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Why Do Some Tropical Forests Have So Many Species of Trees?[1]

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ABSTRACT

Understanding why there are so many kinds of tropical trees requires learning, not only how tree species coexist, but what factors drive tree speciation and what governs a tree clade's diversification rate. Many report that hybrid sterility evolves very slowly between separated tree populations. If so, tree species rarely originate by splitting of large populations. Instead, they begin with few trees. The few studies available suggest that reproductive isolation between plant populations usually results from selection driven by lowered fitness of hybrids: speciation is usually a response to a "niche opportunity." Using Hubbell's neutral theory of forest dynamics as a null hypothesis, we show that if new tree species begin as small populations, species that are now common must have spread more quickly than chance allows. Therefore, most tree species have some setting in which they can increase when rare. Trees face trade-offs in suitability for different microhabitats, different-sized clearings, different soils and climates, and resistance to different pests. These trade-offs underlie the mechanisms maintaining α-diversity and species turnover. Disturbance and microhabitat specialization appear insufficient to maintain α-diversity of tropical trees, although they may maintain tree diversity north of Mexico or in northern Europe. Many studies show that where trees grow readily, tree diversity is higher and temperature and rainfall are less seasonal. The few data available suggest that pest pressure is higher, maintaining higher tree diversity, where winter is absent. Tree α-diversity is also higher in regions with more tree species, which tend to be larger, free for a longer time from major shifts of climate, or in the tropics, where there are more opportunities for local coexistence.

RESUMEN

Comprender por qué hay tantos tipos de árboles tropicales, se requiere aprender no sólo cómo las especies de árboles coexisten, sino también, cuáles factores conducen a su especiación, y qué determina la velocidad de diversificación de un clado de árboles. Muchos reportan que la esterilidad híbrida evoluciona muy lentamente entre poblaciones separadas de árboles. De ser así, las especies de árboles raramente se originarían por la separación de grandes poblaciones; más bien empezarían con pocos árboles. Los pocos estudios disponibles sugieren que el aislamiento reproductivo entre las poblaciones vegetales usualmente resulta de selección derivada del bajo éxito de los híbridos: la especiación generalmente responde a una "oportunidad de nicho". Usando la teoría neutral de Hubbell de dinámica de bosques como hipótesis nula, nosotros mostramos que si las nuevas especies de árboles comienzan como poblaciones pequeñas,

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especies que ahora son comunes deberían haberse expandido más rápido que lo que el azar permite. Por lo tanto, la mayoría de las especies de árboles tendrían alguna condición donde sus poblaciones podrían crecer cuando son raras. Los árboles enfrentan compromisos en su adecuación por diferentes microhábitats, claros de diferentes tamaños, diferentes suelos y climas, y resistencia a diferentes plagas. Estos compromisos sirven de base para los mecanismos que mantienen la diversidad α y al reemplazo espacial de especies. Los disturbios y la especialización de microhabitats parecen ser insuficiente para mantener la diversidad α de árboles tropicales, sin embargo ellos pueden mantener diversidad de árboles al norte de México o en Europa del norte. Muchos estudios muestran que en lugares donde los árboles crecen fácilmente, la diversidad de árboles es mayor donde la temperatura y la lluvia son menos estacionales. Los pocos estudios disponibles sugieren que la presión de las plagas es mayor, manteniendo así la diversidad de árboles en lugares donde no hay invierno. La diversidad α de árboles también es más alta en regiones con más especies de árboles, las cuales tienden a ser más largas, exentas por un largo periodo de tiempo de grandes cambios climáticos, o en los trópicos donde hay más oportunidades de coexistir localmente.

Key words: *α-diversity; β-diversity; Janzen–Connell; neutral theory; pest pressure; regional diversity; stability-time; speciation.*

WHY ARE THERE SO MANY KINDS OF TROPICAL TREES? In particular, why do some tropical hectares contain over 250 species of trees 10 cm DBH or greater, while in the eastern United States, a hectare rarely contains more than 20 species (Leigh 1999)? How can 0.5 km^2 of rain forest in Borneo or Amazonia contain as many tree species as the 4.2 million km^2 of temperate zone forest in Europe, North America, and Asia combined (Wright 2002)? This question has attracted increasing attention ever since it was reopened by Dobzhansky (1950); yet, the explanations proposed for this phenomenon differ as much as ever (Huston 1994, Givnish 1999, Wright 2002, Hawkins *et al.* 2003). Some explanations focus exclusively on the ecological mechanisms that allow so many species to coexist locally, while others focus on latitudinal differences in rates of speciation and extinction, without showing how these species coexist. Moreover, new hypotheses to explain the latitudinal gradient in tree diversity keep appearing (Willig *et al.* 2003).

This paper grew out of a symposium with the same title at the 2002 meeting of the Association for Tropical Biology. The task of both the symposium and this paper was to set out what we know about the factors that promote diversity among tropical trees, and identify what we need to learn in order to understand why some tropical forests contain so many kinds of tropical trees. We focus on four aspects of our question: (1) What factors promote the sympatric coexistence of tree species?; (2) What factors govern the change in tree species composition (β-diversity) along a series of plots spanning a great expanse of forest such as Amazonia?; (3) How do different features of the environment influence the diversity that factors promoting coexistence can maintain?; and (4) What factors influence a biogeographic realm's tree diversity?

We first argue that there must be factors that tend to stabilize species composition, even in tropical forests. Then, we consider possible factors and what we must learn to assess their relative importance in maintaining tree diversity.

TREE DIVERSITY REFLECTS DIFFERENCES AMONG TREE SPECIES

To learn why there are so many kinds of tropical trees, we first ask whether, as a rule, tree species increase in abundance if they are temporarily made rarer. In other words, do tree species coexist because one or more factors tend to stabilize species composition (Chesson 2000)?

We begin our answer by using Hubbell's (1979, 1997, 2001) neutral theory of tropical forest dynamics as a null hypothesis by which to judge whether widespread species began with an advantage over their competitors. Hubbell's theory assumes that what species a tree belongs to is irrelevant to its prospects of mortality or reproduction. In Hubbell's theory, no process stabilizes species composition, and species diversity expresses a balance between speciation and random extinction. Hubbell derived predictions from his theory in analogy with the neutral theory of population genetics for a multi-allelic locus (Ewens 1979) in a haploid population: the population geneticist's reproductive adults correspond to Hubbell's reproductive trees, and the geneticist's allelic types to Hubbell's species.

Here, we use a prediction from the neutral theory of population genetics that follows equally from Hubbell's theory, to judge whether widespread species began with an advantage over their fellows. Fisher (1930) showed that for a neutral allele in a large population, all copies of which descend from a single mutant, the number of adults now carrying this allele cannot greatly exceed the number of generations since this mutant occurred. Indeed, the average time required for an allele originally represented by *y* copies in a huge population to spread by chance alone until there are $n >> y$ copies is likewise *n* generations or more (Kimura & Ohta 1973, equations 13 and 17). Fisher's prediction applies to trees if no one adult leaves many mature offspring, and is irrelevant if a few trees have multitudes of successful young and most have none at all.

Many species of tropical trees range from Central America through all Amazonia as far as Bolivia, each represented by trees 10 cm DBH or greater in a third or more of this region's 1 ha rain forest plots. Such species must each be represented by 10 million or more mature trees. For most of these species, a generation is over 50 years (Gentry 1989: 123). If, as Willis (1922) and Stebbins (1982) have suggested, these species began with very small populations, the neutral theory implies that they appeared well before the origin of angiosperms 140 million years ago. This cannot be true. The tree species *Symphonia globulifera*, for example, reached the Neotropics from Africa in three separate transatlantic dispersal events, all less than 25 million years ago. This species now ranges from Belize and Dominica all through Amazonia as far as Bolivia (Dick *et al.* 2003). The simplest explanation why they have spread so quickly and widely is that such species began with some advantage: they must have exploited a "niche opportunity" (Shea & Chesson 2002) by using some resource or resisting herbivores and pathogens more effectively or economically than their competitors.

Although tree species can become common and widespread only through an advantage over their competitors, no tree species replaces all of its competitors—indeed, in most tropical forests, no species even comes close to doing so. *Symphonia globulifera*, for example, has spread throughout nearly all Neotropical forests. This species now grows on good soils of Western Amazonia and central Panama and on poor soils in Central and Eastern Amazonia, in everwet forests and forests with severe dry seasons (Dick *et al.* 2003), but in almost every forest it accounts for less than 2 percent of the trees 10 cm DBH or greater. Thus rarer, less widespread species also must exploit niche opportunities (less lucrative, to be sure, than those exploited by common species) that have protected them from being replaced by rapidly spreading competitors. Therefore, most tree species must have some setting in which they increase when rare. This circumstance stabilizes tree species composition sufficiently to allow many species to coexist, but it does not ensure each species an equilibrium abundance (Chesson 2000).

These are indeed sweeping conclusions to draw from a single test of Hubbell's null model. After all, to make definite predictions about forests with trees that face no trade-offs, this model assumes, along with many other simplifications, that species always begin from small populations. Later in this paper, we propose and apply more direct tests of the proposition that most new species form in response to niche opportunities. Meanwhile, this first test of the null model will guide our next steps.

CLASSIFYING AND ORDERING EXPLANATIONS FOR TREE DIVERSITY

Abstractly speaking, niche opportunities and the diversity they favor reflect trade-offs. No one species can do everything well; the inevitability of trade-offs allows different species to coexist (MacArthur 1961). We now ask, what are the relevant trade-offs? What circumstances influence the diversity that different trade-offs maintain?

A plethora of factors can influence biotic diversity (Pianka 1994). To understand tree diversity, we must ask questions on at least two scales (Ricklefs & Schluter 1993). First, what governs the tree diversity of a biogeographic region, the number of species available for stocking its various habitats? A region's diversity represents a balance between extinction, and speciation + immigration (MacArthur & Wilson 1967, Terborgh 1973), so we must reckon with mechanisms of speciation in trees and with how this region's climate and topography have varied in the geologic past. Second, what factors control local (α) diversity of trees and the turnover of tree species from one locale to another within the region (β-diversity)? Here, we deal with the properties or circumstances that allow different species to coexist. The two scales of diversity are closely related. Local diversity tends to be higher in regions with higher total diversity (Ricklefs 2004), whereas a species survives only if it is superior to its competitors in some respect, in some setting (Chesson 2000). In this paper, we start from the bottom up. We begin with the factors that maintain local diversity because no species can enter the regional pool unless it spreads initially in some locale by exploiting a local niche opportunity. To evaluate the relative impact of the various factors influencing species diversity, we order our questions as follows:

(1) What factors favor the sympatric coexistence of tree species?

(A) Disturbance.—The fall of individual trees, and the opening of larger clearings by windthrows, allow light-demanding and shade-tolerant tree species to coexist (Skellam 1951); in some regions at least, occasional windstorms may be needed to keep a slow-growing, competitive "supertree" from taking over the forest (Connell 1978, ter Steege & Hammond 2001).

(B) Specialization.—Specialization to various aspects of a complex habitat can allow different species to coexist. Different tree species may coexist because they specialize to different strata of the forest (Terborgh 1985), because their seedlings specialize to different microsites on the forest floor (Molofsky & Augspurger 1992), or perhaps because year-to-year variation in climate and abundances of different types of pollinators, seed-dispersers, and seedling-browsers cause temporal sorting in their recruitment (Chesson & Warner 1981).

(C) Pest pressure.—The presence of a diversity of pests and pathogens able to penetrate different types of plant defense and capable of preventing any one species from taking over the forest can also allow different species to coexist (Gillett 1962).

(2) What factors influence species turnover?

(A) Limited dispersal.—Different species evolve in different places and spread only a limited distance from their points of origin (Willis 1922, Condit *et al.* 2002).

(B) Spatial heterogeneity.—Different species specialize to different habitats within a region—different elevations along a mountainside (Brown 1919, Grubb *et al.* 1963) or different edaphic conditions such as floodplain versus uplands or poor versus better soil (Richards 1952, Phillips *et al.* 2003).

(3) How do different features of the environment influence the diversity that these mechanisms of coexistence can maintain?

(A) Productivity and climate.—How do climate, soil quality, and ecosystem productivity influence tree diversity (Ricklefs 1977, D. H. Wright 1983, Terborgh 1985)?

(B) Stability of productivity and climate.—How does winter or a severe dry season affect the ability of tree species to specialize to different aspects of their habitat (Janzen 1967) or the ability of specialized pests and pathogens to maintain tree diversity (Janzen 1970)?

(C) Diversity and biogeography.—How much is local tree diversity influenced by the tree diversity in its biogeographic region (Ricklefs 2004)?

(4) What factors influence a biogeographic region's tree diversity?

(A) Mechanisms.—What are the mechanisms of speciation among trees? Do new species usually form in response to niche opportunities?

(B) Speciation/extinction balance.—How is a region's tree diversity influenced by the time available for its trees to diversify in response to currently prevailing environmental conditions (Fischer 1960, Morley 2000)? More generally, how does speciation/extinction balance vary in different regions, and why?

(C) Museum or cradle?.—Are the tropics primarily a museum of tree diversity or a cradle of tree speciation?

We now proceed to discuss these questions in the order that they were outlined.

FACTORS MAINTAINING LOCAL (α) DIVERSITY AMONG TREES

Diversity reflects the inability of any one species to do all things well: enhancing one ability usually entails diminishing others. Organisms therefore face trade-offs that allow different species to coexist by exploiting different niche opportunities. What trade-offs play a role in the coexistence of tree species?

Most trade-offs involve more than two characteristics. The relationship between any two of these characteristics will show scatter created by the variation of other characteristics involved in the trade-off. If, for example, birds face a triple trade-off among producing many young, avoiding predators, and competing effectively with other guild members (Cody 1966), a two-factor plot of clutch size against success in avoiding predators will show scatter created by differences in competitive ability. The two-factor trade-offs we discuss are all influenced by other unspecified factors, but they still contribute to the maintenance of tree diversity.

(A) Disturbance as a Generator of Niche Opportunities.—Skellam (1951) showed that a "pioneer" tree species can coexist with a mature forest species even if a mature forest seedling under a pioneer's crown can always grow up to shade and replace that pioneer. To do so, pioneers must colonize light gaps opened by the fall of mature forest trees quickly enough, grow fast enough, and mature soon enough that they can produce enough young to replace themselves before their inevitable displacement. Here, we show what trade-offs allow light-demanding species to coexist with shade-tolerant species. Then we show that, even though tree species are distributed along a continuum from light-demanding to shade-tolerant, there is reason to believe that adaptation to different levels of disturbance is not what allows hundreds of tree species to coexist in the tropics.

The trade-off between competitive ability and the ability to disperse seeds quickly to clearings was long considered to be the primary factor allowing the coexistence of pioneers with mature forest species (Grubb 1977). Indeed, Tilman (1994) argued that the competition–colonization trade-off can allow an indefinite number of species to coexist if these species can be ranked so that any species j is competitively inferior to, but a better colonizer than, species $j - 1$, and if certain other conditions are met. Tilman's result is invalid for two reasons. First, it applies only if a seedling of species j under the crown of a competitively inferior species will replace that inferior equally quickly whatever that inferior's competitive rank. If, however, a seedling under a tree of a competitively inferior species replaces it more slowly when the competitive abilities of the two species are closer, as seems biologically reasonable, this trade-off allows only a few species to coexist (Adler & Mosquera 2000). Second, effective seed dispersal is not the primary factor that enables a species to coexist with superior competitors. For example, seedlings of the tree species that dominate the first few centuries of succession on a growing floodplain in western Amazonia all grow together on this floodplain's new beachfront; differential growth, not differential colonization, orders these stages of succession (Foster *et al.* 1986). Even a large, multi-tree windthrow clearing is not a blank slate; pioneers dominate large clearings by outgrowing the other plants present, not by getting there first. Pioneers must be good colonizers, to be sure, but they must also grow fast.

The primary trade-off allowing pioneer and mature forest tree species to coexist is that between fast growth of saplings in bright light and survival in shade. On Barro Colorado Island, Panama, sapling growth rates in large clearings of three pioneer tree species are inversely related to the minimum size of clearing that will allow new saplings to survive for at least nine years (Brokaw 1987). In general, the more light-demanding canopy tree species on Barro Colorado have shorter-lived and more poorly defended leaves and fewer saplings per adult; their saplings suffer higher mortality and grow faster when they are well lit, and a higher proportion of their germinating seedlings occur in gaps. More shade-tolerant species have more seedlings that germinate in shade, slower-growing saplings with denser wood, lower mortality, longer-lived, better defended leaves, and more saplings per adult (Coley *et al.* 1985; Coley 1987, 1988; King 1994; Wright *et al.* 2003). Judging by these criteria, the canopy tree species of Barro Colorado Island's 50 ha Forest Dynamics Plot are distributed along a continuum from light-demanding to shade-tolerant (Wright *et al.* 2003).

Simulations suggest that the trade-off between fast sapling growth in bright light and survival in shade allows six tree species to coexist in a Connecticut forest if they are subject to a regime of "wide-scale disturbance typical of natural stands" (Pacala *et al.* 1996: 36). On the other hand, frequent gaps of many sizes do not appear to be essential for high tree diversity. Tree diversity in the 50 ha Forest Dynamics Plot in Pasoh Reserve, Malaysia, is nearly three times higher and its most common species much rarer than on Barro Colorado's 50 ha plot. This disparity in diversity occurs even though at Pasoh, tree crowns are narrower and trees usually die standing (Putz & Appanah 1987); so gaps are smaller and less frequent and pioneer trees far less common and diverse at Pasoh than on Barro Colorado (Condit *et al.* 1999). Sixteen of the 141 canopy tree species on Barro Colorado's plot are pioneers with saplings' diameter growth averaging more than 4 mm/yr, compared to 3 of the 422 canopy tree species on the Pasoh plot (Condit *et al.* 1999). Within Sarawak, mixed dipterocarp forest on fertile soil is less diverse than dipterocarp forest on poorer soil (Ashton 1989), even though gaps are larger and more frequent among dipterocarps on more fertile soil (van Schaik & Mirmanto 1985, Ashton & Hall 1992). Here, too, α-diversity is greater where there are fewer, smaller, gaps.

In some regions, such as the Budongo forest in

Uganda, or in Guyana, occasional wide-scale disturbance may be needed to keep a slow-growing, dense-wooded, competitive "supertree" from taking over the forest (Eggeling 1947, Connell 1978, ter Steege & Hammond 2001). These takeovers, however, are rarely complete. In the Congo basin's Ituri Forest, large tracts are dominated by the canopy tree species *Gilbertiodendron dewevrei*, where more than 70 percent of the trees 30 cm DBH or greater belong to this species. Yet, in a 10 ha plot of monodominant forest, the trees 30 cm DBH or greater that belong to other species contain as many species as an equivalent number of such trees on a mixed forest plot (Makana *et al.* 2004). Is the dominant "supertree" *Gilbertiodendron* an intruder in a forest where diversity among non-*Gilbertiodendron* tree species is maintained by factors other than disturbance?

In short, although disturbance can contribute to the maintenance of tree diversity, there is no clear evidence that disturbance is the only factor allowing hundreds of tree species to coexist locally. Moreover, it appears that high tree diversity is maintained in some areas without frequent or widespread disturbance. To understand better what maintains tropical tree diversity, however, we must learn what properties allow a species such as *Pentaclethra macroloba* (Lieberman *et al.* 1985) or *G. dewevrei* (Makana *et al.* 2004) to dominate an otherwise diverse forest.

(B) SPECIALIZATION TO DIFFERENT MICROHABITATS.—A forest's trees create a complex habitat that offers many niche opportunities. The trees create a light gradient from the well-lit canopy to the understory; thus, different tree species can coexist if they specialize to different strata of the forest (Terborgh 1985). In Borneo, even hemiepiphytic figs, which start as epiphytes and later drop roots to the forest floor, also specialize to different strata of the forest, even though their growth form is far rarer than trees (Shanahan & Compton 2001, Harrison *et al.* 2003). Trees also create a mosaic of microsites of different types on the forest floor, each of which favors germination and establishment of a different set of tree species (Grubb 1977). How much tree diversity can the complexity of a forest habitat maintain? To what extent is a tree's regeneration niche governed by its way of life as an adult, that is to say, the adult's size, successional status, or position in the canopy? Do regeneration niches provide different, additional mechanisms of coexistence, or are regeneration niches governed by adult niches (Nakashizuka 2001)?

Specialization to forest stratum is driven in part by the trade-off between fast sapling growth in bright light and survival in shade, the same trade-off that allows coexistence between pioneer and shade-tolerant tree species. In Malaysia's Pasoh Reserve, leaves of understory species have lower photosynthetic capacity per unit area, or per gram of nitrogen, than leaves of young mid-story congeners in the same light environment, which in turn have lower photosynthetic capacity than leaves of young canopy congeners in that light environment (Thomas & Bazzaz 1999). In Borneo, diameter growth decelerates faster once diameter exceeds 11 cm in trees of understory species than in their canopy counterparts, but understory species recruit more saplings 6 cm DBH or greater per unit basal area of conspecific adults than do their canopy counterparts (Kohyama *et al.* 2003), presumably because the more shade-tolerant seedlings and saplings of understory species survive much better than do their more light-demanding canopy counterparts (*cf.* Wright *et al.* 2003). A species' degree of shade tolerance, however, is not the only factor influencing its stratum in the forest. Shade-tolerant and light-demanding species coexist in forest canopies (Grubb 1977). Indeed, the 73 most common species of canopy tree on Barro Colorado's 50 ha plot span the spectrum from extremely light-demanding to extremely shade-tolerant (Wright *et al.* 2003).

Rain forests, however, have no more than five strata of trees (Terborgh 1985). Does the complexity of the forest habitat offer other opportunities for coexistence? Specialization to soil type contributes greatly to species turnover (Richards 1952, Ashton 1964). Tilman (1982) proposed that nutrient availability is heterogeneous at all scales, and that small-scale nutrient heterogeneity enhances tree α-diversity to the greatest degree on moderately infertile soils. Ashton (1989) uses Tilman's (1982) theory to explain why the most diverse forests in Sarawak occur on moderately infertile soils. No one, however, has yet been able to associate seedlings of particular tree species on a "uniform" forest hectare with specific soil qualities or to provide independent criteria for predicting the precise relationship between soil fertility and tree diversity. Moreover, given the prevalence of dispersal limitation (Harms *et al.* 2000, Dalling *et al.* 2002), especially in rare species (Muller-Landau *et al.* 2002), is it reasonable to expect seedlings of particular species to establish on specific microsites? The specialization of plants to microsites with particular soil qualities needs to be documented before we can assess its importance.

Grubb (1977) considered that different tree species could coexist because their seedlings were favored by different microhabitats. Fallen logs, tip-up mounds from uprooted trees, and variation in thickness of litter and in amount of light reaching the ground offer a variety of different microsites, each favoring different species of seedlings. In southern Chile, litter thickness seems to be a microsite's decisive attribute; small-seeded species favor fallen logs and tip-up mounds because they are free of litter (Christie & Armesto 2003). Seeds of some light-demanding pioneers persist in the soil and grow when exposed by an uprooted tree, an event that usually opens a large gap (Putz 1983), but in other cases, there is no obvious relationship between regeneration niche and way of life as an adult. At Yasuní in Amazonian Ecuador, small juveniles of *Oenocarpus bataua* are distributed independently of light level, while those of *Iriartea deltoidea* tend to occur in the better lit understory sites—yet most adult *Oenocarpus* occur in major canopy gaps, while the majority of 15 m tall *Iriartea* are shaded by closed canopy (Svenning 2001: 14).

Can different "regeneration niches" allow tree species with the same "adult niche" to coexist? Greenhouse experiments in central Panama suggest that in gaps, the large seeds of the successional tree *Gustavia superba* germinate and survive better under thick litter, whereas the small seeds of other successional species do better where litter is thin or absent (Molofsky & Augspurger 1992). If thick- and thin-litter microsites are close together in the same gap, one sapling will reproduce after crowding out the others on these various microsites. On the other hand, if whole gaps differ in litter thickness, different successional species could coexist because their seedlings are favored by different thicknesses of litter. Different saplings also differ in their ability to survive damage by branches fallen from above (Guariguata 1998). If some sites escape branch-falls and others not, a more susceptible, faster-growing species might coexist with a slower-growing, more damage-resistant species of the same forest stratum. We have much to learn about how the complexity of forest habitats contributes to maintenance of tree diversity.

Do the year-to-year fluctuations in climate and in the abundance of different pollinators, seed dispersers, and seedling browsers create a temporally sorted array of regeneration niches that allow different species to coexist because they recruit in different years (Grubb 1977, Chesson & Warner 1981)? There is some temporal sorting in fruit production among a forest's tree species (Grubb 1977, Connell & Green 2000). Coexistence, however, demands temporal sorting in recruitment, not just reproduction; coexistence requires, for example, that each species occupy a disproportionately high fraction of the gaps that occur in those years when it fruits heavily. This can rarely be true. Seedlings of most mature forest tree species grow slowly (Hubbell 1998, Connell & Green 2000), so slowly that differences in their growth rates will prevent temporal sorting in reproduction from assuring temporal sorting in tree recruitment.

Kelly and Bowler (2002) argued that in dry forest at Chamela, Mexico, coexistence within a genus reflects temporal sorting in recruitment, whereby the faster-growing species only recruits in good years (with abundant rain or low herbivory?). Their evidence consists of five pairs of sympatric congeners in which the rarer, faster-growing congener has a less regular size distribution, presumably reflecting more pulsed recruitment (Kelly *et al.* 2001, Kelly & Bowler 2002). Their evidence, however, suggests that each pair of congeners coexists simply because one is more gap-demanding and the other more shade-tolerant; is a more subtle explanation needed?

Their argument shares another problem with other explanations of tree diversity by habitat specialization: Kelly and Bowler (2002) fail to explain how different genera coexist. The coexistence of 34 palm species at Yasuni (Svenning 1999, 2001), 27 species of hemiephytic figs at Lambir, Sarawak (Harrison *et al.* 2003), or 11 species of pioneer *Macaranga* at Lambir (Davies 1998, Davies *et al.* 1998) are all three explained in terms of differences in shade tolerance and different preferences for forest stratum, soil quality, and topographic position. The figs, being hemiepiphytes, also differ according to what parts of a tree they colonize (Harrison *et al.* 2003). Otherwise, species in each group coexist by the same types of difference in habitat preference. Large, varied families such as Euphorbiaceae have each evolved species suitable for all tropical forest microhabitats. In the Solomon Islands, Corner (1967: 32) describes a forest with canopy trees, understory trees, treelets, and lianas all belonging to the genus *Ficus.* Neither disturbance nor the complexity and heterogeneity of forest habitats explains why 30 or more plant families coexist on a hectare of tropical forest. Does diversity of defenses against pests promote the coexistence of plant families?

(C) PESTS, PATHOGENS, AND TREE DIVERSITY.—Pathogens and insect herbivores face trade-offs in what plants they can eat. In those tropical forests where neither winter nor prolonged dry season depresses insect populations, pest pressure is intense (Ridley 1930, Gillett 1962, Janzen 1970, Connell 1971, Coley & Barone 1996). Young, tender leaves are easiest to eat (Coley 1983), so the defenses of young, expanding tropical leaves are particularly strong (Coley *et al.* 2003). Therefore, trade-offs between eating young leaves of species with different defenses should be particularly acute, so that the most damaging pathogens and insect pests should be specialists. If specialist pests are the attackers, we expect: (1) that these pests will find and kill most quickly those young plants nearest conspecific adults, making space for plants of other species between adults and their surviving young; and (2) as adult hosts become rarer, specialist pests are less likely to spread to other adults, and the adults' load of specialist pests should decrease, until this plant species can maintain its density. As a result of (1) and (2), wide-scale seedling survival in a species should decrease as the abundance of its adults increases, and seedlings of this species should survive less well in patches where they are more abundant or closer to conspecific adults. All three propositions are true for rain forest trees in Borneo (Webb & Peart 1999).

Can pest pressure maintain the diversity of tropical trees? This can only be so if the most damaging tropical pests are specialists. In most forests, caterpillars (larvae of Lepidoptera) "consume more living leaves than all other animals combined" (Janzen 1988: 120). Tropical caterpillars appear to face a trade-off between fast growth and a generalized diet (Janzen 1984, Bernays & Janzen 1988). In any one tropical forest, the most damaging caterpillars usually consume leaves of a particular species (Janzen 1988) or genus (Novotny *et al.* 2002) of plants. The same is true of seed-eating weevils (Janzen 1980, 1981).

Specialized pests can maintain tree diversity by causing mutual repulsion among conspecifics. Some pests are known to do so. In Central America, seedlings or saplings of *Casearia corymbosa* (Howe 1977), *Platypodium elegans* (Augspurger 1983), *Dipteryx panamensis* (Clark & Clark 1985), *Quararibea asterolepis* (Wong *et al.* 1990), and *Ocotea whitei* (Gilbert *et al.* 1994, 2001) suffer more from pathogens and/or herbivores when they are closer together or closer to adult conspecifics.

In other tree species, such as *Attalea butyracea* (*Scheelea zonensis*: S. J. Wright 1983) and *Virola surinamensis* (Howe *et al.* 1985) on Barro Colorado, *Astrocaryum murumuru* in western Amazonia (Terborgh *et al.* 1993), and *Maximiliana maripa* in northern Amazonia (Fragoso *et al.* 2003), insects cause mutual repulsion among conspecifics by inflicting more damage on seeds near conspecific adults. The mutual repulsion acts on very different scales; a toucan greatly improves the survival prospects of a *Virola* seed by carrying it 40 m from its parent's crown before dropping it, whereas *Maximiliana* palm seeds may have a future only if a tapir defecates them a kilometer or more from existing palm clumps. In general, many insects and some pathogens, but very few mammals, preferentially attack seeds or seedlings near conspecific adults (Hammond & Brown 1998, Gilbert 2002). A meta-analysis by Hyatt *et al.* (2003) suggests that seed predation is as likely to be heavier farther from, as nearer to, parent plants. If so, mutual repulsion may be governed mostly by heavier mortality of seedlings or saplings, rather than seeds, near conspecific adults.

Is mutual repulsion among conspecifics the rule for tropical trees? In the two commonest canopy tree species on Barro Colorado's 50 ha Forest Dynamics Plot, *Trichilia tuberculata* and *Alseis blackiana*, the number of juveniles per adult on a hectare is sufficiently depressed by increased numbers of conspecific adults on that hectare to regulate the populations of their species (Hubbell *et al.* 1990). Other populations may be regulated on more local scales. Per capita recruitment of stems 1 cm DBH or greater of a species onto 10 x 10 or 20 x 20 m quadrats of the 50 ha plots on Barro Colorado, Panama, or Pasoh, Malaysia, is lower on plots in which this species has higher density or basal area (Wills *et al.* 1997, Wills & Condit 1999). On Barro Colorado's 50 ha plot, the probability that a stem 1 cm DBH or greater in 1983 survived to 1995 was lower if there were more conspecifics among its 20 nearest neighbors (Ahumada *et al.* 2004). For shade tolerant plants, the probability of surviving from 1983 to 1995 was diminished by an average of 1 percent for each extra conspecific among its 20 nearest neighbors (Fig. 8D in Ahumada *et al.* 2004).

In another analysis, Peters (2003) divided stems on the 50-ha plots at Pasoh and Barro Colorado into three diameter classes: DBH < 5 cm, 5 cm $\leq$ DBH < 10 cm, and DBH ≥ 10 cm. For each species with 30 or more stems in some diameter class, he calculated the partial correlation between the prospects of a stem of that size class surviving from the first census (1983 on Barro Colorado, 1987 at Pasoh) to 1995 and the density of conspecifics within its size class ≤5, ≤10, ≤15, or ≤20 m away from it, holding the density of heterospecifics in the neighborhood constant. He tested significance relative to the correlation from 100 data sets in each of which the survival fate of each tree was randomly reassigned to another tree of the same species and size class. For over half the species in each plot, he found a correlation for at least one diameter class and neighborhood size that he considered significant or nearly so. Such correlations were most prevalent among small stems, but they occurred among trees 10 cm DBH or greater in 40 percent of the species tested. On each plot, over 75 percent of these correlations were negative; a stem was less likely to survive if there were more conspecifics nearby (Peters 2003). Unfortunately, local density of conspecific trees and local mortality rates among stems of all species are both spatially autocorrelated on BCI's 50 ha plot (Condit *et al.* 2000, Hubbell *et al.* 2001: 861). The simulations underlying the significance tests of both Peters (2003) and Wills *et al.* (1997), however, removed the spatial autocorrelations in mortality, invalidating the tests. This topic needs more work.

Nonetheless, what might these results mean? First, many species are increasing in numbers even though their stems die faster when more conspecifics are nearby. Species having stems that survive better with fewer conspecific neighbors include some that can increase quite rapidly when rare (Condit *et al.* 1996, Ahumada *et al.* 2004).

Secondly, some species whose stems survive better when more conspecifics are nearby are habitat specialists. On Barro Colorado, stems of the habitat specialists *Erythrina costaricana*, which grows along streams, and *V. surinamensis*, which grows on slopes where soil moisture content is higher during the dry season, survived better when more conspecifics were nearby (Condit *et al.* 1996, Ahumada *et al.* 2004); however, this was not true for all habitat specialists.

Also, there is other evidence that specialized pests affect forest dynamics in a way that enhances tree diversity. Rausher (1981) found that specialist swallowtail caterpillars located *Aristolochia* vines more readily if surrounding plants of different species within 50 cm of an *Aristolochia* were cleared away. Similarly, Wills and Green (1995) proposed a herd immunity hypothesis which, applied to trees, predicts that a stem survives better when more stems of other species are nearby, because they "hide" that stem from pests specialized to its species. At Pasoh, the average stem survives better when the density of stems of other species within 15 m or less is higher, even though it survives less well when the basal area of stems of other species is higher (Peters 2003). The discrepancy occurs because most stems are small, and small stems suffer less from the competitive impact of other stems their size than from the shade and root competition of bigger trees nearby. On Barro Colorado, the average stem survives worse when the density of nearby stems of other species is higher. Nonetheless, for 69 of the 188 species on the plot that were common enough to test, the "herd immunity" effects of extra heterospecifics nearby overrode the competitive impact of these heterospecifics enough to significantly enhance survival (Peters 2003). It is not obvious what, besides pest pressure, would cause neighboring stems of other species to enhance a plant's survival.

Finally, if the pressure of specialized pests is responsible for the mutual repulsion among conspecifics documented by Peters (2003), can the observed degree of mutual repulsion among conspecifics (and the observed degree of herd immunity) maintain observed levels of tree diversity? Tree seeds disperse only a limited distance from their parents (Harms *et al.* 2000), while a seed's recruitment prospects, and a plant's survival prospects, depend on nearness to stems of different sizes and on what species these stems belong to. Learning how repulsion among conspecifics governs tree diversity demands a dynamics of spatial pattern, which is not an easy task (Molofsky *et al.* 1999) even in the neutral case (Nagylaki 1976).

(D) Conclusions.—Testing Hubbell's (2001) neutral theory suggested that if species begin as small populations, common species must have become so thanks to some advantage, and other species must avoid replacement by new competitors spreading through their region by increasing when rare enough, at least in some habitat (Chesson 2000). Therefore, some mechanisms must promote the coexistence of tree species. Disturbance, habitat complexity, and pressure of specialized pests all provide opportunities for different species to coexist. At the moment, it is easier to visualize how pest pressure, rather than microhabitat specialization, maintains many tree species in a single forest stratum. To assess the relative contributions of different factors to the α-diversity of trees, (1) we need a more comprehensive understanding of the various possible modes of habitat specialization; (2), we must learn whether pest pressure is the prime cause of mutual repulsion among conspecifics; and (3) we must learn whether or not observed levels of mutual repulsion among conspecifics can maintain observed levels of tree diversity. Now, however, we turn to causes of species turnover.

CAUSES OF SPECIES TURNOVER (β-DIVERSITY)

Differences in tree species composition among biogeographic realms separated by oceans or by regions of very different climate have long been known (Good 1964). Changes in tree species composition (β-diversity) along elevational gradients (Brown 1919) or along gradients of climate and soil (Gleason & Cronquist 1964: chapter 22) have likewise long been known, especially in the north temperate zone. Data on the rate at which tree species composition changes with location in a tropical region such as Amazonia have become available more recently (Ashton 1964, Schulze & Whitacre 1999, Pyke *et al.* 2001, Pitman *et al.* 2001, Pitman, Terborgh, Silman, Nuñez *et al.* 2002). What factors influence species turnover among tropical trees?

(A) Local Speciation and Dispersal Limitation.—One cause of species turnover is that different species originate in different places and spread only a limited distance from their points of origin. Differences in tree species composition among different biogeographic realms arise largely from this cause.

To learn how local speciation and dispersal limitation might influence species turnover within a biogeographic realm, Chave and Leigh (2002) modified Hubbell's (2001) neutral theory by incorporating limited dispersal. They imagined a forest in an endless, uniform habitat in which the distribution of seeds about their parents is the same for all reproductive trees regardless of their species, and each tree has the same minute probability of producing a young of an entirely new species. They calculated the probability $F(r)$ that two trees r km apart belong to the same species, as a function of tree density, speciation rate, and mean square dispersal distance of seeds from their parents, when speciation is in balance with random extinction.

Condit *et al.* (2002) used this theory to fit data from censuses of trees 10 cm DBH or greater on 1 ha plots separated by 200 to 100,000 m in Amazonian Peru near Manu, Amazonian Ecuador near Yasuni, and central Panama near Barro Colorado. They used observed values of tree density, assumed that mean square dispersal distance was near that observed on Barro Colorado, and adjusted speciation rate to fit the data. They fit the trend of the data, and they found more scatter about the trend in central Panama, which has a strong rainfall gradient and marked variation in soil type, than in the more uniform expanses of upland forest in western Amazonia. To fit these data, however, Condit *et al.* (2002) had to assume that speciation rate was a thousand-fold lower near Yasuni than in central Panama, and a thousand-fold lower near Manu than near Yasuni. The speciation rate fitting the data near Manu is so low that it would take several times the age of the universe for random extinction to balance speciation (Chave & Leigh 2002).

In later attempts to compare the relative contributions of dispersal limitation and habitat heterogeneity to species turnover, the partial correlation of distance or the logarithm of distance between plots with the divergence in their species composition, holding topography and soil constant, was used as a surrogate for the impact of dispersal limitation (Potts *et al.* 2002; Phillips *et al.* 2003; Tuomisto, Ruokolainen, Aguilar *et al.* 2003; Tuomisto, Ruokolainen, & Yli-Halla 2003). All these authors, especially Tuomisto, Ruokolainen, and Yli-Halla (2003), found that distance explains some differences after the effects of soil and topography are accounted for. They ascribe this distance effect to the limited dispersal of species that originate in different places. They all, however, consider that differences in soil and topography contribute far more to species turnover. We now turn to this contribution.

(B) Habitat Heterogeneity and Species Turnover.—Plants face a fundamental trade-off between competing for light and competing for water and nutrients (Tilman 1982, King 1993); resources expended on roots and mycorrhizae are not available for making leaves or lifting them above neighboring crowns. Forests on drier (Murphy & Lugo 1986) or less fertile soil (Medina & Cuevas 1989) must expend more energy procuring water or nutrients and have larger proportions of their total biomass underground (Table 6.6 in Leigh 1999). Moreover, in poorer soils, trees conserve their nutrients by making tougher, better-defended, longer-lived leaves (Janzen 1974, Reich *et al.* 1992). Finally, trees on waterlogged soils and those subject to seasonal floods, have special features which, among other things, assure their roots an adequate supply of oxygen (Junk 1989). These features presumably render these species less competitive in upland forests.

The long-recognized impact on tree species composition of habitats as different as floodplain forests, swamp forests, white sand forests, and "normal" upland forests (Richards 1952, Brunig 1983, Proctor *et al.* 1983, Balslev *et al.* 1987, Medina & Cuevas 1989, Dumont *et al.* 1990, Terborgh *et al.* 1996, Schulze & Whitacre 1999), reflect these trade-offs, as does the impact of dry season length on tree species composition (Richards 1952, Pyke *et al.* 2001, Condit *et al.* 2004). Within upland forests, differences in soil quality influence tree species composition. In the 52 ha Forest Dynamics Plot at Lambir, none of the six most common canopy species, or the seven most common subcanopy species in a 4 ha subplot on fertile soil were among their most common counterparts in a 4 ha subplot on very poor soil (Lee *et al.* 2002).

Nearby hectares on very different soils can differ greatly in tree diversity as well as species composition. In a national park in Sarawak, a hectare of dipterocarp forest contains 214 species of tree 10 cm DBH or greater; a hectare of heath forest, 123; and a hectare of forest on limestone, 73 (Proctor *et al.* 1983). In Pakitza, along the Río Manú in southwestern Amazonia, a hectare of upland forest averages 128 tree species, whereas a hectare of swamp forest contains 61 (Appendix in Pitman *et al.* 1999). If they are distinctive enough, rare habitats, like small regions, have fewer tree species.

Gradients in climate also have a marked impact on species turnover. In a network of 22 small plots spanning 6.5° of latitude in south India's Western Ghats, at elevations ranging from 400 to 1400 m, species turnover is most rapid along axes where the length and severity of the dry season varies most rapidly (Davidar & Puyravaud 2002). Heterogeneity in soil and climate is clearly a major contributor to species turnover.

(C) WHAT FACTORS LIMIT SPECIES TURNOVER?.—Some tree species, in some places, are much less influenced by habitat heterogeneity than others. In the rain forests of Sarawak, species composition of trees 10 cm DBH or greater depends much less on soil type when soil fertility exceeds a certain threshold (Potts *et al.* 2002). On Barro Colorado, Panama, where soil is relatively fertile (Leigh & Wright 1990), 26 of the 41 most common species on the 50 ha Forest Dynamics Plot are equally common on the flat plateau, on slopes exceeding 10 percent in ravines and along streambeds, and in a 2 ha seasonal swamp (Hubbell & Foster 1986), even though in the dry season, soil moisture is more readily available on the slopes (Becker *et al.* 1988) or along streambeds than on the plateau. On the relatively fertile soils of western Amazonia, common species tend to grow in many habitats (Pitman *et al.* 1999). In a network of 15 1 ha upland forest plots near Yasuni, 15 percent (150) of their species averaged at least one tree 10 cm DBH or greater per hectare. These 150 species accounted for 63 percent of these plots' trees (Pitman *et al.* 2001) and for 32 percent of the trees on floodplain and swamp forest plots nearby (Pitman, Terborgh, Silman, Thompson *et al.* 2002). Where soils are fertile, many tree species live in a variety of habitats.

Smaller plants can be more sensitive to habitat type. Indeed, common species of ferns and melastomes of Western Amazonia are rather more sensitive to habitat type than rare ones (Tuomisto, Ruokolainen, & Yli-Halla 2003). Ferns and melastomes include mostly herbs and shrubs, but tree species composition also changes with habitat type, even in Western Amazonia (Phillips *et al.* 2003; Tuomisto, Ruokolainen, Aguilar *et al.* 2003). Tuomisto, Ruokolainen, Aguilar *et al.* (2003: 754), however, noticed a tendency "at least among Amazonian trees and palms, that large-statured trees are more wide-spread both geographically and ecologically than small-statured trees," a result quantified for geographical range by Ruokolainen *et al.* (2002). Pitman *et al.* (2001) likewise found that common species on their plots averaged greater maximum height than their rarer counterparts. Likewise, canopy or emergent tree species that occur in at least half of lowland or mid-elevation plots were more common than species occurring in fewer plots in south India's Western Ghats (Davidar & Puyravaud 2002). Although common plants of smaller size are often habitat specialists, canopy trees of common species, at least those that grow on more fertile soils, are more likely to be habitat generalists.

Bigger trees probably disperse their seeds farther than shrubs or treelets. This circumstance may hinder speciation among bigger trees (Davidar & Puyravaud 2002). Does some other factor allow common species to override the trade-offs that inhibit growing successfully in different habitats? Is effective defense against specialized pests what allows a tree species to grow in many habitats? There is some evidence that invasive plants that have escaped the largest proportion of the fungal pathogens plaguing them in their native habitats are the most widespread in North America (Mitchell & Power 2003). More detailed study of invasive plants may well reveal the extent to which freedom

TABLE 1. *Annual rainfall,* P, *and evapotranspiration,* AET[a] *(mm); annual wood production,* WP; *total fine litter fall,* LF; *and total aboveground production,* TP; *measured as* WP + LF, *(tons dry weight/ha·yr); the total number* N *of trees ≥10 cm DBH in a plot sample and the number* S *of species among them at selected sites.*

Site	Lat.	*P*	*AET*	*WP*	*LF*	*TP*	*N*	*S*
1. New Hampshire	44°N	1295	494	5.7	5.7	11.4	156	8
2. Western Oregon	44°N	2370	825	2.7	4.3	7.0	2825[b]	12
3. Eastern Maryland	39°N	1080	758	6.5	6.9	13.4	435	15
4. W. North Carolina	35°N	1813	858	2.9	5.5	8.4	579	22
5. Chamela, Mexico	20°N	707	<700	2.4	3.6	6.0	451[c]	75
6. Costa Rica	10°N	3600		3.0	8.7	11.7	529	102
7. Panama	9°N	2600	1600	5.5	12.9	18.4	409	91
8. French Guiana	6°N	3357	1492	3.1	7.8	10.9	654	175
9. Amazonia, Brazil	2°S	2609	1319	4.4	8.4	12.8	618	285

[a] *AET* measured as rainfall minus runoff except at sites 3 and 9.
[b] Trees ≥15 cm DBH in a 10.24 ha catchment.
[c] Freestanding woody stems ≥2.5 cm DBH in ten 100 m^2 plots scattered over 5 ha.
Data Sources:
Site 1, Hubbard Brook: *P* and *AET*, Likens *et al.* (1977); *WP*, Whittaker *et al.* (1974); *LF*, Gosz *et al.* (1972). *N* and *S* are from a forest in central Vermont (Bormann & Buell 1964).
Site 2, Andrews Experimental Forest, WS 10: *P* and *AET*, Sollins *et al.* (1980); other data from Grier & Logan (1977).
Site 3, SERC, Edgewater, MD: G. G. Parker, pers. comm.
Site 4, Coweeta WS 18: *P* and *AET*, Johnson & Swank (1973); *WP* and *LF*, Monk & Day (1985); *N* and *S*, J. A. Yeakley, pers. comm.
Site 5, dry deciduous forest; *P, WP, LF*, Martinez-Yrizar *et al.* (1996); *N* and *S*, Lott *et al.* (1987).
Site 6, everwet forest, La Selva; *P, WP*, Lieberman *et al.* (1990); *LF*, Parker (1994; Fig. 5.1); *N* and *S*, Lieberman *et al.* (1985).
Site 7, seasonal forest, Barro Colorado Island: data from Leigh *et al.* 2004.
Site 8, rain forest, ECEREX site, Piste de St. Elie: *P, AET* and *LF*, Sarrailh (1989); *WP* is standing crop, 318 tons/ha (Sarrailh 1989) times the average proportional increase in basal area from recruitment and growth, Pelissier & Riera (1993); *S*, Sabatier & Prévost (1989); *N*, average number of trees ≥10 cm DBH/ha in ECEREX plots of Puig & Lescure (1981).
Site 9, Biological Dynamics of Forest Fragments Project; *P*, W. Laurance, pers. comm. *AET* from nearby Ducke Reserve where *P* = 2648 mm (Shuttleworth 1988); *WP* and *LT* from Fazenda Dimona (Clark *et al.* 2001); *N* and *S*, de Oliveira & Mori (1999).

from pests allows plants to invade a wider range of habitats.

ENVIRONMENTAL INFLUENCES ON TREE DIVERSITY

How do different aspects of the environment influence the diversity that different modes of coexistence among trees can support? Disentangling causes from correlates is not easy because different aspects of the environment often vary concurrently. For example, when average annual temperature is higher, winter is usually less severe; when rainfall is higher, the dry season is usually shorter and wetter.

(A) Climate and Productivity.—Here, we assume that a forest's productivity reflects its "average" climate (Scheiner & Rey-Benayas 1994). Productivity, or an environmental factor such as rainfall or evapotranspiration that probably governs productivity for the region in question, is the best predictor of plant diversity in 20 of 21 studies of changes in plant diversity over distances exceeding 800 km (Hawkins *et al.* 2003). And indeed, aboveground productivity is higher in tropical forests than in the "average" natural forest of the temperate zone. In the tropics, moreover, tree diversity tends to be low on the least fertile and least productive soils, such as white sands (Bruenig 1996).

On the other hand, gradients in productivity do not predict gradients of tree diversity within a region. Over gradients of 500 km or less, plant diversity peaks at intermediate productivity (Tilman & Pacala 1993, Waring *et al.* 2002). More generally, tree diversity is not closely related to either aboveground productivity or actual evapotranspiration (Table 1). The forest at Hubbard Brook, New Hampshire, has higher productivity than a forest at Coweeta in western North Carolina, but the Coweeta forest is more diverse than forests of the Hubbard Brook region (Table 1). Indeed, aboveground productivity is higher in eastern Maryland than in French Guyana, La Selva, Costa

Rica or north of Manaus, Brazil, which have forests that are much more diverse, and actual evapotranspiration is higher in western Oregon and Coweeta than at Chamela, although tree diversity is much higher at Chamela (Table 1).

In the tropics, net forest productivity levels off at an annual rainfall of 2000 mm, and declines from 3000 mm onward (Clark *et al.* 2001; Fig. 1 in Schuur 2003). Diversity of woody stems 2.5 cm DBH or greater on 0.1 ha plots increases with annual rainfall up to 3500 mm, and is no lower in wetter places (Gentry 1988a). Here, rainfall, not productivity, appears to be the best predictor of diversity. Productivity is necessary for tree diversity, but within the tropics, other factors such as total annual rainfall and brevity of dry season exert greater influence on tree diversity.

How might productivity constrain tree diversity? There is no consistent variation of tree density from boreal forest to the tropics (Tilman & Pacala 1993); the increased productivity of tropical climes does not allow finer "niche partitioning" merely by supporting more trees per hectare. Higher productivity can increase tree diversity by providing enough resources to support viable populations of energetic animal pollinators able to travel long distances in search of appropriate pollen and such pollinators can maintain adequate genetic variation in low-density tree populations (Regal 1977, Nason *et al.* 1998). Higher productivity also supports more trophic levels, multiplying the number of ways different tree species can coexist (Paine 1966, Oksanen *et al.* 1981). Both these effects, however, are more pronounced where productivity is less seasonal.

(B) Tree Diversity and Environmental Stability.—The most obvious contrast between the tropics and the temperate zone is winter. The frost-free parts of South Florida shelter a diverse array of tree species that do not grow farther north (Gleason & Cronquist 1964). Adapting to frost is costly. Wide xylem vessels transport water far more rapidly, but freezing embolizes wider vessels (Zimmermann & Brown 1971). Temperate zone trees must somehow parry the effects of frost. Ring-porous trees, such as oaks and elms, build a new set of wide vessels each year after the danger of frost is over and before leafing out: they opt for a shorter growing season in return for rapid water transport during this season. Other kinds of trees have short, narrow vessels, as do diffuse-porous maples, or even narrower tracheids, as do conifers, sacrificing rapid water transport in return for a longer growing season and reduced danger of embolism. There should accordingly be rapid species turnover near the southernmost boundary of frosts. But does frost limit tree diversity? Why cannot many frost-adapted tree species coexist?

Winter has other effects. At higher latitudes, the low and variable sun angle reduces the number of strata a forest can support and diminishes the ability of understory trees to specialize to particular light environments (Terborgh 1985). A low and variable sun angle also reduces the contrast between light gaps and shaded understory (Ricklefs 1977). Finally, while trees at high latitudes must face a great variety of temperatures during their growing season, tropical trees can specialize more closely to particular temperature conditions; so species turnover should be more rapid on the slopes of tropical mountains than on mountains at higher latitudes (Janzen 1967). Can such factors, however, increase the number of tree species on a hectare from 16 in Maryland to 91 in Panama and more than 280 in Amazonia (Leigh 1999)?

Many believe that the latitudinal gradient in tree diversity occurs because the absence of winter enhances pest pressure. Is this true? Many types of organisms suffer heavier predation in the tropics (Paine 1966, Moles & Westoby 2003). Specialist seed-eaters are considered a major cause of mutual repulsion among conspecifics (Hammond & Brown 1998). Moles and Westoby (2003) were therefore surprised to discover that there was no latitudinal gradient in the proportion of seeds destroyed prior to dispersal, or the proportion of seeds removed after dispersal, among the 122 and 205 plant species of different latitudes in which these types of seed predation were measured. If, however, the most damaging tropical seed predators are specialists (Janzen 1980), their ability to destroy the seeds of rare tropical plant species as effectively as their counterparts destroy seeds of the more common plant species of the temperate zone suggests that if a plant species in a tropical setting became much more common, it would suffer intolerable seed predation. To test this proposition, we must learn whether most seed predation is the work of specialists and if predation on the seeds of a tree species is heavier where that species is more common.

Leaf-chewing and seedling-eating insects also cause mutual repulsion among conspecifics. Absence of winter lengthens their activity season (Wolda 1983), intensifying their pressure on plants. Because young, expanding leaves should be equally tender everywhere, a comparative measure of an area's pest pressure should assess the rate at which young leaves are eaten in relation to their toxicity and the area's plant diversity. Young tropical leaves are eaten much more rapidly even though they are far more poisonous and are produced by much rarer tree species than young dicot leaves in the north temperate zone (Coley & Barone 1996). Perhaps because young tropical leaves are more poisonous, butterfly caterpillars are more specialized in the tropics than in the temperate zone (Scriber 1973, 1995; Marquis & Braker 1994); this is presumably true of moth caterpillars as well, the main chewers of plant leaves (Janzen 1988). Phloem-sucking treehoppers (Membracidae) are less specialized in the tropics (Marquis & Braker 1994), presumably because phloem is not poisonous. Even so, the enormous pressure of consumers on seeds, seedlings, and young leaves of tropical tree species, despite their low density, suggests that increased pest pressure entailed by absence of winter could account for the latitudinal gradient in tree diversity.

On the other hand, there must be a "niche opportunity" in the coniferous forests of eastern Canada for a tree species resistant to spruce budworms. Is that habitat more difficult to adapt to than others? Are cold winters so difficult to adapt to, and habitats with cold winters so temporary, geologically speaking, that there has not been time enough for a tree species resistant to spruce budworms to evolve in this habitat?

Within the tropics, tree diversity tends to be higher where dry season is shorter (Givnish 1999, Leigh 1999), that is to say, where climate and productivity vary less from season to season. In India's Western Ghats, annual rainfall is not correlated with the length of the dry season; there, tree diversity on small plots is not correlated with total annual rainfall, but it is higher where dry season is shorter (Davidar & Puyravaud, pers. obs.). In Amazonia, the average tree diversity on 1 ha plots within a 1° latitude x 1° longitude block is higher where dry season, as measured by the number of months averaging less than 100 mm of rain, is shorter ($R^2 = 0.35$, $P << 0.001$; ter Steege *et al.* 2003). If all the plots in this study with one dry month or less are assigned to one group, those with two dry months to another, those with three dry months to a third, and so forth, then the average diversity of the most diverse 10 percent of the plots in each group is quite tightly correlated with dry season length ($R^2 = 0.91$, $P << 0.001$; ter Steege *et al.* 2003); here, dry season length is a decisive constraint on tree diversity.

More generally, tree diversity is highest where environmental conditions vary least. "Hyperdiverse" forests with over 250 tree species per hectare are restricted, not only to everwet climates, but to latitudes between 4°40′N (Davies & Becker 1996) and 5°S (de Lima Filho *et al.* 2001), where sun angle at zenith varies least (Table 3). Are light environments partitioned more finely in these "hyperdiverse" forests? There is little evidence to support this proposition.

Everwet climates usually allow year-round herbivory. The abundance of insect herbivores varies far less with the season in a forest of central Guyana with only one dry month a year (Basset 2000) than on Barro Colorado, with its four-month dry season (Wolda 1983). In a deciduous dry forest of south India, insect herbivores are sufficiently less common during the dry season that trees reduce their "herbivore tax" by leafing out before the rains come (Murali & Sukumar 1993). In a Brazilian Cerrado, however, trees and shrubs avoid pathogen damage, not herbivore damage, by flushing leaves before the rainy season; leaves flushed after the rains come suffer more pathogen damage than those flushed beforehand (Marquis *et al.* 2001).

Is insect herbivory more intense in everwet forests where it is less seasonal? We summarize the few available data. Young leaves are eaten much more rapidly in the seasonal forest of Barro Colorado than in drier Brazilian Cerrado or Mexican dry forest (Table 2), despite Barro Colorado's higher tree diversity; insect pressure is higher on Barro Colorado than at these drier sites. Mutual repulsion among conspecifics is as prevalent on the 50 ha Forest Dynamics Plot at Pasoh, Malaysia, as on Barro Colorado's plot, even though tree diversity is far higher and tree species correspondingly rarer at Pasoh (Peters 2003). Were Pasoh less diverse, its plants would be more damaged by specialist pests than Barro Colorado's. On the other hand, the everwet forest at La Selva, Costa Rica, has hardly greater tree diversity than Barro Colorado (Table 1); yet, on average, both young and mature leaves of both pioneer and mature forest species are eaten much more rapidly on Barro Colorado than at La Selva (Table 2). Indeed, young leaves appear to be consumed most rapidly in forests with dry seasons of intermediate length (Marquis *et al.* 2002). Are anti-herbivore defenses so much stronger at La Selva than on Barro Colorado? A contrast within central Panama suggests that this may be true. In dry forest near Panama City, trees need birds to help defend them against insect herbivores (Van Bael *et al.* 2003), whereas in forest near Colón, where an-

TABLE 2. *Consumption rate by chewing herbivores, percent area per day, of young and mature leaves at selected sites.*

Site	Lat.	Young Leaves	Mature Leaves
1. Deciduous dry forest	19.5°N	0.352	0.097
2. Cerrado	15.9°S	0.254 + 0.113[a]	0.007 + 0.060[a]
3. Seasonal forest	9.1°N	0.97[b]	0.04[b]
4. Everwet forest	10.4°N	0.143[b]	0.012[b]

[a] Damage rate from pathogens.
[b] Average for mature forest species.
Data Sources:
Site 1, Chamela, Mexico: Filip *et al.* (1995).
Site 2, Fazenda Agua Limpa, Brazil: Marquis *et al.* (2001).
Site 3, Barro Colorado Island, Panama: Coley (1983).
Site 4, La Selva, Costa Rica: Marquis & Braker (1994).

nual rainfall is 50 percent higher and dry season shorter and wetter, trees suffer no more insect damage when birds are excluded (S. Van Bael, pers. comm.), as if the leaves of wetter forests have far better anti-herbivore defenses. To learn if pest pressure is what maintains higher tree diversity in more nearly everwet forests, the relation between seasonality, anti-herbivore defenses, predation pressure on herbivores, and the resulting damage from pests needs far more exact study, at many more sites.

On the other hand, it appears that trees 10 cm DBH or greater are no more likely to be habitat specialists in western Amazonia than in South Carolina (Pitman, Terborgh, Silman, Thompson *et al.* 2002). We also need to learn whether species turnover contributes to the latitudinal gradient in tree diversity (Pitman, Terborgh, Silman, Thompson *et al.* 2002), and whether this answer depends on the size of the plants considered.

In summary, even within the tropics, less seasonal climates allow higher tree diversity. More work is needed to learn why this is so. The mystery of how 43 species of *Inga* can coexist on a 25 ha plot in Amazonian Ecuador (Bermingham & Dick 2001) demands attention. Moreover, some forests in everwet climates, such as that at San Carlos de Rio Negro, have very low tree diversity (Table 3). This circumstance reflects the effects of past history, which we will consider later.

(C) THE RELATION BETWEEN LOCAL AND GLOBAL TREE DIVERSITY.—Local tree diversity tends to be higher in regions with high regional tree diversity (Ricklefs 2004). Does this mean that in regions with more tree species, local diversity is enhanced by species unfit for the locale, which would inevitably be replaced by superior competitors were it not for immigration from outside (Shmida & Wilson 1985)? Would this circumstance imply that mechanisms promoting stable coexistence of tree species are irrelevant to gradients in tree species diversity?

If we have interpreted our test of Hubbell's (1997, 2001) neutral theory correctly, each tree species in the region started off with some advantage over its competitors, and a tree species usually has some setting in which it can increase when rare. A region's tree diversity cannot exceed the diversity of that region's local niche opportunities. To be sure, a larger proportion of such opportunities may remain unexploited in rarer habitats or smaller regions such as oceanic islands.

We know too little of the ecology of most tropical tree species to even think of assessing what proportion of the species on a hectare, or in a 50 ha plot, is unsuited to that plot's environment. It is reasonable to believe, however, that more species will spill over from habitats offering more niche opportunities than from those offering fewer (MacArthur & Wilson 1967). Immigration into unsuitable habitats may render diversity gradients less steep, but immigration cannot reverse these gradients (Rohde 1992). These gradients require explanation in terms of the relative abundance of niche opportunities.

WHAT FACTORS INFLUENCE A REGION'S TREE DIVERSITY?

A region's tree diversity represents a balance between speciation (and some immigration) and extinction (MacArthur & Wilson 1967, Terborgh 1973). We must first review mechanisms of speciation among woody plants to learn what conditions are necessary for speciation, whether or not species usually begin from small populations, and if, as our test of Hubbell's (2001) neutral theory has suggested, speciation is usually a response to a niche

TABLE 3. *Latitude, annual rainfall* P *(mm), rainfall during year's driest quarter* P_3 *(mm), number* N *of trees* ≥ 10 *cm DBH, number* S *of species among them, and Fisher's* α^a *in selected everwet forests, and in selected pairs of sites with similar climates. In each pair of sites, the upper site was much less disrupted by Pleistocene climate change.*

Site	Lat.	P	P_3	N	S	α
Everwet Sites						
1. Papua New Guinea	6.7°S	6400	1350	693	228	119
2. Amazonia, Brazil	5°S	3404	<300	769	322	208
3. Amazonia, Brazil	5°S	2715	365	779	271	147
4. Amazonia, Peru	4°S	2845	513	608	295	226
5. Amazonia, Brazil	2.4°S	2609	344	618	285	205
6. Lambir, Sarawak	4.3°N	2664	498	637	247	148
7. Andulau, Brunei	4.7°N	3000	500	572	256	178
8. San Carlos, Venezuela	1.9°N	3500	600	744	83	23.4
Paired Sites						
9. Manu, SW Amazonia, Peru	12°S	2028	186	586	174	83.6
10. Korup, Cameroon	5°N	5272	172	492	87	30.7
11. E. Amazonia, Brazil	5°S	1900	87	530	98	35.4
12. W. Ghats, S. India	8.9°N	2499	90	482	57	16.8

[a] Fisher's α is calculated recursively from the equation $S = \alpha \ln(1 + N/\alpha)$. Fisher's alpha depends less on sample size N than does S (Leigh 1999).

Data sources:
Site 1, Crater Mt: Wright *et al.* (1997).
Site 2, Ha 3, Rio Urucu: de Lima Filho *et al.* (2001).
Site 3, Mungaba plot, Rio Juruá; Lima da Silva *et al.* (1992).
Site 4, Allpahuayo, plot 2: Vásquez-Martínez & Phillips (2000); rainfall for nearby Iquitos from Müller 1982.
Site 5, Ha C, 90 km N of Manaus: de Oliveira & Mori (1999); rainfall from W. Laurance, pers. comm.
Site 6, Lee *et al.* 2004.
Site 7, Davies & Becker (1996); P_3 from nearby Site 6.
Site 8, San Carlos de Rio Negro, forest on Oxisol: Uhl and Murphy (1981).
Site 9, Average Manu ha from Pitman *et al.* (2002); rainfall from Gentry (1990, facing p. 1).
Site 10, Chuyong *et al.* 2004.
Site 11, Salomão (1991).
Site 12, Parthasarathy & Karthikeyan (1997).

opportunity. Next, we ask what factors affect the diversity different regions support, and how long it takes speciation and immigration to build up the tree diversity of a region newly opened, say, by retreating glaciers or a major, favorable change in climate. Finally, we ask whether the tropics are primarily a cradle of tree speciation or a museum of tree diversity.

(A) MECHANISMS OF SPECIATION AMONG WOODY PLANTS.—This paper's argument hinges on the propositions that speciation in woody plants is normally a response to a niche opportunity and that new species arise from small populations. Thus, we inquire into mechanisms of speciation among woody plants, especially tropical ones.

The first question is, do tropical woody plants usually speciate allopatrically? Sympatric speciation can occur in woody plants. Polyploidy seems a logical means of sympatric speciation, but only 2–4 percent of today's species of flowering plants evolved by polyploidy, and this proportion is far lower among woody plants (Otto & Whitton 2000). Sympatric speciation sometimes occurs among tropical trees when a sexual species gives rise to an obligately asexual clade (Ehrendorfer 1982, Gentry 1989), but asexual species can hardly last long in competitive, pest-ridden tropical forests. Gentry (1989) proposed that sympatric speciation is contributing to the "explosive" diversification of smaller woody plants in the topographically heterogeneous lower slopes of the northern Andes, but he provided no evidence for how it happened. In groups such as Bignoniaceae and Dipterocarpaceae, however, the most closely related species have adjacent rather than overlapping or distantly separated ranges (Ehrendorfer 1982, Ashton 1988, Gentry 1989). Although the prevalence of allopatric speciation among tropical woody plants needs far more comprehensive and careful study, for the moment it appears reasonable to conclude with Ehrendorfer (1982: 505) that for woody plants, "Initial steps of speciation mostly are on the basis of allopatric (often peripatric) geographical or parapatric ecological differentiation."

Second, how local is speciation? In woody plants, it is usually possible to hybridize members of populations many million years after they were separated (Ehrendorfer 1982, Carr & Kyhos 1986, Baldwin *et al.* 1991). This rule needs more careful, and more comprehensive, testing. If true, then when a barrier splits a tree population, different, mutually incompatible alleles of the sort mentioned by Dobzhansky (1937) and Orr and Turelli (2001) do not accumulate fast enough to make hybrid breakdown a driving force in tree speciation. Most tree species do not arise because an impenetrable barrier split big populations of trees in half. Speciation in woody plants must usually be a more "local" process, perhaps a form of "budding" (Stebbins 1982) in which a subpopulation invades a new habitat, and selection, driven by the lower fitness of hybrids for either parent's niche, favors its reproductive isolation from the parent population.

The final question is, do new species form in response to niche opportunity, or is speciation as little related to niche opportunity as mutation is to opportunities for organismic adaptation? One of the few relevant studies of speciation among tropical plants concerns speciation among large herbs, *Costus* (Costaceae) in Central America (Schemske 1981, Kay & Schemske 2003). As a rule, a *Costus* species is pollinated by either bees or hummingbirds, rarely both. Sympatric *Costus* with different pollinators exchange few genes, even though artificial hybrids do well in the laboratory (Kay & Schemske 2003). Is there selection against hybridizing? If so, it cannot be driven by the kind of genetic incompatibility invoked by Dobzhansky (1937); hybridizing must therefore be disadvantageous because hybrids are unfit for either parent's way of life (Schluter 1998).

There is further evidence for selection against hybridizing in *Costus*. At La Selva, Costa Rica, a pair of bee-pollinated *Costus* avoid hybridizing by flowering at different times (Kay & Schemske 2003). In a pair of hummingbird-pollinated *Costus* species that flower simultaneously at both Barro Colorado and La Selva, pollen–stigma incompatibility prevents hybridization between plants at the same site, but a plant of either species can be fertilized successfully by pollen from a plant of the other species at the other site (Kay 2002). The pollen–stigma incompatibility occurs only when needed to prevent hybridizing. If cross-site hybrids grow well in the laboratory, hybridizing must be disadvantageous because hybrids are fit for neither parent's way of life.

Now that access to the canopy has become more practicable (Ozanne *et al.* 2003), the studies of Schemske (1981) and Kay and Schemske (2003) on *Costus* can be repeated on tropical trees. As this has yet to happen, we confine ourselves to extrapolating the conclusions of Kay and Schemske (2003) to those many woody genera with fully distinct species, which are easily hybridized artificially but rarely hybridize in nature. When they are sympatric, species in these genera flower at different times or use different pollinators (Ehrendorfer 1982, Gentry 1989). We therefore infer that, in these genera, speciation is a response to a niche opportunity and that selection reduces the probability that sympatric species hybridize because hybrids are unfit for either parent's way of life.

What might drive speciation? What role might pest pressure play in speciation? "It is a commonplace of African botany that genera very often have one or more species in the rain forest and other species in the savannah" (Gillett 1962). In South America, 14 of the 18 most common woody species in a hectare of cerrado savanna near the Tropic of Capricorn censused by Silberbauer-Gottsberger and Eiten (1987: 77) are congeneric with some tree 10 cm DBH or greater in one of the three rain forest hectares north of Manaus censused by de Oliveira and Mori (1999). The woody genus *Ruprechtia* (Polygonaceae), which originated in "chaco" savannas over ten million years ago, has since radiated into deciduous dry forest. During the last million years, this genus has invaded and diversified in forests of Central America (Pennington *et al.* 2004). The vine genera *Chaetocalyx* and *Nissolia* have diversified back and forth from wet to dry forests during the last ten million years. How could a genus that evolved in rain forest compete successfully in dry forests or savannas with genera that evolved in those settings, or vice versa? A shift of habitats may be advantageous if it entails escape from pests (Gillett 1962; Janzen 1970: 523; Mitchell & Power 2003).

Based on these limited data, it appears that (1) speciation among tropical woody plants is usually allopatric or parapatric; (2) new species arise locally, with, initially, small populations; and (3) speciation usually occurs in response to divergent selection between a parental way of life and a new "niche opportunity."

(B) WHAT FACTORS INFLUENCE A REGION'S TREE DIVERSITY?.—If each tree species initially spreads and avoids subsequent extinction by exploiting a unique niche opportunity, then a region's tree diversity will be enhanced by a greater number of local niche opportunities, which may arise either from a greater variety of habitats or from more opportunities per habitat.

Large extent also enhances a region's tree diversity. Other things being equal, larger regions should support higher regional diversity, and therefore higher local diversity, than smaller ones (Terborgh 1973; Rosenzweig 1995: 287ff; Ricklefs 2004). Regional diversity represents a balance between speciation (and some immigration) and extinction (MacArthur & Wilson 1967, Terborgh 1973). In larger regions, extinction rate is lower because their species can spread more widely, reducing the probability of extinction by environmental variation (Rosenzweig 1995). In larger regions, speciation occurs more often. Larger regions offer more opportunities for isolation and divergence of peripheral tree populations (Ricklefs 2004) and more opportunities for speciation and diversification among herbivores and pathogens, thereby multiplying niche opportunities for trees (Ehrlich & Raven 1964, Dussourd & Eisner 1987, Becerra & Venable 1999, Becerra *et al.* 2001).

Temperate zone forests in east Asia contain more species than forests of equal area and comparable climate in North America (Latham & Ricklefs 1993b). This was true even before glaciations started in the Pleistocene, presumably because Eurasia has a far larger area of temperate zone habitat than North America. A hectare of everwet forest in Amazonia contains more tree species than one in New Guinea (Table 3), presumably because Amazonia's total area of rain forest is far larger than New Guinea's. On the other hand, despite the small area and profound isolation of Madagascar's rain forest, a hectare of rain forest at 18°S musters 146 tree species 10 cm DBH or greater (Rakotomalaza & Messmer 1999), far more than can be found in any hectare of temperate zone forest. Except for very small regions, limited regional area does not override the impact on local tree diversity of the variety of local niche opportunities.

A region's tree diversity is also enhanced by a longer period of freedom from major environmental change. It takes millions of years of freedom from such change for speciation and immigration to build up the tree diversity of a newly opened region to the level it can support. Tree diversity is lower in northern Europe than in the eastern United States because glaciation devastated Europe's tree flora, and there has been too little time for immigration and speciation to replenish its diversity (Latham & Ricklefs 1993a). On the Hawaiian islands, the "Big Island" has 14 times Maui's area of alpine/subalpine habitat, but only 94 plant species in that habitat compared to Maui's 102—apparently because Maui's alpine/subalpine habitat is nearly two million years old compared to less than 600,000 years for the "Big Island's" (Price 2004). For 1 ha plots in a given climate, tree diversity is lowest in areas such as Australia, south India, and west Africa (Table 3), where the forest retreated farthest into the most scattered refuges during Pleistocene glaciations (Morley 2000). The everwet upland forest at San Carlos de Rio Negro, Venezuela, has uncommonly low tree diversity for its climate (Table 3), apparently because the region was much drier during the Pleistocene: during the Last Glacial Maximum, sand dunes were active near San Carlos in what is now everwet forest (Carneiro Filho *et al.* 2002). Tree diversity is greatest in Western Amazonia (Gentry 1988b), most of which was covered by rain forest all through the Pleistocene (Piperno 1997). Developing a western Amazonian level of tree diversity, however, does not require the whole Cenozoic. Twenty million years ago, Malesia was covered by seasonal monsoon forest; the diversity of Sarawak's everwet forest has developed since then (Morley 2000).

(C) ARE THE TROPICS A CRADLE OF TREE SPECIATION OR A MUSEUM OF TREE DIVERSITY?.—We have seen how tree diversity is highest in those tropical regions where climates have varied least during the last 10 or 15 million years, and lowest in those areas where forests were most disrupted by the cyclic revolutions of climate during the Pleistocene (Morley 2000). Indeed, Amazonian tree diversity was higher before the Pleistocene changes began than it is now (Hooghiemstra & van der Hammen 1998).

The cyclical drying and wetting of tropical habitats during Pleistocene glaciations, whereby rain forests were fragmented during glacial periods (Guillaumet 1967, Haffer 1969, Prance 1982) and dry forests fragmented during interglacials (Pennington *et al.* 2004), enhanced speciation rates in some groups (Pennington *et al.* 2004). In Central America, especially, the expansion of depauperate rain forest during interglacials provided niche opportunities for dry forest lineages to invade this rain forest (Pennington *et al.* 2004). Such speciation, however, did not compensate for the diversity lost through the extinctions caused by climate change.

The latitudinal gradient in tree diversity is old. A hectare of forest on Barro Colorado includes 73 genera and 36 families among its 91 species 10 cm DBH or greater (Leigh *et al.* 2004), and a hectare of depauperate tropical forest in India's Western Ghats has 47 genera and 32 families among its 57 species 10 cm DBH or more (Parthasarathy & Karthikeyan 1997), more genera and families than a temperate zone hectare has tree species. Many of a tropical plot's tree genera and most of its families evolved long enough ago to have spread to more than one continent; 30 percent of the tree genera recorded from Makokou, Gabon, also occur in the Neotropics (Gentry 1982: 564). The number of lowland species that occur on both sides of the Ecuadorian Andes suggests that at least 30 percent of the plant species in Ecuador's lowland rain forests evolved before the Andes sundered these rain forests in the late Miocene (Jørgenson and Léon-Yánez 1999, Raven 1999). Tropical forests are clearly museums of diversity.

Tropical environments, however, especially those in the wet tropics, also offer plants more ways to achieve reproductive isolation, making speciation easier there (Fischer 1960). For example, a greater variety of pollinators and a longer growing season provide more scope for achieving reproductive isolation by pollinator shift or change of flowering season (Gentry 1989, Kay & Schemske 2003). How might these factors influence gradients in tree diversity?

Some tropical lineages diversify much more rapidly than others. *Inga* (Leguminosae), with 300 species, began diversifying 10 or fewer million years ago (Richardson *et al.* 2001); *Ficus* (Moraceae), with 750 species, originated 90 million years ago (Machado *et al.* 2001). Do lineages diversify more rapidly if they have cheaper or more effective anti-herbivore defenses that allow them to invade already occupied habitats (Ehrlich & Raven 1964)? In Central America, trees and canopy lianas usually belong to slowly diversifying lineages, centered on lowland Amazonia; treelets and shrubs usually belong to rapidly diversifying clades centered on the foothills and lower slopes of the lower Andes (Gentry 1982). Do the shrubs and treelets diversify more rapidly simply because their seeds disperse less efficiently (Givnish 1999)? What factors drive speciation in these "Andean" lineages?

CONCLUSIONS AND OPEN QUESTIONS

A test of Hubbell's (2001) neutral theory suggests that tree diversity is no accident. Rather, each species has some setting where it increases when rare. It appears that neither disturbance nor microhabitat specialization can explain the diversity of tropical trees, even though larger-scale habitat and climate differences are the primary causes of species turnover. Increased activity of specialized pests and pathogens in less seasonal climates appears to be a primary cause of the latitudinal gradient in tree diversity. Further work is needed to assess the role of pest pressure and other factors in generating within-tropical diversity gradients. To establish and develop these conclusions, we need to learn (1) the various ways habitat complexity can enhance tree diversity. How many tree species can coexist locally by this means?; (2) whether mutual repulsion among conspecifics is usually driven by specialist pests or pathogens; (3) whether or not the observed degree of mutual repulsion among conspecifics suffices to maintain observed tropical tree diversity; (4) whether leaves of wet tropical forests have sufficiently effective anti-herbivore defenses to reduce herbivory rates on young leaves by 75 percent compared to a forest with a four-month dry season; (5) how much species turnover contributes to the latitudinal gradient in tree diversity; and (6) why species turnover is higher for herbs, shrubs, and treelets than for large trees.

Local tree diversity is influenced by regional tree diversity. Regional tree diversity is higher in regions with more local niche opportunities (for which variety is greater at lower latitudes and in less seasonal environments), in larger regions, and in regions that have been free of major environmental shifts for a longer period.

To attain a clearer understanding of the factors that maintain tree diversity, we must learn more about the mechanisms, and driving forces, of speciation in woody plants. We must learn (1) if speciation is usually allopatric; (2) how long a time after a tree population is split by an impenetrable barrier before hybrids between the two halves are no longer viable. If this time is very long, then reproductive isolation must usually be the outcome of natural selection driven by the unfitness of hybrids for either parent's way of life; (3) what factors drive tree speciation? Is speciation usually associated with invading new habitats?; and (4) why some lineages diversify rapidly, while other equally diverse lineages have diversified more slowly. Why the difference? Do cheaper, or more effective, anti-herbivore defenses allow a clade to diversify more rapidly?

To understand why some tropical forests have so many kinds of trees, we will have to learn more about the natural history of these trees, the history of their biomes, and the driving forces of tree evolution.

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