barriers between the tropics and the subtropics and the boreal biome and the temperate biome do restrict species distributions (Fig. 4). Just as frost tolerance probably restricts tropical species from living north of the frost line, there is an analogous physiological threshold at the boreal/temperate barrier. This is at –40°C, the temperature of spontaneous nucleation of supercooled water (Woodward, 1987). Trees must be specially adapted to survive temperatures below that, and this trait presumably also trades off against growth rate (Loehle, 1998).

What is the evidence for MacArthur's (1972) suggestion that interspecific competition limits southern range expansion? First, only three species with a centre of distribution in the subtropics also live in the tropics (Fig. 4). Second, consider how trees are distributed in South Florida, an area that experiences a tropical climate and supports a mixture of trees from tropical and extra-tropical origins. Extra-tropical trees only dominate where there are frequent wildfires (Alexander, 1967; Snyder *et al.*, 1990). In the absence of fire, northern trees (which are frost-tolerant) get excluded by tropical trees, presumably because tropical trees have a faster growth rate (Loehle, 1998). Third, extra-tropical trees are grown in many tropical areas where humans restrict natural competition, for example in arboretums and in towns, demonstrating that the hot tropics do not overwhelm the physiologies of cold-tolerant trees (personal observation).

Zonal endemicity (or the percentage of biome-endemics) decreases away from the equator (Table 2). This makes sense for North American trees: the further north, the more extreme and unpredictable are the temperature ranges, making it more difficult for a tree to specialize upon a specific geographic area (Janzen, 1967). Thus, independent of area, climate imposes restrictions on diversity.

In summary, frost tolerance defines the boundaries between the extra-tropical and tropical biomes for North American trees, and causes the latitudinal gradient in tree diversity to resemble a step function. But other physiological stresses impose barriers to range expansion. Drought may well be the second most important factor in restricting species distributions (Woodward, 1987). I suspect that, as with frost tolerance, few species can tolerate severe drought and successfully compete against species without drought tolerance in drought-free areas. Future research could define biomes by drought and frost tolerance, and I predict that area should be the primary factor for worldwide comparisons of diversity *within* biomes – for example, comparing all of the drought-free subtropical biomes between continents. This approach would complement previous studies that have ignored the effect of area and simply correlated tree diversity with productivity or precipitation (Currie and Paquin, 1987; Adams and Woodward, 1989).

ACKNOWLEDGEMENTS

I wish to thank P.D. Coley for advice and support at all stages of this project. I also gratefully acknowledge S.D. Torti, S.W. Brewer, J.S. Dukes and M.L. Rosenzweig for reading and providing comments on previous drafts of the manuscript, and B.S. Weinstein, A.R. Masters and D.H. Feener, Jr for helpful discussions concerning my data. This work was supported in part by a NSF Predoctoral Fellowship.

REFERENCES

Adams, J.M. and Woodward, F.I. 1989. Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature*, **339**: 699–701.

Alexander, T.R. 1967. A tropical hammock on the Miami limestone: A twenty-five year study. *Ecology*, **48**: 863–867.

Begon, M., Harper, J.L. and Townshend, C.R. 1990. *Ecology*: *Individuals*, *Populations*, *and Communities*. Boston, MA: Blackwell Scientific.

Blackburn, T.M. and Gaston, K.J. 1997. The relationship between geographic area and the latitudinal gradient in species richness in New World birds. *Evol. Ecol.*, **11**: 195–204.

Colwell, R.K. and Hurtt, G.C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *Am. Nat.*, **144**: 570–595.

Currie, D.J. and Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature*, **329**: 326–327.

Endler, J.A. 1977. *Geographic Variation*, *Speciation*, *and Clines*. Princeton, NJ: Princeton University Press.

Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Gard.*, **75**: 1–34.

Gentry, A.H. and Dodson, C. 1987. Contribution of nontrees to species richness of a tropical rain forest. *Biotropica*, **19**: 149–156.

Gilinsky, N.L. 1998. Evolutionary turnover and volatility in higher taxa. *Biodiversity Dynamics* (M.J. McKinney and J.A. Drake, eds.). New York: Columbia University Press.

Givnish, T.J. 1999. On the causes of gradients in tropical tree diversity. *J. Ecol.*, **87**: 193–210.

Janzen, D.H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.*, **101**: 233–249.

Larcher, W. and Bauer, H. 1981. Ecological significance of resistance to low temperature. In *Encyclopedia of Plant Physiology*, Vol. 12A (O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler, eds), pp. 403–437. Berlin: Springer-Verlag.

Latham, R.E. and Ricklefs, R.E. 1993. Global patterns of tree species richness in moist forests: Energy-diversity theory does not account for variation in species richness. *Oikos*, **67**: 325–333.

Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. *J. Biogeogr.*, **25**: 735–742.

Long, R.W. and Lakela, O. 1971. *A Flora of Tropical Florida*. Coral Gables, FL: University of Miami Press.

Lyons, S.K. and Willig, M.R. 1999. A hemispheric assessment of scale dependence in latitudinal gradients of species richness. *Ecology*, **80**: 2483–2491.

Mabberley, D.J. 1997. *The Plant-Book*. Cambridge: Cambridge University Press.

MacArthur, R.M. 1972. *Geographical Ecology*. New York: Harper & Row.

McGlone, M.S. 1996. When history matters: Scale, time, climate, and tree diversity. *Global Ecol. Biogeogr. Lett.*, **5**: 309–314.

Neill, D. and Palacios, W. 1989. *Arboles de la Amazonia ecuatoriana. Lista preliminar de especies*. Quito: Ministerio de Agricultura y Ganaderia.

Petrides, G.A. 1998. *A Field Guide to the Eastern Trees*: *Eastern United States and Canada*, *including the Midwest*. New York: Houghton Mifflin.

Petrides, G.A. and Petrides, O. 1992. *A Field Guide to Western Trees*: *Western United States and Canada.* New York: Houghton Mifflin.

Pianka, E.R. 1966. Latitudinal gradients in species diversity: A review of the concepts. *Am. Nat.*, **100**: 33–46.

Rice, W.R. 1989. Speciation via habitat specialization: The evolution of reproductive isolation as a correlated character. *Evol. Ecol.*, **1**: 301–314.

Rohde, K. 1997. The larger area of the tropics does not explain latitudinal gradients in species diversity. *Oikos*, **79**: 169–172.

Rosenzweig, M.L. 1975. On continental steady states of species diversity. In *The Ecology and Evolution of Communities* (M. Cody and J. Diamond, eds), pp. 121–140. Cambridge, MA: Harvard University Press.

Rosenzweig, M.L. 1992. Species diversity gradients: We know more and less than we thought. *J. Mammal.*, **73**: 715–730.

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

Rosenzweig, M.L. and Sandlin, E.A. 1997. Species diversity and latitudes: Listening to area's signal. *Oikos*, **80**: 172–176.

Sakai, A. and Weiser, C.J. 1973. Freezing resistance of trees in North America with reference to tree regions. *Ecology*, **54**: 118–126.

Schall, J.J. and Pianka, E.R. 1978. Geographical trends in numbers of species. *Science*, **201**: 679–686.

Schultz, J. 1995. *The Ecozones of the World*: *The Ecological Divisions of the Geosphere*. Berlin: Springer-Verlag.

Snyder, J.R., Herndon, A. and Robertson, W.B., Jr. 1990. South Florida rockland. In *Ecosystems of Florida* (R.L. Myers and J.J. Ewel, eds), pp. 230–277. Orlando, FL: University of Central Florida Press.

Terborgh, J. 1973. On the notion of favorableness in plant ecology. *Am. Nat.*, **107**: 481–501.

Terborgh, J. 1992. *Diversity and the Tropical Rain Forest*. New York: Scientific American Library.

Tilman, D. and Pacala, S. 1993. The maintenance of species richness in ecological communities. In *Species Diversity in Ecological Communities* (R.E. Ricklefs and D. Schluter, eds), pp. 13–25. Chicago, IL: University of Chicago Press.

Valencia, R., Balslev, H. and Guillermo Paz y Mino, C. 1994. High tree alpha-diversity in Amazonian Ecuador. *Biodivers. Conserv.*, **3**: 21–28.

Wallace, A.R. 1876. *The Geographical Distribution of Animals*, Vols 1 and 2. London: Macmillan.

Woodward, F.I. 1987. *Climate and Plant Distribution*. Cambridge: Cambridge University Press.

APPENDIX

List of species that have ranges that span the tropics and the subtropics, and their habitats, if notable

---

1. *Acacia farnesiana* (Fabaceae)
2. *Acacia tortuosa* (Fabaceae)
3. *Avicennia germinans* (Avicenniaceae), mangroves
4. *Baccharis halimifolia* (Asteraceae), seashores, marshes
5. *Bumelia celastrina* (Sapotaceae), coastal ridges
6. *Caesalpinia mexicana* (Fabaceae), sandy soils
7. *Celtis laevigata* (Celtidaceae)
8. *Cephalanthus occidentalis* (Rubiaceae), wetlands
9. *Cordia sebestena* (Boraginaceae), poor soils, seashores
10. *Ehretia anacua* (Boraginaceae)
11. *Forestiera segregata* (Oleacaea), seashores
12. *Leucaena pulverulenta* (Fabaceae)
13. *Lyonia ferruginea* (Ericaceae), acid soils
14. *Myrica cerifera* (Myricaceae), wet sandy soils
15. *Pithecellobium flexicaule* (Fabaceae), roadsides, disturbed areas
16. *Rhus copallina* (Anacardiaceae)
17. *Sabal mexicana* (Arecaceae), oases
18. *Sabal palmetto* (Arecaceae)
19. *Salix taxifolia* (Salicaceae), oases in deserts and grasslands
20. *Sapindus saponaria* (Sapindaceae)
21. *Zanthoxylum fagara* (Rutaceae)