

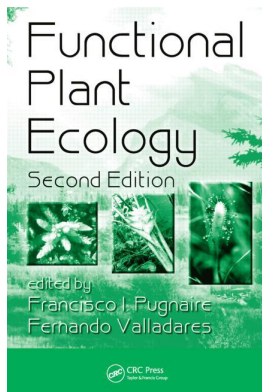
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S. Joseph Wright

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INTRODUCTION

Plant species diversity is greatest in tropical forest. The highest plant species density yet recorded, 365 species in just 1000 m², is for the only complete enumeration of tropical forest plants (Gentry and Dodson 1987). The diversity of lowland tropical forest at a local scale may exceed the diversity of extratropical forests at a continental scale. The combined temperate forests of Europe, North America, and Asia support 1166 tree species in 4.2 × 10⁶ km² (Latham and Ricklefs 1993). In contrast, 1175 tree species occur in just 0.5 km² of lowland dipterocarp forest in Borneo (LaFrankie 1996). Trees comprise just 25% of the plant species in tropical rain forests (Gentry and Dodson 1987). There are 65% of all flowering plant species, 92% of fern species, and 75% of moss species that are tropical (Prance 1977).

These levels of diversity challenge modern ecology (Rosenzweig 1995). Theory and experiment confirm that two species cannot coexist if they use resources in an identical manner (Gause 1934). This competitive exclusion principle has become the touchstone against which theory addresses the coexistence of species. Plants compete for light, water, and perhaps a dozen of mineral nutrients. Plants must also disperse their progeny and survive the depredations of their pests. Are interspecific differences in these few parameters sufficient to explain the levels of plant diversity observed in tropical forests? Do other mechanisms

contribute to the coexistence of tropical forest plants? Or is the competitive exclusion principle an inappropriate touchstone?

This chapter addresses these questions in three steps. First, five mechanisms are evaluated that are frequently invoked to explain the coexistence of extraordinary numbers of plant species in tropical forests. Second, four appendices present significant attributes of plant diversity within and among tropical forests. A successful theory must explain these observations. Finally, the origination of tropical forest plant diversity is considered. The extraordinary species densities of tropical forests may have more to do with the evolutionary history of plants, especially angiosperms, than with any unique ecological attribute of tropical forests.

COEXISTENCE OF TROPICAL FOREST PLANTS

This chapter focuses on five mechanisms that may contribute to the coexistence of very large numbers of species of plants and is not intended to be exhaustive. Many potential mechanisms are omitted (see Palmer 1994). The five mechanisms were selected for two reasons: (1) they dominate the literature for tropical forests and (2) each mechanism is amenable to experimental and comparative tests. The relationship to plant species density is briefly described for each mechanism. Principal tests in tropical forests are then evaluated. Finally, the mechanisms are related to one or more of the patterns of plant diversity observed among tropical forests ([Appendix 11.1](#) through [Appendix 11.4](#)).

NICHE DIFFERENTIATION

Species may exploit limiting resources in ways that are sufficiently distinctive to permit stable coexistence in equilibrium communities (Ashton 1969, MacArthur 1969). Coexistence occurs when resources vary spatially, and each species occurs where it is a superior competitor.

Treefalls create spatial heterogeneity. Light intensities are highest near the center of a treefall and lowest nearby, beneath the intact forest canopy. Treefalls also create soil heterogeneity. Clays from depth are exposed when roots tip up, when rich humic material accumulates where fallen canopies decompose. Tropical forest plants may segregate along both light and soil gradients created by treefalls (Ricklefs 1977, Connell 1978, Denslow 1980, 1987, Orians 1982, Platt and Strong 1989).

This treefall gap hypothesis has been evaluated thoroughly. A few species do segregate treefall gaps by size and light intensity (Brokaw 1987). However, in large mapped plots, the spatial distributions of saplings of most tree species were indifferent to treefall gaps (Hubbell and Foster 1986, Lieberman et al. 1995). Saplings of just 5% of the tree species evaluated were specialized to treefall environments in repeated surveys of the performance of 250,000 trees in Panama (Welden et al. 1991). The great majority of species survived well and grew slowly, both in treefall gaps and in the deeply shaded understory. Interspecific differences in performance in response to gaps are necessary to promote coexistence. Recent experimental studies have failed to identify such differences (Uhl et al. 1988, Denslow et al. 1990, Brown and Whitmore 1992, Osunkjoya et al. 1992). The emerging conclusion is that spatial heterogeneity associated with treefalls maintains a relatively small number of light-demanding, shade-intolerant species in the forest landscape and makes a limited contribution to tropical forest plant diversity.

An intriguing extension of the treefall gap hypothesis relates the frequency of treefalls to forest productivity. Tree mortality increases with rainfall in tropical forests and with soil fertility in temperate-zone forests (Grubb 1986, Phillips et al. 1994). More productive forests with higher tree mortality rates have higher rates of gap formation and are predicted to have higher spatial heterogeneity of forest light environments. To the extent that plants

differentiate light environments, this enhanced spatial heterogeneity contributes to the increase in plant species diversity with rainfall in tropical forests and with soil fertility in temperate forests (Grubb 1986, Phillips et al. 1994). However, we have seen that tropical forest plants show limited niche differentiation with respect to light environments. Still, the hypothesis of Phillips et al. (1994) is one of the few that addresses the ubiquitous increase in tropical-forest plant diversity with rainfall ([Appendix 11.1](#)) and merits further examination.

Variation in soil resources related to topography and underlying geological formations may also introduce spatial variation and promote species coexistence. Many tropical forest plant species have restricted distributions along soil moisture and soil fertility gradients (Hubbell and Foster 1983, Lieberman et al. 1985, Baillie et al. 1987, Tuomisto and Ruokolainen 1994, Swaine 1996, Sollins 1998). However, in most of these studies, many more species were indifferent to the edaphic gradient and occurred everywhere. Most tropical plant species are generalists with respect to both edaphic gradients and treefall microhabitats.

A modal relationship has been predicted between plant species density and soil fertility when three conditions are met (Tilman 1982): (1) few species survive the least fertile soils; (2) soil resources vary spatially; and (3) the most fertile soils provide ample resources everywhere, effectively negating spatial heterogeneity. Under these conditions, species diversity increases with the pool of tolerant species from infertile to intermediate soils and then decline on the most fertile soils as effective spatial heterogeneity declines and competitive dominance develops. The predicted modal relationships between tropical tree species' densities and soil fertility have been reported ([Appendix 11.2](#)). The postulated mechanisms remain untested, however, and the declining portion of the diversity–fertility relationship may be an artifact ([Appendix 11.2](#)).

In conclusion, spatially heterogeneous resources and ecologically segregated plant species are obvious to even casual observers of tropical forests. Niche differentiation undoubtedly contributes to tropical forest plant diversity. However, there are many ecologically similar plant species ([Appendix 11.4](#)). Moreover, there is no indication that levels of ecological differentiation among species distinguish dry from wet tropical forest or tropical forest from other forest biomes. Additional mechanisms must contribute to the diversity of tropical forest plants.

PEST PRESSURE

Microbes, fungi, and animals consume living plant tissue. These pests may contribute to the coexistence of their host plant species if the more abundant plant species or the superior competitors suffer disproportionately high levels of damage (Gillett 1962).

Pest pressure is severe in tropical forests. Insect herbivores alone consume an average of 11% of the leaf area produced in the understories of wet tropical forest (Coley and Barone 1996). Granivorous and browsing mammals reduce seedling recruitment, survivorship, and growth in a wide range of tropical forests (Dirzo and Miranda 1991, Osunkjoya et al. 1992, Terborgh and Wright 1994, Asquith et al. 1997). Pathogens kill entire seedling crops as well as significant numbers of adult trees (Augspurger 1984, Gilbert et al. 1994). Pathogens that impair but do not kill the host plant have received less attention, but are likely to be very important. Herbivores consume a larger proportion of leaf production in tropical forests than in temperate forests, despite greater plant investment in antiherbivore defenses in tropical forests (Coley and Aide 1991, Coley and Barone 1996). High levels of activity of plant pests may set tropical forests apart from other forested biomes.

Pest pressure may vary on several spatial scales. At the smallest scale, pests may cause disproportionately high levels of damage on the concentrations of conspecific seeds or seedlings found near fruiting trees. Conspecific may be prevented from recruiting successfully near one another, freeing space for other plant species, and potentially raising plant diversity

(Janzen 1970, Connell 1971). Seeds, seedlings, and saplings experience high mortality rates near conspecific adults (Clark and Clark 1984, Hubbell et al. 1990, Condit et al. 1992). However, the mechanism is not necessarily pest pressure. The alternative is intraspecific competition, occurring either among juvenile plants or between juveniles and the nearby adult (Clark and Clark 1984).

The relationship between pest pressure and the local population density of host plants becomes critical at larger spatial scales ([Appendix 11.3](#)). Pest pressure is positively density dependent when pest pressure increases more rapidly than host density. Positively density-dependent pests cause the highest levels of damage on the most abundant hosts and potentially contribute to the coexistence of host species. Alternatively, pest pressure is negatively density dependent when pests are unable to keep in pace with host densities. High host densities satiate pests (Schupp 1992). Negatively density-dependent pests cause the greatest damage on rarer hosts and potentially reduce host diversity. Negative density dependence occurs when factors other than host density control pest populations. Possibilities include control of pest populations by their own predators and parasites or by social behavior, especially territorial behavior. Thus, at spatial scales over which the densities of reproductive plants vary, pest pressure may be positively or negatively density dependent with the potential to increase or decrease plant diversity, respectively.

Keystone predators control community organization through their impact on prey species (Paine 1966). Terborgh (1992) hypothesized that felids and raptors are keystone predators in tropical forests. The hypothesis has two components. First, felids and raptors collectively limit midsized terrestrial mammals. Second, when their numbers are not checked by predation, these prey species alter forest regeneration. This hypothesis has profound implications. Felids and raptors may indirectly control plant diversity in tropical forests just as starfish control the diversity of sessile organisms in some marine environments.

The second component of this hypothesis has recently been falsified. Fences were used to exclude mammals from seeds and seedlings at Cocha Cashu, Peru, where the biota is intact, and at Barro Colorado Island, Panama, where several large predators are missing (Terborgh and Wright 1994). The enclosures had large and virtually identical effects at both sites, enhancing all indices of seedling performance. Browsing and granivorous mammals clearly alter plant regeneration, but the presence or absence of large felids and raptors had no additional effect.

Pest pressure may contribute to the increase in plant species diversity with rainfall ([Appendix 11.1](#)). Wet forests have higher and more constant pest pressure if seasonal temperature and rainfall reduce pest populations in drier forests. Plant diversity is, in turn, enhanced in wet forests if the more abundant plant species or the superior competitors suffer disproportionately high levels of damage. The premise of this hypothesis, higher pest pressure in wetter forests, is yet to be established. Levels of herbivory are actually higher in dry forests than in wet forests in the tropics (Coley and Barone 1996). Realized levels of herbivory result from the interaction between herbivores and plant defenses. In dry deciduous forests, leaves live less than 1 year and are poorly defended. In wet evergreen forests, long-lived leaves are better defended. The full cost of pests includes the diversion of resources to pest defenses as well as direct pest damage. Evaluation of pest pressure along tropical rainfall gradients awaits this information, as well as information on levels of activity of fungal and microbial pests.

In conclusion, pest pressure is greater in tropical forests than in other forest biomes. Positively density-dependent pest pressure increases plant diversity. At very small spatial scales, pest pressure almost certainly reduces recruitment near conspecific adults (Clark and Clark 1984). For larger spatial scales, there have been almost no tests for density-dependent pest pressure for tropical forests (see Schupp 1992). Pest pressure remains a promising but unproven mechanism of plant species coexistence in tropical forests.

INTERMEDIATE DISTURBANCE

Windstorms, lightning, fire, landslides, and other disturbances kill trees. Connell (1978) predicted that species diversity varies during succession after such disturbances. Diversity is low immediately after a disturbance as just those species with the greatest ability to disperse their seeds arrive. Diversity reaches a maximum at intermediate times after a disturbance as many more species arrive. Diversity then declines with time as the best competitor or the species most resistant to pests or physical stress comes to dominate the forest. Species diversity over entire landscapes is low at (1) high disturbance frequencies, because recently disturbed patches and the few species with the greatest dispersal abilities dominate the landscape; and (2) low disturbance frequencies, because old patches and the few species best able to persist dominate the landscape. Diversity is greatest at intermediate disturbance frequencies because the landscape includes patches of a great variety of ages supporting a wide mix of species.

Connell (1978) applied the intermediate disturbance hypothesis to treefall gaps. He predicted that species best able to persist would perform poorly when transplanted into large gaps. These experiments have since been conducted with generally negative results. Performance improves for all species when seedlings are transplanted into gaps (Denslow et al. 1990, Brown and Whitmore 1992, Osunkjoya et al. 1992). Connell (1978) also failed to recognize that saplings of species capable of persisting in deep shade survive the formation and closure of treefall gaps (Uhl et al. 1988). Treefalls do not wipe the ground clean as envisioned by Connell (1978).

Intermediate disturbance may be important at larger spatial scales. Blowdowns caused by downburst of wind associated with severe storms are an important disturbance. Blowdowns larger than 30 ha can be identified from satellite images. The frequency of large blowdowns over Amazonian Brazil increases with storm activity and annual rainfall (Nelson et al. 1994). Such large disturbances may contribute to the ubiquitous increases in plant species density with rainfall in tropical forests ([Appendix 11.1](#)).

Huston (1979, 1994) extended the intermediate disturbance hypothesis by incorporating environmental factors postulated to affect rates of competitive exclusion. Huston reasoned that productivity controls the rate of competitive exclusion. Given a constant frequency of disturbances, diversity is low in the least productive environments where few species can tolerate physical stress, highest in intermediate environments where many species can tolerate the environment but recurrent disturbance prevent competitive exclusion, and low again in the most productive environments where competitive exclusion occurs more rapidly than disturbance. Huston (1980, 1993, 1994) used soil fertility as a proxy for productivity in tropical forests. This proxy is evaluated in [Appendix 11.2](#). Chesson and Huntly (1997) recently overturned the postulated connection between disturbance and rates of competitive exclusion. They demonstrated theoretically that disturbance either has no effect on or enhances rates of competitive exclusion. Huston's extension of the intermediate disturbance hypothesis must be reconsidered.

In conclusion, the intermediate disturbance hypothesis remains largely untested for tropical forests. One reason is overlap among hypotheses (see Palmer 1994). For example, the mechanisms postulated by Connell (1978) for treefall gaps incorporate interspecific differences in response to light intensity considered here under niche differentiation (see [Section "Niche Differentiation"](#)). The intermediate disturbance hypothesis also implicitly assumes a trade-off between the abilities to disperse and persist so that the species with the greatest dispersal abilities are poor competitors and vice versa (Petraitis et al. 1989; see [Section "Life History Trade-Offs"](#)). Finally, the intermediate disturbance hypothesis is most likely to be important for large disturbances that kill all advanced regeneration. These types of disturbances await further study.

LIFE HISTORY TRADE-OFFS

Sessile organisms live in communities with rigid spatial structure. Each individual occupies a space. Direct interactions are limited to colonists of the same space and near neighbors. The ability to colonize empty space, compete within a space, and persist once established jointly determines success. Trade-offs in these abilities, such that a superior colonist was an inferior competitor, might facilitate species coexistence.

Life history trade-offs occur among tropical forest plants. The number of seeds produced and the mass of individual seeds are inversely related. Presumably, species producing many small seeds disperse to rare high-resource environments, whereas species producing a few large seeds tolerate frequent low-resource environments (Hammond and Brown 1995). At the leaf level, maximum photosynthetic potentials and leaf longevity are inversely related (Reich et al. 1992). Presumably, species with long-lived leaves tolerate low-light environments, and species with short-lived leaves are superior competitors in high-light environments. At the level of individuals, maximum potential growth rates and survivorship in deep shade are inversely related (Kitajima 1994). Presumably, allocation to defense against pests limits growth rates but enhances shade survivorship. These trade-offs may facilitate species coexistence.

An infinite number of species can coexist when there is a strictly ordered trade-off between longevity, dispersal ability, and competitive ability (Tilman 1994). However, a critical assumption of this spatial competition hypothesis is violated in tropical forests. Tilman assumed a strict trade-off between longevity and competitive ability, such that superior competitors had short longevity and vice versa. Superior competitors in tropical forests are likely to tolerate deep shade as seedlings and cast deep shade as adults. Such species invest heavily in defenses against pests, have long-lived tissues including leaves, and are characterized by low growth and mortality rates (Kitajima 1994). Tilman acknowledged the possibility that long lifetimes and superior competitive ability may co-occur, falsifying the spatial competition hypothesis.

A very large number of species can also coexist if dispersal limits recruitment (Hurtt and Pacala 1995). Hurtt and Pacala modeled spatially heterogeneous environments and environmentally dependent competitive abilities. Sites vacated by the death of an adult were won by the best competitor among the species that reached the site. When the absolutely best competitor for the environment at the site did not arrive, the site was won by forfeit, and dispersal limitation occurred. Hurtt and Pacala proposed a positive feedback between species diversity and dispersal limitation. Dispersal limitation becomes more important as diversity increases because all species become rarer, produce fewer propagules, and reach fewer sites. However, a negative feedback may disrupt dispersal limitation. If a superior competitor became abundant, its seeds would approach ubiquity and only the rarer, less-competitive species would be dispersal limited. The two most common tree species on Barro Colorado Island, Panama, have dispersed seeds to each and every one of 200 tiny (0.5 m^2) litter traps randomly located throughout a 50 ha forest plot. Both species are superior competitors whose abundant, widespread seedlings grow and survive well both in the deeply shaded understory and in treefall gaps. Such abundant species have escaped dispersal limitation, even in a species-rich tropical moist forest.

Empirically driven simulation models may elucidate the relationship between species diversity and life history traits. Pacala et al. (1996) have successfully applied this approach to North American forests with nine tree species. Model inputs determined empirically for each species included seed dispersal, light-dependent growth rates, growth-dependent death rates, and light interception. The model tracked the performance of individual trees, where each tree competed for light with its immediate neighbors. Important trade-offs were evident between maximum potential growth rates and (1) dispersal, (2) light interception, and (3) survivorship

under low light. A similar approach for a species-rich tropical forest has the potential to identify life history trade-offs that facilitate the coexistence of tropical forest plants.

CHANCE

A recurrent hypothesis postulates that many tropical forest plants are ecologically equivalent ([Appendix 11.4](#); Aubréville 1938, Hubbell 1979, Hubbell and Foster 1986, Gentry 1989, Wright 1992, Federov 1966). Ecologically equivalent species might coexist for a very long time, given the large population sizes and random birth and death processes (Hubbell 1979, Hubbell and Foster 1986). Ecological equivalence might arise through common descent (Federov 1966), convergent evolution for a generalized ability to tolerate diffuse competition (Hubbell and Foster 1986), or the chance dynamics of life in the deeply shaded understory (Gentry and Emmons 1987, Wright 1992). The latter possibility is developed here.

Competitive exclusion requires that species compete and that the better competitor consistently wins. Consider competition among forest understory plants. There is an asymmetry between strata in tall forests. Large trees and lianas form the canopy and dominate understory environments. Trees and lianas intercept up to 99.5% of the photosynthetically active radiation reaching tropical forest canopies (Chazdon and Pearcy 1991), and tree and liana roots dominate the underground environment. Trees and lianas suppress understory plants, and, as a result, direct interactions among understory plants are unlikely. Understory environments may violate the two requisites for competitive exclusion.

First, competition among understory plants is unimportant. Pests maintain low understory stem densities that minimize direct competition. For example, the densities of understory plants increase dramatically after the experimental removal of mammalian herbivores (Dirzo and Miranda 1991, Osunkjoya et al. 1992, Terborgh and Wright 1994). Manipulations of understory stem densities provide direct evidence for limited competition among understory plants. The removal of all understory plants (less than 5 cm diameter at breast height [dbh]) had no effect on seedling recruitment and survival in a wet tropical forest (Marquis et al. 1986). Suppression by canopy plants limits direct competitive interactions in the deeply shaded understory.

Second, chance, not competitive ability, determines which individuals succeed in the understory. Chance is introduced by severe light limitation. Understory irradiance has two components. Dim, diffuse irradiance occurs throughout the understory, whereas direct solar irradiance occurs in sunflecks. Sunflecks contribute 32%–65% of the daily carbon gain of understory plants in closed canopy forests (Chazdon and Pearcy 1991). The occurrence of a sunfleck depends on the juxtaposition of the solar path and a canopy opening, cloud cover that diffuses solar irradiance, and wind that moves the vegetation, altering canopy openings. Most sunflecks are small in tall tropical forests (hundreds to thousands of square centimeters). Sunfleck location and intensity vary on a variety of timescales as wind, cloud cover, solar declination, and canopy openings change (Chazdon and Pearcy 1991). Sunflecks introduce chance as a primary determinant of performance in the understory.

Treefalls reinforce the importance of chance. Understory plants are temporarily released from canopy suppression when canopy trees die and open large gaps (Denslow 1987). Canopy gaps occur at random with respect to understory plants. Most importantly, canopy gaps close before competition causes mortality among previously suppressed understory plants. For example, more than 80% of the stems present 4 years after gap formation were present before gaps were formed in an Amazonian rain forest (Uhl et al. 1988). Likewise, more than 80% of tree saplings survived the opening and the closure of experimental treefall gaps in central Panama (N. Brokaw and A.P. Smith, unpublished data, 1993). Treefall gaps close before competition reduces species richness. Both sunflecks and treefalls introduce chance as an important determinant of the performance of understory plants.

To summarize, pests maintain low stem densities that prevent competition among understory plants, and chance sunflecks and treefall gaps largely determine which individuals succeed. Differences in competitive abilities are never realized among herbs and shrubs that spend their entire lives in the understory or among the seedling and saplings that form the advanced regeneration for the canopy. The absence of competition and the important role of chance in the understory contributes to species coexistence in all forest strata.

An extreme form of the chance hypothesis has been advanced by Hubbell (Hubbell 1979, Hubbell and Foster 1986). Species composition is predicted to fluctuate randomly as identical species experience random births and deaths. Species composition is, in fact, very similar for forests in similar abiotic environments, falsifying this prediction (Leigh et al. 1993, Terborgh et al. 1996). A more sophisticated version of the chance hypothesis must incorporate the ecological differences that so obviously exist among species. Chance enhances the potential for coexistence, but is not the sole explanation of population dynamics. It is clear that chance plays a large role in the deeply shaded understory. A renewed theoretical effort is required to explore the consequences for species coexistence.

ORIGINS OF TROPICAL PLANT DIVERSITY

Perhaps the most robust rule in ecology is that species richness and area increase together (Rosenzweig 1995). Terborgh (1973) ascribed high tropical species richness to the large areas with tropical climates. Terborgh noted that the area within each degree of latitude is greatest at the equator and decreases poleward, and that mean temperatures are uniformly high within 25° of the equator and then decrease poleward. As a consequence, tropical biomes cover four times more area than do subtropical, temperate, or boreal biomes (Rosenzweig 1992). Considerations of area alone suggest that species richness should be exceptionally high in the tropics.

Tropical biomes have been even more important in the past. In particular, the earth was largely tropical while the angiosperms radiated. Angiosperms appeared approximately 140 million years (Myr) ago in the early Cretaceous. The first angiosperms were tropical and required 20–30 Myr to spread beyond the tropics (Friis et al. 1987). The mean duration of angiosperm species in the fossil record exceeds 2 Myr (Niklas et al. 1983), making the last few tens of millions of years most relevant to modern angiosperm diversity. Tropical forests extended to 65° latitude in the Eocene (50 Myr ago), contracted to 15° latitude in the Oligocene (30 Myr), expanded to 35° latitude in the Miocene (20 Myr), and finally contracted to 25° latitude today (Behrensmeyer et al. 1992). The angiosperm radiation had a 20–30 Myr head start in the tropics and occurred when tropical climates covered up to 80% of all land (Eocene). The great species richness of tropical angiosperms may have ancient origins.

CONCLUSIONS

Tree and epiphyte diversity is greatest in everwet tropical forests ([Appendix 11.1](#)), and when terrestrial herbs and shrubs are included, it is probable that plant diversity is greatest in everwet tropical forests on fertile soils ([Appendix 11.2](#)). Several factors enhance plant diversity in these forests. First, temperature, moisture, and nutrients do not limit the pool of species able to survive in the most diverse tropical forests. Second, negative dependence characterizes common species, limiting competitive exclusion ([Appendix 11.3](#)). Both intra-specific competition and pest pressure may contribute to negative density dependence. In particular warm, moist conditions favor pathogens and small insects, and year-round pest pressure may reinforce negative density dependence in moist tropical forests.

High productivity may also indirectly enhance plant diversity in everwet tropical forests. Wet tropical forests are the most productive tierra firme biome and fertile soils may further enhance production (Vitousek 1984, Grubb 1986, Silver 1994). High tree turnover rates are associated with high production and year-round growth, and high frequencies of large blow-downs are associated with high rainfall (Nelson et al. 1994, Phillips et al. 1994). The most productive forests may be characterized by a mosaic of successional microhabitats on spatial scales ranging from single treefall gaps to blowdowns covering tens to thousands of hectares. This may permit coexistence through microhabitat specialization and life history trade-offs wherein inferior competitors are superior colonists and vice versa.

These possibilities are all mutually compatible, and there is ample evidence for each of the postulated mechanisms. Performance is habitat dependent (Section “Niche Differentiation”), pests do attack concentrations of conspecific plants (Section “Pest Pressure”), disturbances do kill trees (Section “Intermediate Disturbance”), and life history traits do covary (Section “Life History Trade-Offs”). What remains unclear is how these events affect species coexistence.

Future research in three areas is particularly valuable. First, are plant pests specific to particular hosts, are pest depredations density dependent, and does pest pressure vary among forest biomes? Second, do life history traits covary among the 905 tropical forest species that persist in deep shade as seedlings and saplings? And, third, does that 90% include species that require the spatial heterogeneity introduced by treefalls and other disturbances to recruit successfully? Until these questions are answered, the chance events that determine the success of understory plants and a tacit denial of the competitive exclusion principle continue to fascinate tropical ecologists.

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APPENDIX 11.1: PLANT SPECIES DENSITY INCREASES WITH RAINFALL

Plant species densities increase with rainfall in tropical forests. The increase is greatest for epiphytes, intermediate for terrestrial herbs and shrubs, and least for lianas and trees (Gentry and Dodson 1987, Gentry and Emmons 1987, Gentry 1988). Even for trees, however, species densities increase several-fold along rainfall gradients in Ghana, the Neotropics, and Southeast Asia (Whitmore 1975, Hall and Swaine 1976, 1981, Gentry 1988, Clinebell et al. 1995). The gross primary production of tropical forests also increases with rainfall (Brown and Lugo 1982, Jordan 1983, Medina and Klinge 1983). Plant species densities are greatest in the most productive tropical forests.

At least these mechanisms may contribute to the increase in plant species densities with rainfall. First, rates of tree turnover and treefall formation are higher in more productive forests (Grubb 1986, Phillips et al. 1994). Treefalls create a mosaic of forest patches recovering from past treefalls. This may increase diversity by increasing the spatial heterogeneity of forest light environments (see Section “Niche Differentiation”), by preventing competitive dominance (see Section “Intermediate Disturbance”), or by introducing spatiotemporal variation (see Section “Life History Trade-Offs”).

Pest pressure provides a second mechanism that may contribute to the increase in plant species densities with rainfall. Many microbes, fungi, and small insects are vulnerable to desiccation. Density-dependent attacks by these pests may be more severe in high-rainfall forests that lack a dry, desiccating season (see Section “Pest Pressure”).

Finally, the most productive forests occur where rainfall and soils are most favorable for plant growth. Here, the physiological requirements for moisture and mineral nutrients are

fulfilled for the greatest number of species. Allocation can be shifted from roots to photosynthetic functions permitting the greatest number of species to maintain a positive carbon balance and regenerate from the shaded understory (see Section “Chance”). Regardless of the mechanism, it is clear that the most productive tropical forests also support the greatest plant diversity.

APPENDIX 11.2: PLANT SPECIES DENSITY AND SOIL FERTILITY

The relationship between plant species density and soil fertility has variously been reported to be positive, modal, negative, or absent for tropical forests. This diversity of results has at least two causes.

First, soils and climate covary. Plant species densities increase (Appendix 11.1) and soil nutrient concentrations decrease with rainfall (Clinebell et al. 1995). Apparent negative relationships between plant species density and soil fertility may be caused by parallel variation in rainfall. The negative relationship between tree species density and soil fertility reported by Huston (1980, 1993, 1994) are suspected for this reason. Huston (1980) omitted rainfall from a multiple regression analysis even though rainfall was the single best predictor of tree species density. Huston (1993, 1994) reproduced a relationship between plant species density and the first axis of an ordination performed by Hall and Swaine (1976, 1981). Hall and Swaine (1981, p. 31) state that this axis was “closely correlated with the moisture gradient.” Huston (1993, 1994) refers to the same axis as a “composite soil fertility index.” In a recent multiple regression analysis, annual rainfall and rainfall seasonality were the most important variables explaining tree species richness; soil nutrient concentrations were negatively correlated with rainfall; and, after rainfall was included, soil attributes explained little additional variation in plant species richness. Clinebell et al. (1995) concluded that “tropical forest species richness is surprisingly independent of soil quality.”

The second problem suggests that this conclusion is premature. Only surface soils (0–10 cm depths) and shallow subsurface soils (most often 30–40 cm depths) are considered. Forest trees have roots to 12 m depths in Amazonia, and lianas have roots to at least 5 m depths in Panama (Nepstad et al. 1994; M. Tyree and S.J. Wright, personal observation, 1994). Deep roots reach decomposing rock, a rich and overlooked source of mineral nutrients. Many analyses of the relationship between tropical plant species densities and soils have been limited to the most deeply rooted life-forms: either trees more than 10 cm dbh (Holdridge et al. 1971, Hall and Swaine 1976, 1981, Huston 1980) or trees and lianas more than 2.5 cm dbh (Clinebell et al. 1995). These analyses omit a potentially large source of nutrients from deeper soils.

Shrubs and herbs have relatively shallow roots (Wright 1992), and surface and shallow subsurface soils are more relevant for shrubs and herbs than for trees and lianas. The species densities of ferns and melastomes (mostly shrubs and small treelets) increase with soil fertility in Amazonian Peru (Tuomisto and Ruokolainen 1994, Tuomisto and Poulsen 1995). More generally, the species densities of fertile understory plants increase with soil fertility throughout the Neotropics (Gentry and Emmons 1987). The number of rain forest genera also increases with soil phosphorus in Australia (Beadle 1966). Species densities increase with soil fertility when fertility is measured for the soil volume reached by roots (i.e., for ferns, herbs, and shrubs). We await comparable analyses that include nutrients available from decomposing rock in the very deep soil horizons reached by tree and liana roots.

APPENDIX 11.3: DENSITY DEPENDENCE

Negative density dependence occurs when high local densities of conspecifics impair performance. One possible mechanism, intraspecific allelopathy, is unknown for tropical forests.

Pest pressure and the competition for resource implicit to niche differentiation also mediate interspecific coexistence through negative density dependence. Negative density dependence prevents any species from becoming dominant and excluding others. The search for negative density dependence has been intense.

Only weak tests for density dependence are possible for long-lived organisms. Strong tests evaluated population fluctuations over many generations, searching for density-dependent temporal variation. Tests for long-lived organisms are limited to spatial variations, specifically to comparisons of performance among sites that differ in conspecific density. An implicit assumption is that population fluctuations are asynchronous among sites. Spatial tests fail to detect density dependence if populations vary synchronously among sites. Spatial tests are also compromised if resources vary spatially. Spatially variable resources introduce apparent positive density dependence. High resource sites support high performance and high population densities. Spatially variable resources are important in tropical forests (see Section “Niche Differentiation”). Negative density dependence must overcome spatial variation in resources and performance. Therefore, we expect evidence for negative density dependence from spatial tests to be rare.

However, this is not the case. Strong evidence for negative density dependence comes from the 50 ha forest dynamics plot on Barro Colorado Island, Panama. The performance of more than 300,000 stems greater than or equal to 1 cm dbh of 314 species was monitored in 1982, 1985, 1990, and 1995. Negative density dependence is evident at scales ranging up to 100 m for recruitment, growth, and survivorship of several of the more abundant species (Hubbell et al. 1990, Condit et al. 1994). Tests for density dependence in rarer species were usually not significant; however, trends were consistent in the direction of negative density dependence. A very local negative density dependence, reduced performance near a conspecific adult, has also been documented in many tropical forests (see Section “Pest Pressure”). Negative density dependence is a fact for the more abundant trees in tropical forests. It only remains to determine the contribution of negative density dependence to interspecific coexistence (Hubbell et al. 1990, Condit et al. 1994).

Negative density dependence has also been reported for much rarer trees (Connell et al. 1984, Wills et al. 1997). The evidence consists of negative correlations between the number of recruits per conspecific adult (R/A) and the number of conspecific adults (A) or the basal area of conspecifics (BA). These correlations are suspected because the independent variable (A) is also the denominator of the dependent variable (R/A). Note that A and BA are closely related.

Wills et al. (1997) performed Monte Carlo simulations to evaluate the significance of R/A versus BA correlations. The size (dbh) and intercensus performance of randomly chosen pairs of conspecific trees were switched while maintaining the mapped location of each tree. Performance included death versus survival for trees present in the first census and recruitment for trees that appeared only in the second census. Adults were larger than a species-specific threshold dbh. After a large number of random switches, simulated correlations between R/A and BA were calculated. This procedure was repeated 99 times for each of a wide range of quadrat sizes, and the observed correlation coefficient for each quadrat size was compared with the distribution of simulated correlations. A subtle bias compromises these simulations for analyses of recruitment.

Two facts unrelated to density dependence affect the relative values of observed and simulated correlations. First, recruits are always small. Second, recruits are never adults. Consider a quadrat for which R/A is large and BA is small. This quadrat includes a relatively large number of recruits. The net effect of the randomization is likely to switch a recruit for an adult. This decrease is small. This quadrat includes a relatively large number of recruits. The net effect of the randomization is likely to switch a recruit for an adult. This decreases R/A and increases BA because the adult gained is larger than the recruit lost. The opposite tends to

be true for quadrats for which R/A is small and BA is large. The randomization tends to move quadrats in R/A –BA space so that simulated correlations between R/A and BA are less negative than the observed correlations. This bias is unrelated to density.

This bias explains the spatial pattern of significant result reported by Wills et al. (1997). Recruitment was negatively density dependent for small quadrats but not for large quadrats. This bias identified only arises when there is a net loss or gain of recruits. Net changes are likely for small quadrats with small numbers of individuals. The randomization is less likely to cause net changes for large quadrats where larger numbers of individuals are switched back and forth. Artifact explains the spatial scale of significant results for recruitment.

A size-stratified randomization would avoid this artifact. Small recruits would only be switched with small survivors. This would eliminate the correlated change in R/A and BA that occurs whenever a small recruit and large adult are switched. Until a size-stratified randomization is performed, we must conclude that negative density dependence only affects recruitment for the most common trees in tropical forests (Hubbell et al. 1990, Condit et al. 1994).

APPENDIX 11.4: SYNTOPIC CONGENERS

As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle is generally more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera (Darwin 1859).

Interactions between syntopic congeners often select for character divergence (Grant 1986). Coexistence is then possible through niche differentiation. Hubbell and Foster (1986) proposed instead that syntopic tropical forest plants are selected to converge on a generalized ability to tolerate diffuse competition. Which outcome is more likely? A full answer requires a phylogenetic analysis because convergence and evolutionary stasis are indistinguishable unless the character state of the common ancestor is known (Harvey and Pagel 1991). Still, we can inquire whether syntopic congeners are now ecologically similar or dissimilar.

Large numbers of congeneric plants coexist in tropical forests. Gentry (1988) and Gentry et al. (1987) drew attention to this phenomenon, describing species swarms in *Piper* (Piperaceae), *Miconia* (Melastomataceae), *Psychotria* (Rubiaceae), and several herbaceous genera in southern Central America and northwestern South America. Other examples include *Eugenia* (Myrtaceae) with 45 tree species in a 50 ha plot at Pasoh, Malaysia; *Pouteria* (Sapotaceae) with 22 tree species in a single hectare in Amazonian Ecuador; and *Inga* (Mimosoideae) with 22 tree species in a 0.16 ha plot also in Amazonian Ecuador (Manokaran et al. 1992, Valencia et al. 1994, R. Foster, personal communication, 1996). Are these syntopic congeners ecologically distinct or ecologically similar?

Reproductive phenologies illustrate both possibilities. Cross-pollination and competition for pollinators and fruit dispersal agents select for divergent phenologies that minimize temporal overlap. The fruiting phenologies of Tinidadian *Miconia* (Melastomataceae) and the flowering phenologies of Malaysian *Shorea* (Dipterocarpaceae) and Costa *Heliconia* (Musaceae) are segregated in time (Snow 1965, Stiles 1977, Ashton et al. 1988). These congeners have diverged despite recent common descent. The attraction of larger numbers of pollinators or fruit dispersal agents and the satiation of pests select for coincident reproductive displays that maximize temporal overlap. Flowering phenologies overlap completely for different species of Panamanian *Costus* (Zingiberaceae) with morphologically similar flowers that attract the same pollinator species to the same microhabitats (Schemske 1981). Both divergence and convergence or stasis are evident among the reproductive phenologies of syntopic congeners. Which is more likely?

When all genera in a local flora are evaluated, a clear answer emerges. Phenologies are remarkably similar in an overwhelming proportion of genera (Wright and Calderon 1995). Strong demonstrable similarities among species motivate the hypothesis that chance population dynamics contributes to the maintenance of tropical forest plant diversity (see Section “Chance”).

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