Oecologia (2002) 130:1–14
DOI 10.1007/s004420100809

S. Joseph Wright

Plant diversity in tropical forests: a review of mechanisms of species coexistence

Received: 10 August 2000 / Accepted: 14 August 2001 / Published online: 12 October 2001

Abstract Evidence concerning mechanisms hypothesized to explain species coexistence in hyper-diverse communities is reviewed for tropical forest plants. Three hypotheses receive strong support. Niche differences are evident from non-random spatial distributions along micro-topographic gradients and from a survivorship-growth tradeoff during regeneration. Host-specific pests reduce recruitment near reproductive adults (the Janzen-Connell effect), and, negative density dependence occurs over larger spatial scales among the more abundant species and may regulate their populations. A fourth hypothesis, that suppressed understory plants rarely come into competition with one another, has not been considered before and has profound implications for species coexistence. These hypotheses are mutually compatible. Infrequent competition among suppressed understory plants, niche differences, and Janzen-Connell effects may facilitate the coexistence of the many rare plant species found in tropical forests while negative density dependence regulates the few most successful and abundant species.

Keywords Alpha diversity · Density dependence · Disturbance · Host-specific pests · Janzen-Connell hypothesis

Introduction

A central question in community ecology concerns the control of alpha diversity, or the number of species able to coexist at small spatial scales. Plant alpha diversity reaches astonishing levels in equatorial forests. For example, a single hectare of Amazonian forest can support more than 280 tree species with diameter at breast height (d.b.h.) ≥10 cm (Valencia et al. 1994; Oliveira and Mori 1999). Tree diversity is equally remarkable at slightly larger spatial scales. A 0.52-km^2 plot in Borneo and a 0.25-km^2 plot in Ecuador support 1,175 and 1,104 tree species with diameter at breast height (d.b.h.) ≥1 cm, respectively (LaFrankie 1996; R Condit, personal communication). In contrast, the 4.2×10^6 km^2 of temperate forests that cover Europe, North America and Asia support just 1,166 tree species with maximum height >7 m (Latham and Ricklefs 1993). For trees, alpha diversity in the tropics can rival hemispheric diversity in the North Temperate Zone. Other life forms augment alpha diversity in tropical forests, particularly in rain forests where trees comprise just 25% of the plant species (Gentry and Dodson 1987). Plant alpha diversity is greater in equatorial rain forests than in any other vegetation type (Gentry 1988).

Evolutionary biogeography contributes to this diversity. Angiosperms dominate tropical forests (Prance 1977). Warm, wet climates, which are now restricted to equatorial latitudes, predate the first angiosperms and characterized immense landmasses throughout the angiosperm radiation (Terborgh 1973; Morley 2000). Hyper-diverse angiosperm floras have repeatedly developed through long distance dispersal and in situ evolution within 5–10 million years after a warm, wet climate replaced a cool, dry climate (Morley 2000). Today, the most diverse tree floras are found in Borneo and in a broad band across the central and western Amazon basin (Ashton 1993; Ter Steege et al. 2000). The persistent, extensive, and benign physical environment combine to insure that the pool of tropical forest plant species is large.

Here I ask how hundreds of these species can coexist within a single hectare. Competition limits diversity when superior competitors increase in abundance until other species are excluded. More than 100 mechanisms have been proposed that delay or prevent competitive exclusion. Palmer (1994) organized this “huge mass of competing hypotheses” around six conditions required to realize competitive exclusion. I use the same six conditions to organize this review (Table 1). Each condition is violated by one or more of the principal hypotheses ad-

S.J. Wright (✉)
Smithsonian Tropical Research Institute,
Apartado 2072, Balboa, Ancón, Republic of Panama
e-mail: wrightj@tivoli.si.edu
Tel.: +507-212-8132, Fax: +507-212-8148

Table 1 The principal hypotheses advanced to explain species coexistence among tropical forest plants. Each hypothesis violates one (or more) of six conditions required to realize competitive exclusion. The hypotheses are associated with the principal condition violated. Citations are to studies that applied the hypotheses to tropical forest plants. Adapted from Palmer (1994)

The competitive exclusion principle:

Given a suite of species, interspecific competition will result in the exclusion of all but one species

Conditions of the competitive exclusion principle	Hypotheses that violate the condition
(1) Rare species are not favored demographically	Janzen-Connell hypothesis (Janzen 1970; Connell 1971) Compensatory mortality (Connell et al. 1984)
(2) Species have the opportunity to compete	Recruitment limitation (Hubbell et al. 1999); Low understory densities (this review)
(3) (a) The environment is temporally constant	Regeneration Niche or Gap dynamics (Grubb 1977; Denslow 1987)
(b) The environment has no spatial variation	Many authors (reviewed by Sollins 1998; Svenning 2001)
(4) Time has been sufficient to allow exclusion	Dynamic equilibrium (Huston 1994) and Intermediate disturbance (Connell 1978) Chance population fluctuations (Hubbell 1979)
(5) Growth is limited by one resource	Nutrient resource ratios (Ashton 1993; Tilman and Pacala 1993)
(6) There is no immigration	Mass effects (Stevens 1992)

Corollary:

The greater the degree to which these conditions are broken, the greater the number of species that can coexist

vanced to explain the coexistence of tropical forest plants (Table 1). The long generation times of most tropical forest plants have precluded experiments to evaluate these hypotheses relative to alpha diversity. This has left two approaches to study plant species coexistence in tropical forests.

The first assumes Palmer's corollary holds (see final line in Table 1) and evaluates correlations between alpha diversity and proxy variables, which are believed to reflect the degree to which a condition of the competitive exclusion principle is violated. Three examples follow. Evidence for the (1) niche differentiation and nutrient resource ratio hypotheses, (2) regeneration niche and gap dynamic hypotheses, and (3) Janzen-Connell and compensatory mortality hypotheses comes from correlations between alpha diversity and (1) soil attributes believed to reflect spatial heterogeneity (Ashton 1993; Tilman and Pacala 1993), (2) tree mortality rates believed to reflect temporal environmental variation (Phillips et al. 1994); and (3) several conditions believed to reflect pest pressure (Givnish 1999). This valuable approach has recently been reviewed elsewhere and is not considered here (Wright 1999).

The second approach to the study of plant species coexistence in tropical forests concerns the detection and strength of hypothesized mechanisms. If a mechanism cannot be demonstrated to occur, then it can be discounted. If a mechanism can be detected but its signal is weak, then its influence on plant diversity is doubtful. A large literature has demonstrated that the mechanisms underlying the niche differentiation, regeneration niche, gap dynamic, and Janzen-Connell hypotheses operate in tropical forests (reviewed by Denslow 1987; Hammond and Brown 1998; Sollins 1998). Hubbell and associates have, however, marshaled evidence that each of these mechanisms is too weak to maintain observed levels of plant alpha diversity (Hubbell 1979, 1980; Hubbell and Foster 1986, 1992; Hubbell et al. 1990, 1999; Welden et al. 1991; Condit et al. 1992, 1994). This review re-evaluates the evidence and this conclusion for conditions 1–4 and the associated hypotheses from Table 1. Conditions 5 and 6 from Table 1 are omitted because mechanisms postulated for the mass effect and nutrient resource ratio hypotheses are unexplored for tropical forests.

Several critical attributes characterize plants and forest environments. As sessile autotrophs, plants must disperse pollen and seeds, survive environmental variation and pest depredations in situ, and tolerate competition with a few near neighbors for water, mineral nutrients and light. In forests, herbivore and pathogen activity may be intense, low resource levels often limit plants, and resource levels and in particular understory light levels can vary tremendously in both time and space. These attributes of plants and forest environments underlie the hypotheses considered here.

Are rare species favored? Negative density dependence

Negative density dependence occurs when nearby conspecifics impair performance. Allelopathy, intraspecific competition, and pest facilitation may all contribute. Negative density dependence constrains locally abundant species, which opens space for otherwise less successful species and facilitates species coexistence. Three methods have been used to detect density dependence among tropical forest plants. The Janzen-Connell hypothesis has motivated comparisons of juvenile performance near and far from reproductive conspecifics. A second single-species approach has contrasted performance among plots characterized by the density of a focal species; and a multi-species approach has contrasted performance among species characterized by different density. I review each method as applied to tropical forest plants. Throughout performance refers to survival, growth, or recruitment.

The Janzen-Connell hypothesis

Janzen (1970) and Connell (1971) hypothesized that host-specific pests reduce recruitment near conspecific adults (or where conspecific seed density is greatest) thereby freeing space for other plant species. Hammond and Brown (1998) reviewed 46 studies that compared seed or seedling performance near and far from conspecific adults. Performance was lower near conspecific adults for 15 of 19 populations whose principal herbivore was an insect, but for just 2 of 27 populations whose principal herbivore was a vertebrate. Vertebrates forage over large areas, are polyphagous, and do not reduce seed and seedling performance disproportionately near conspecific adults. Insects and the few microbial pathogens studied to date do, however, act in a manner consistent with the Janzen-Connell hypothesis (Augspurger 1984; Gilbert et al. 1994; Gilbert and DeSteven 1996; Packer and Clay 2000). Do insects and pathogens reduce recruitment near conspecific adults for most species? Does this, in turn, influence alpha diversity? Community-level analyses are required to answer these questions.

There have been four community-level evaluations of the distance or density dependence postulated by Janzen and Connell. Condit et al (1992) contrasted distances to reproductive adults for conspecific versus heterospecific recruits on Barro Colorado Island (BCI), Panama. Recruits were concentrated near conspecific adults for 27 species, were indifferent to the identity of the nearest adult for 38 species, and were repelled from the vicinity of conspecific adults for 15 species. The repelled distribution extended for just one crown width for 14 of the final 15 species. Condit et al. (1992) concluded recruitment is consistent with the Janzen-Connell hypothesis for very few species and then only over very short distances. This conclusion must be qualified. Limited seed dispersal and appropriate microhabitat (as demonstrated by the presence of a conspecific adult) favor recruits near conspecific trees. Host-specific pests could reduce recruits substantially without offsetting these advantages (Hamill and Wright 1986). Condit et al. (1992) recognized this limitation of their analysis. They did not, in fact, test the hypothesis that juvenile performance declines near conspecific adults.

The three remaining community-level analyses provide evidence for distance or density dependence. Hubbell et al. (1990) contrasted saplings located under conspecific versus heterospecific adults for 11 abundant species on BCI. Nearby conspecific adults reduced growth for 9 species for small (significant for 5 species) and intermediate sized saplings (significant for 3 species) and also reduced survival significantly for the 2 most abundant species. Connell et al. (1984) contrasted plants whose nearest larger neighbor was conspecific versus heterospecific for two sites in northern Australia. Species were pooled to increase sample size and 26 analyses were performed (two sites, first and second nearest neighbors, multiple juvenile size classes; I disregard 'near' and 'far' nearest neighbors.). Near conspecific neighbors reduced growth in 17 analyses (5 significantly) and survival in 24 analyses (14 significantly). Harms et al. (2000) evaluated density dependence during the seed-to-seedling transition for 53 species from BCI. They used 200 census stations to fit recruit (*R*) and seed (*S*) density to the following function: $R=c\times S^{b}$, where c and b are fitted constants. Negative density dependence ($b<1$) was evident for every species, and the median b-value was just 0.23. These three studies provide strong community-level evidence for the distance and density dependent recruitment postulated by Janzen and Connell.

It remains to explore the consequences for alpha diversity. The theoretical development of the Janzen-Connell hypothesis has been contentious. Janzen (1970) reasoned that recruitment would fail completely near conspecific adults freeing space for other species. Hubbell (1980) showed that when recruitment failed completely within 1, 2, 3, 4, 5, and 6 crown diameters of a conspecific adult just 3, 7, 12,19, 27, and 37 species could coexist at equilibrium, respectively. Hubbell concluded that this effect was quantitatively unimportant because reduced performance occurs over relatively short distances and most tropical forests support hundreds to thousands of plant species. Becker et al. (1985) questioned Hubbell's choice of equilibrium conditions and showed that a minimum spacing rule could greatly prolong species persistence times in simulated communities. Armstrong (1989) developed an analytical model to demonstrate that a minimum spacing rule always stabilizes the coexistence of competing species. This theory has limited relevance to real forests where there is no minimum spacing rule. Recruitment does not fall to zero near conspecific adults. Rather, the large numbers of seeds falling near conspecific adults overwhelm distance and density dependent differences in per capita recruitment so that recruit density is greatest where seeds were initially most numerous (Hubbell 1980; Condit et al. 1992; Harms et al. 2000). A renewed theoretical effort is needed to relate alpha diversity to partial reduction of recruitment near conspecifics.

There has, in the meantime, been one empirical attempt to relate alpha diversity to partial reduction of recruitment near conspecifics (Harms et al. 2000). The BCI seed rain is heavily dominated by a few species while first-year seedling recruits are much more diverse. The plant directly overhead dominated the seed rain at the small spatial scale of single census stations (~ 0.5 m^2) while a few species that produced copious numbers of small seeds dominated the seed rain at the larger spatial scale of 200 census stations (50 ha). Harms et al. (2000) partitioned the increase in diversity between seed rain and seedling recruits into components due to density dependent recruitment and species-specific differences in seed-to-seedling transition probability (generally greater for species with larger seeds). Density dependence made a substantial contribution to the increase in diversity even though recruit density increased with conspecific seed density for 41 of the 53 focal species ($0<b<1$). The partial reduction of recruitment near conspecifics increased alpha diversity.

To summarize, the depredations of host-specific insects and possibly pathogens are greatest near reproductive host trees. As a consequence, juvenile performance is often impaired near conspecific adults and where conspecific seed density is greatest. This effect has almost certainly been underestimated because performance has been evaluated for short time intervals for plants of different sizes with no attempt to integrate the cumulative effect over time. Negative effects on growth and survival are particularly likely to reinforce one another over longer time intervals, and the eventual reduction in recruitment near conspecific adults may be much greater than is now appreciated. As demonstrated by Harms et al. (2000), even a partial reduction of recruitment near conspecifics can increase alpha diversity. The Janzen-Connell mechanism is likely to play an important role in the maintenance of plant diversity in tropical forests.

Analyses among plots characterized by density of a single species

The second method used to detect density dependence contrasts performance among plots characterized by different densities of single focal species. Density and performance are implicitly assumed to fluctuate asynchronously among plots and to vary over a similar range for each plot. Temporal and spatial variation may falsify both assumptions. Interannual variation in climate synchronizes seed production, tree growth, and tree mortality over large areas and may override a spatial signature of density dependence (Clark and Clark 1994; Condit et al. 1995; Wright et al. 1999). Spatially heterogeneous resources may constrain the potential range of density and performance in different plots and even introduce apparent positive density dependence, with elevated performance and population density in plots with appropriate resources. For these reasons, plot-based analyses may rarely detect negative density dependence.

Plot-based analyses have, in fact, repeatedly detected negative density dependence for abundant species [An appendix critiques reports of negative density dependence among rarer species (Wills et al. 1997; Wills and Condit 1999)]. Hubbell and Foster (1986) used 50 1-ha plots to fit the densities of juveniles (J) and adults (A) of their 48 most abundant species to the following model: $J = a_0 + a_1 A + a_2 A^2$, where a_0, a_1 and a_2 are fitted constants. Strong negative density dependence was evident for the most abundant species ($a_1 < 0$), weak negative density dependence was evident for another 20 species ($a_1 > 0$; $a_2 < 0$), and there was no evidence for density dependence for 27 species. Negative density dependence was also detected in five of six studies of single abundant species (Martinez-Ramos et al. 1988; Alvarez-Buylla 1994; Condit et al. 1994; Gilbert et al. 1994; Silva Matos et al. 1999). Schupp (1992) reported positive density dependence for an abundant small tree on BCI; however, both seedling recruitment and sapling performance were negatively density dependent in subsequent studies of the same population (Condit et al. 1994; Harms et al. 2000). Plot-based analyses frequently detect negative density dependence among the more abundant plant species in tropical forests.

Hubbell and associates reasoned that most tropical trees are too rare to be regulated by density dependence, which therefore is unlikely to promote species coexistence (Hubbell 1979; Hubbell and Foster 1986; Hubbell et al. 1990). Density-dependent population regulation is difficult to demonstrate for long-lived organisms like tropical trees. The one approach attempted has been to incorporate observed density-dependent vital rates into numerical simulations of population fluctuations. Negative density dependence regulated population density at observed levels for *Trichilia tuberculata*, the most abundant tree on BCI (Hubbell et al. 1990). Populations were, in contrast, growing rapidly at all densities for *Euterpe edulis*, *Astrocaryum mexicanum* and *Cecropia obtusifolia* (Alvarez-Buylla 1994; Alvarez-Buylla et al. 1996; Silva Matos et al. 1999). Additional studies are needed to determine whether negative density dependence regulates population size and facilitates coexistence among tropical forest plants.

Analyses among species: the community compensatory trend

Connell et al. (1984) coined the phrase community compensatory trend (CCT) to describe an inverse interspecific relationship between performance and population density. A CCT will facilitate species coexistence by protecting rare species from extinction and preventing common species from further increases at the expense of rare species. A CCT is consistent with equilibrium species composition if one aspect of performance improves with population density and offsets the CCT (C.O. Webb, personal communication). A CCT otherwise implies that species composition fluctuates through time.

There have been four attempts to detect a CCT. Growth and survival were independent of conspecific density in northern Australia (Connell et al. 1984; I discount their regressions between per capita recruitment and adult density, which took the form y/x versus x). Sapling survival increased with population size, which is the reverse of a CCT, at Pasoh Forest, Malaysia (He et al. 1997). CCTs were observed for recruitment on BCI and for sapling survival at Gunung Palung, Borneo (Welden et al 1991; Webb and Peart 1999). Density dependence may be the mechanism responsible for the two observed CCTs; however, other possibilities should be considered.

A CCT might be observed if rare species were associated with a rare microhabitat characterized by high recruitment, rapid growth, or high survival. Gap-dependent pioneers are rare in most tropical forests, and gaps favor recruitment, growth, and survival (Hubbell and Foster 1986; Denslow 1987; Brown and Whitmore 1992). The recruitment CCT observed for BCI spanned a severe El Niño drought, which increased tree mortality and numbers of tree fall gaps (Welden et al. 1991; Condit et al. 1996). An alternative explanation for this CCT might be an increase in habitat available to rare pioneers. Other analyses have indicated that rare species perform poorly on BCI (Hubbell and Foster 1986). The survival CCT observed for Gunung Palung contrasts with the opposite pattern observed for a second Dipterocarp forest (He et al. 1997; Webb and Peart 1999). This may reflect different methods. He et al. (1997) evaluated all saplings in a 50-ha plot, the vast majority was in deep shade, and rare pioneers probably survived poorly. In contrast, Webb and Peart (1999) evaluated saplings from similar numbers of plots in treefall gaps and the shaded understory. An alternative explanation for their CCT might be that pioneers tended to be rare and pioneer saplings were disproportionately represented in tree fall gaps where high light levels favored survival. Future efforts to detect a CCT should consider microhabitat associations and other possible alternative mechanisms.

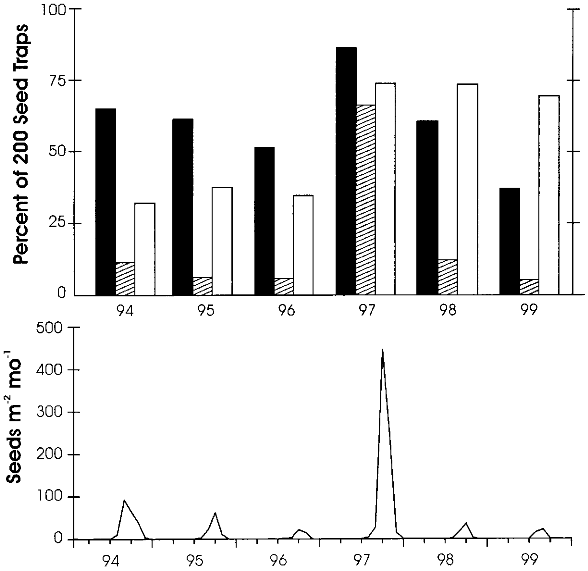

Fig. 1 Evidence that *Trichilia tuberculata* escapes dispersal limitation on Barro Colorado Island (BCI), Panama. The *lower panel* presents seed rain density (number of seeds m^{-2} $month^{-1}$) estimated from 200 randomly located, 0.5-m^2 seed traps (for methods see Wright et al. 1999). The *upper panel* presents percentages of seed traps that received at least one seed (*filled bars*) and percentages of 600 nearby 1-m^2 plots where at least one seedling recruited (*hatched bars*) or where at least one seedling was present regardless of its age (*open bars*). Seeds reached most traps in most years and particularly in the 1997 El Niño year when seed production was very heavy (Wright et al. 1999). Seedlings are shade tolerant, and the surge of seedling recruits following the 1997 El Niño persisted until 1999 and beyond (personal observation)

The opportunity for competition

Potential competitors must encounter one another to compete. Both recruitment limitation and low population densities reduce such encounters.

Recruitment limitation

Recruitment limitation occurs when species fail to reach otherwise suitable regeneration sites. Recruitment limitation may facilitate species coexistence when (1) each species is a superior competitor somewhere in the environment, (2) each species fails to reach some otherwise suitable regeneration sites, and (3) inferior competitors win those sites by default (Hurtt and Pacala 1995). Hubbell et al. (1999) addressed the second condition by identifying 1.3×10^6 seeds collected in 520 weekly censuses of 200 0.5-m^2 seed traps located on BCI. Just 3 of 314 species reached all 200 traps, and a mean of just 31 species arrived at each seed trap in 10 years. Hubbell et al. (1999) concluded that dispersal limitation and, hence, recruitment limitation was nearly universal.

This conclusion is premature. Dispersal limitation decreases as (1) each seed is dispersed more effectively, (2) each tree becomes more fecund, and/or (3) the number of reproductive trees increases (Nathan and Muller-Landau 2000). The third possibility is particularly problematical for species coexistence. If a superior competitor became sufficiently abundant, it could escape dispersal and recruitment limitation. This may describe *Trichilia tuberculata*, which comprises 13% of all canopy trees on BCI (Muller-Landau et al., in press). The modestly sized seed (140 mg dry mass) is embedded in a rich aril and is dispersed by vertebrates capable of long distance movements. In years of heavy seed set, *T. tuberculata* seeds arrived at more than 90% of the 200 seed traps and seedlings recruited into more than 66% of 600 1-m^2 plots (Fig. 1). The seedling of *T tuberculata* is among the most shade tolerant on BCI, and the recruitment pulse observed in 1997 is persistent with seedlings present in more than 66% of 1-m^2 plots from 1997 through 1999 (Fig. 1). The small 1-m^2 seedling plots contrast with the 21-m^2 canopy area of the smallest (20 cm d.b.h.) reproductive adults of *T. tuberculata* (O’Brien et al. 1995). One or more *T. tuberculata* seedlings are expected in 14 of 21 1-m^2 subplots at the spatial scale relevant to regeneration. This species has escaped recruitment limitation. More generally, the combination of high adult density, shade-tolerant seedlings, and well-dispersed seeds will minimize recruitment limitation (Muller-Landau et al. in press). To summarize, recruitment limitation has the potential to limit interactions among the many rare tropical trees; however, some other mechanism must check the abundance of species like *T. tuberculata* that are characterized by high adult density, shade-tolerant seedlings, and well-dispersed seeds.

Low population density among understory plants

Plants compete when zones of resource depletion of near neighbors overlap. Hence, low plant densities can preclude direct competition particularly for light, water, and nutrients. Canopy trees and lianas have contiguous or overlapping crowns (and probably also root systems). The situation may be very different among understory plants.

Two types of interaction limit the summed density of all understory species. The first is the competitive asymmetry between forest strata. Canopy trees and lianas dominate forest light and rooting environments. The canopy intercepts or reflects as much as 99.5% of photosynthetically active radiation, and low light levels limit all understory plants (Canham et al. 1990; Chazdon and Pearcy 1991). Trees and lianas also dominate the rooting environment. Dried fine root (≤2 mm diameter) biomass averages 372 g m^{-2} for the upper 30 cm of soil on BCI (Yavitt and Wright, in press). In contrast, the entire root systems of 48 excavated understory shrubs averaged just 34 g m^{-2} (excavation methods follow Wright et al. 1992). Canopy plants account for more than 90% of the roots in the soil volume occupied by understory shrubs on BCI. Not surprisingly, understory plants often grow more rapidly after experimental trenches sever competing roots both in the shaded understory and in tree fall gaps (Coomes and Grubb 1998, 2000; Lewis and Tanner, 2000). Root and shade competition from canopy plants suppresses understory plants.

Herbivores further reduce understory plant density. Seedling density was 230% greater where most mammalian herbivores were absent compared to a second forest with an intact mammal fauna (Dirzo and Miranda 1991). Exclusion experiments provide additional insight. Insect plus vertebrate exclusion increased the growth rate of an understory shrub by an order of magnitude in Panama (Sagers and Coley 1995). Vertebrate exclusion alone had a greater positive impact on seedling survival than did the difference in microenvironments between tree fall gaps and the shaded understory in both Panama and Australia (Fig. 2). Vertebrate exclusion also increased seedling recruitment in Panama and Peru and understory plant density in Panama and tropical Australia (Terborgh and Wright 1994; W.P. Carson and J.H. Connell, personal communication). Herbivores and competition with canopy plants both suppress understory plant density.

Do low population densities preclude competition among understory plants? The experimental removal of part of the understory could provide an answer. If competition were important, the remaining understory plants should experience competitive release. This experiment has been performed twice. Seedling germination and survival were unaffected by the removal of all plants smaller than 5 cm d.b.h. from the understory of a Costa Rican forest (Marquis et al. 1986). In the second experiment, all non-dipterocarps were removed from half of ten tree fall gaps and saplings of three focal dipterocarp species were monitored in the removal and control halves of each gap for 40 months (Brown and Whitmore 1992). Survival and height growth were similar in both halves of the nine smaller gaps (canopy openness ≤17.5%) and were consistently reduced in the *removal* half of a single large gap (30% canopy openness). Competitive release was absent after understory plants were removed.

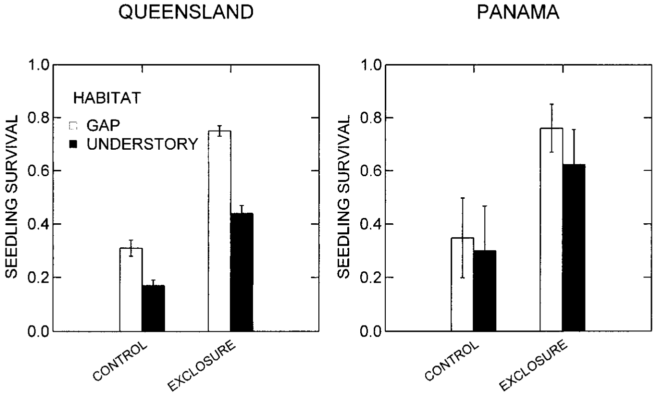

Fig. 2 Evidence that vertebrate herbivores have a greater impact on seedling survival than do microhabitat differences between the shaded understory and recent tree fall gaps for northern Australia and Panama. Experimental treatments indicated along the horizontal axis include unfenced controls open to vertebrates and fenced exclosures that excluded vertebrates. Seedling survival was greater in tree fall gaps (*open bars*) than in the shaded understory (*solid bars*), inside vertebrate exclosure than in unfenced controls, and for fenced seedlings in the deeply shaded understory than for unfenced seedlings in recent tree fall gaps. Mean survival (± 1 SE) is presented for six species and two sites for Queensland, Australia and for three species for BCI, Panama. Drawn from data presented by Howe (1990), Osunkoya et al. (1992), and Molofsky and Fisher (1993)

The implications of the possible lack of competition among understory plants for light, water and nutrients are profound. The understory is home to juveniles for canopy trees and to all life stages for smaller trees, shrubs and terrestrial herbs. The notion of competitively superior and competitively inferior species becomes moot for the smaller life forms if low density prevents competition with similar sized plants. Juveniles of canopy trees and lianas might also be shielded from direct competition with all but the canopy tree directly overhead. Every species able to tolerate the understory environment could potentially coexist.

Additional experiments will be required to explore the role of competition in the understory. Understory plants might be manipulated along environmental gradients that alter the level of suppression of understory plants. Competition among understory plants would be predicted to increase in importance as the level of suppression by herbivores and canopy plants declined. If this prediction were realized, forests with more favorable understory environments (more light, fewer herbivores), greater understory plant density, and a greater potential for competitive exclusion among understory plants would be predicted to have lower alpha diversity.

Spatial and temporal variation in the environment

Plants potentially compete for pollinators, seed dispersal agents, light, water, and mineral nutrients. Plant species may coexist by utilizing these resources in different ways. This possibility has been evaluated separately for biotic and abiotic resources.

Biotic resources

Plants serviced by different animal species avoid competition for pollination and seed dispersal. Figs, for example, never compete for pollinators because each fig species is pollinated by a different wasp species. Such species-specific mutualisms could greatly facilitate plant species coexistence. Species-specific mutualisms are, however, rare. Flower morphology and observations of flower visitors suggest that most plant species attract one or more large groups of taxonomically related pollinators, but rarely just one pollinator species (Feinsinger 1983 Bawa et al. 1985; Bawa 1990; Roubik 1992; Kress and Beach 1994; Momose et al. 1998). The species of insects that visit conspecific flowers can also vary widely among years (Horvitz and Schemske 1990). Most seed dispersal agents are equally non-specific. Fruit morphology and observations of seed dispersal suggest a small number of syndromes each involving many plant and animal species (Howe and Smallwood 1982). Most plant species share seed dispersal agents and potential pollinators with many other plant species.

Temporal segregation of flower and seed production could still minimize competition for shared pollinators and seed dispersal agents and thereby facilitate species coexistence (Snow 1965; Stiles 1977; Ashton et al. 1988; Poulin et al. 1999). The potential for temporal segregation is, however, limited. Most species bear flowers (mature fruit) for weeks to months, and more than 500 species may flower (fruit) in every calendar month in species rich tropical forests (Croat 1978). Flowers, fruits, and reproductive phenologies are also evolutionarily conservative (Lord et al. 1995; Wright and Calderon 1995). Closely related species are likely to have similar flowers and fruits, to share pollinators and seed dispersal agents, and to flower and mature fruit at similar times. Generalized pollinators and seed dispersal agents service most tropical forest plants, and temporal segregation of flower and seed production is rare. I conclude that the potential for pollinators and seed dispersal agents to promote plant species coexistence is severely limited.

Abiotic resources: spatial heterogeneity

The mobility of pollinators and seed dispersal agents precludes spatial heterogeneity at scales relevant to alpha diversity. Many abiotic resources are, in contrast, fixed in space. Micro-topography, for example, causes drainage, moisture, and possibly nutrients to vary from ridges to slopes and nearby streams often over just tens of meters. Many tropical forest plants are non-randomly distributed with respect to such micro-topographic gradients (Clark et al. 1998; 1999; Svenning 1999; earlier studies reviewed by Sollins 1998).

A detailed case study hints at the implications for alpha diversity. Drainage influences the distributions of two congeners with contrasting physiology in Guyana (Ter Steege 1994). *Mora excelsa* occurs near streams, its seeds float and survive well in water, and its seedlings transpire rapidly. *Mora gongrijpii* occurs a few meters above stream level, its seeds sink and die once submerged, and its seedlings transpire slowly and are able to extract water from relatively dry soil. Each *Mora* species occupies the end of the drainage gradient where its seed and seedling physiology provides a regeneration advantage. Together the two *Mora* species occupy the entire drainage gradient. These last two points are crucial and recur elsewhere. For example, just two species were associated with intermediate slopes in a survey of the distributions of 110 tree species along micro-topographic gradients in Costa Rica (Clark et al. 1999). Species restricted to the middle of micro-topographic gradients are rare.

This places an upper limit on the potential contribution of micro-topography to alpha diversity. If equal numbers of species were restricted to each end of a micro-topographic gradient and no species were widely distributed, then micro-topography would make a two-fold contribution to alpha diversity. The actual contribution will be lower because many species are widely distributed across micro-topographic gradients (Sollins 1998). Spatial variation alone is unlikely to explain the high levels of plant alpha diversity observed in tropical forests unless important sources of spatial heterogeneity have gone undetected.

Abiotic resources: spatiotemporal variation

Theory suggests that indefinite numbers of sessile species may coexist when resources vary through space at any instant in time and also through time at any point in space (Comins and Noble 1985; Tilman 1994). Such spatiotemporal variation characterizes understory environments, particularly light levels and possibly rooting environments. Tree death and replacement is the greatest source of variation, and expected resource distributions are identical for all locations given a sufficiently long time period (many cycles of tree death and replacement).

This spatiotemporal variation underlies the regeneration niche and gap dynamic hypotheses (Grubb 1977; Ricklefs 1977; Denslow 1980; Orians 1982). The death of a branch, a tree or several neighboring trees opens a gap. This alters light levels, rooting environments, litter depth and/or surface soils. Each new gap includes a range of microhabitats from its center to the adjacent understory, and larger gaps include more extreme conditions in their more open centers. Early in regeneration species segregate spatially in and around gaps according to their requirements for establishment and onward growth. Nonetheless, species with very different regeneration requirements are often near neighbors as adults for two reasons.

First, environmental gradients change over short distances within gaps. Second, a patchwork develops through time as new gaps are superimposed on older gaps. Established plants that regenerated in one microhabitat in an earlier gap are often located near a very different microhabitat when a new gap forms. Species with different regeneration requirements coexist through spatial segregation during regeneration, yet end up as near neighbors as adults. As a consequence, alpha diversity is high.

Recent criticisms of the gap dynamic hypothesis focus on spatial segregation during regeneration. The role of gap dynamics is unexplored for the overwhelming majority of tropical tree species, which are shade tolerant as juveniles (Brown and Jennings 1998). More than 80% of the shade-tolerant saplings present before gap formation survive after gap formation (Uhl et al. 1988; Fraver et al. 1998). The size advantage of survivors often offsets the high growth rates achieved by light-demanding pioneers that germinate in gaps (Brown and Whitmore 1992; Grubb 1996). As a consequence, both alpha diversity and species composition are largely independent of gap size and the history of gap forming events (Lieberman et al. 1995; Hubbell et al. 1999). The spatial heterogeneity introduced by gaps does not create predictable regeneration niches in space for most tropical plant species.

Most trees also regenerate too slowly to germinate and reach the canopy in a single gap cycle. Temperate tree saplings, for example, show repeated cycles of large and small annual growth rings (Wu et al. 1999). These saplings survived and grew slowly beneath a closed canopy, survived a gap-forming event and grew more rapidly in the gap, and then repeated this cycle many times. Clearly, spatial heterogeneity within any single gap can only make a limited contribution to the successful regeneration of such species. A longer temporal scale that integrates survival and growth in deep shade and in gaps is required to understand the regeneration of slow-growing, shade-tolerant trees.

This temporal scale is addressed by studies that demonstrate a tradeoff between potential growth rates in gaps and survivorship in deep shade. For example, *Shorea johorensis* and *Hopea nervosa* grew to mean heights of 10 m and 4 m in large gaps and had survivorship of 35% and 60% in the shaded understory, respectively, over 77 months at Danum Valley, Sabah (Whitmore and Brown 1996). Among three relatively light-demanding pioneers on BCI, *Trema micrantha* grew most rapidly but only survived in the largest gaps, *Cecropia insignis* was intermediate on both counts, and *Miconia argentea* grew most slowly and survived in the smallest gaps (Brokaw 1987). Similar tradeoffs have been documented in multi-species comparisons for BCI trees. Growth rates measured with ample resources in the growing house were inversely related to survivorship measured for wildings in the shaded understory for 18 species (Kitajima 1994). Finally, sapling growth rates measured in gaps were inversely related to sapling survival measured beneath closed canopy forest (Fig. 3, Hubbell and Foster 1992).

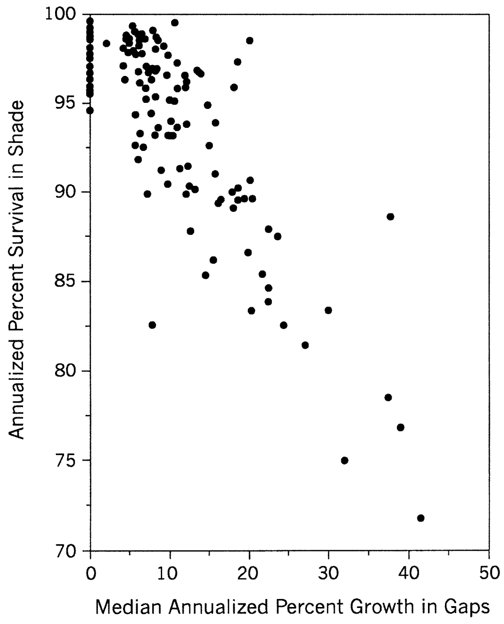

Fig. 3 The tradeoff between survivorship and growth for trees from BCI, Panama. The annual survival rate (*vertical axis*) is for saplings in the shaded understory. The annual growth rate (*horizontal axis*) is for saplings in tree fall gaps. Sapling d.b.h. was initially between 1 cm and 4 cm. Many slowly growing species have median growth rates of zero because d.b.h. was measured to the nearest 5 mm and slow growth was undetectable. Drawn from data in Welden et al. (1991) following Hubbell and Foster (1992)

The tradeoff in Fig. 3 defines combinations of traits that permit species to coexist. An inferior species whose growth and survivorship fell below the relationship would be excluded, while a super species whose growth and survivorship fell above the relationship would exclude other species. Super species are presumably impossible because the tradeoff reflects allocation of a fixed total amount of resource to functions that maximize growth (leaves, stem extension, roots) or survivorship (storage, defenses against herbivores) (Kitajima 1994). The critical role for herbivore defenses is illustrated by the reduction in seedling survivorship caused by vertebrate herbivores, which is greater than the reduction observed between gaps and shaded understory (Fig. 2). The tradeoff in Fig. 3 also suggests a mechanism for coexistence given strict spatiotemporal variation. Conservative species (slow growth, high survival) regenerate where resource availability is low over time, and aggressive species (rapid growth, low survival) regenerate where resource availability is higher over time. This tradeoff facilitated species coexistence in the SORTIE model of temperate forest dynamics (Pacala et al. 1996).

Has there been sufficient time for competitive exclusion to occur?

The temporal dynamics of competitive exclusion has become intertwined with the possible coexistence of ecologically equivalent species in the tropical forest literature. Tropical forests may harbor large numbers of ecologically equivalent plant species (Aubréville 1938; Federov 1966; Van Steenis 1969; Hubbell and Foster 1986). Ecological equivalence may arise through common descent (Federov 1966; Van Steenis 1969) or through convergent evolution for a generalized ability to tolerate diffuse competition (Hubbell and Foster 1986). In either case, ecologically equivalent species with non-overlapping distributions would enhance diversity at large spatial scales (Federov 1966; Van Steenis 1969). Ecologically equivalent species will not, however, enhance local alpha diversity unless their prolonged coexistence is possible.

Slow population dynamics may permit ecologically equivalent species to coexist. Huston (1994) considered relative rates of population growth and of disturbances that reduce population size. Each species persists where the rate of disturbance permits population recovery but prevents competitive exclusion between disturbances. The proposed balance between population dynamics and disturbance has yet to be evaluated for tropical forest and seems unlikely for three reasons. First, rapid population dynamics characterize many tropical forest plants with population density fluctuations frequently exceeding 5% per annum (Alvarez-Buylla et al. 1996; Condit et al. 1996, 1999; Silva Matos et al. 1999). Second, few disturbances reset population sizes (reviewed by Whitmore and Burslem 1998). Anthropogenic disturbance can be discounted because tropical paleofloras that predate man were as diverse as modern floras (Burnham and Graham 1999; Morley 2000). Extreme windstorms can be discounted because the advanced regeneration survives and species composition is quickly re-established (Burslem et al., 2000). The final reason to discount the Huston hypothesis is that tree alpha diversity is often greatest where tree population dynamics are most rapid and the two types of disturbance that do reset population sizes (fire and climate change) are least likely. In the western Amazon for example, tree alpha diversity is greatest (Gentry 1988), tree population dynamics are most rapid (Phillips et al. 1994), and fire and climatic drying are least likely where annual rainfall now exceeds 4,000 mm. These inconsistent data contrast with an impressive array of consistent data marshaled by Huston (1994). A direct test of the dynamic equilibrium hypothesis is needed.

Chance population dynamics may permit ecologically equivalent species to coexist even in the absence of disturbances. Hubbell (1979, 1997) developed the community drift model to demonstrate that identical species can coexist indefinitely when births and deaths occur by chance. The community drift model is considered to be the single plausible explanation for coexistence without niche differentiation (Chesson and Huntly 1997).

Recent criticism of the community drift model has focused on the assumption that all species are identical. In the community drift model, each individual has the same probability of death, each survivor has the same probability of successful reproduction, and individuals are arbitrarily divided among species. Zhang and Lin (1997) and Yu et al. (1998) relaxed the assumptions of identical probabilities of reproduction and survival, respectively. Expected times to extinction declined by two orders of magnitude when species-specific probabilities differed by just one or two percent in both cases. Since probabilities of reproduction and survival differ by at least 2% among real species, Zhang and Lin (1997) and Yu et al. (1998) concluded that the community drift model was unable to explain prolonged coexistence.

In real forests, a mixture of chance and species-specific events influence recruitment and survival. Falling debris, lightning strikes and wind throws introduce chance. For example, falling debris killed 33% of the liana saplings that died in 2 years on BCI and buried 19% of artificial seedlings in 1 year at the La Selva Biological Station (Aide 1987; Clark and Clark 1989). Demographic events only occurred with species-specific probabilities in the models of Zhang and Lin (1997) and Yu et al. (1998). How would coexistence times change if instead some portion of the births and deaths occurred by chance and the remainder occurred according to species-specific probabilities?

I used the community drift model to answer this question with demographic events partitioned among chance and species-specific causes. Hubbell (1979) simulated a community of K individuals initially divided into equally abundant species and selected D individuals (without replacement) to die and D individuals from among the survivors (with replacement) to reproduce completing one model iteration. To introduce species-specific mortality, I first determined the species of a randomly selected individual, then compared its species-specific probability of dying to a random uniform number, and repeated the process until D deaths were recorded (without replacement). An analogous procedure (but with replacement) was used to introduce species-specific reproduction. The proportion of demographic events attributed to chance versus species-specific causes was then varied, and each set of conditions was simulated 100 times to estimate the mean number of model iterations until half of the species initially present were lost.

Coexistence times decayed rapidly as the proportion of demographic events attributed to species-specific causes increased from zero to 10% or 20% of all events (Fig. 4). The diversity reducing power of a few species-specific demographic events was unexpected. In retrospect, demographic events controlled by species-specific probabilities recur, and, even when the proportion of such events is small, their directional effect accumulates over model iterations and disadvantaged species are rapidly lost. Figure 4 was created using probabilities of death observed for BCI trees (taken from Condit et al. 1995). Additional simulations varied the variance of species-specific probabilities of birth and death and demonstrated a strict equivalence between this variance and the proportion of demographic events occurring by chance (not shown). Chance births and deaths can do very little to enhance transitory species coexistence unless chance

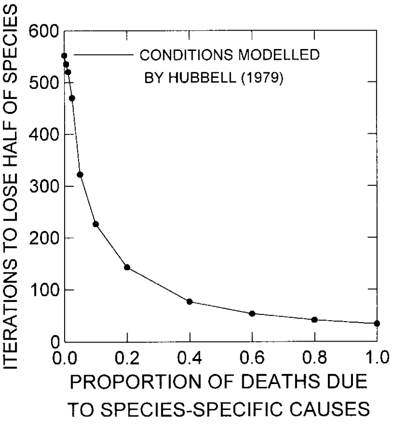

Fig. 4 The transitory maintenance of community diversity by chance (*vertical axis*) decays rapidly as the proportion of deaths determined by chance declines and the proportion determined by species-specific causes increases (*horizontal axis*). Hubbell (1979) simulated the indicated conditions. In contrast, Yu et al. (1998) simulated conditions similar to those at the opposite extreme along the horizontal axis. I used annual probabilities of mortality observed for different tree species on BCI (Condit et al. 1995) for species-specific deaths and equal probabilities for every individual regardless of species for chance deaths and for all births. Following Hubbell (1979), the simulated community included 1,600 trees initially divided among 40 equally abundant species with 160 tree deaths per model iteration

accounts for a very large proportion (80% or more) of all demographic events or interspecific differences are artificially small. Real differences among species quickly overwhelm chance demographics and diversity declines.

Synthesis and future directions

There is ample evidence among tropical forest plants for (1) niche differences associated with micro-topography, (2) niche differences associated with a trade-off between survivorship and growth, (3) the reduction of recruitment near fruiting conspecifics by host-specific pests (the Janzen-Connell effect), and (4) negative density dependence among the more abundant species at larger spatial scales. These mechanisms of species coexistence are mutually compatible. Niche segregation and Janzen-Connell effects could facilitate the coexistence of the many rare species found in tropical forests while negative density dependence checked populations of the most successful and abundant species.

Janzen-Connell effects may be much more important than is now generally realized. The full extent of the reduction of recruitment near fruiting conspecifics has been systematically underestimated by short-term studies focused on the very earliest stages of regeneration. With one exception, distance dependence has been evaluated for initial seedling establishment, first-year seedling performance, or the onward growth of small seedlings of unknown age (reviewed by Hammond and Brown 1998). The one exceptional study documented reductions in performance for saplings as large as 8 cm d.b.h. when located near larger conspecific adults (Hubbell et al. 1990). Distance dependent reductions in performance must accumulate as juveniles grow. Future studies that integrate distance dependence from seed to first reproduction are required to appreciate the real strength of Janzen-Connell effects.

There may also be an interesting synergism between recruitment limitation and the life history niches described in “Abiotic resources: spatio-temporal variation” above. Many tree species pass through several cycles of gap formation and closure before reaching the canopy. Their saplings experience a wide range of light and rooting environments as gaps form and close. No single sapling is the best possible competitor in all environments. Established saplings enjoy a size advantage, however, and may resist displacement by a superior competitor particularly when the environmental conditions that favor the superior competitor change relatively rapidly (i.e., as gaps close). Inferior competitors may routinely hold regeneration sites, making recruitment limitation an ongoing process (Brown et al. 1999). The implications for species coexistence are unexplored.

We are, finally, left with intriguing possibilities. Field measurements only demonstrate that niche differences, Janzen-Connell effects, and negative density dependence occur. Implications for species coexistence and plant diversity remain conjectural. Large size, low population density, and long generation times may well preclude experimental evaluation of mechanisms of plant species coexistence in tropical forests. A promising alternative uses field measurements to parameterize multi-species models, which are then used to determine which field attributes facilitate species coexistence (e.g., Pacala et al. 1996). The Center for Tropical Forest Science coordinates a network of 16 forest plots from 15 to 52 ha in area where all trees and shrubs larger than 1 cm d.b.h. are enumerated at 5-year intervals (http://www.ctfs.si.edu). These enumerations will soon make it possible to parameterize species rich models to evaluate how plant diversity is affected by negative density dependence, Janzen-Connell effects, and niche differences associated with the trade-off between survivorship and growth.

Acknowledgements I thank Allen Herre, Will Edwards, and two anonymous reviewers for comments. The manuscript was rewritten during a sabbatical at the Rainforest CRC, James Cook University, Cairns, Australia. The Environmental Sciences Program of the Smithsonian Institution funded Fig. 1.

Appendix 1

Critique of Wills et al. (1997) and Wills and Condit (1999)

Wills and associates used a Monte Carlo simulation to evaluate density dependence for two 50-ha plots where all trees and shrubs larger than 1 cm d.b.h. were censused twice. They found evidence for negative density dependent recruitment for most species. In contrast, Condit et al. (1992) concluded that recruits were spatially aggregated near conspecific adults for one of the same 50-ha plots ("The Janzen-Connell hypothesis" above). To resolve this discrepancy, I describe the Monte Carlo simulations then offer an alternative explanation for the result.

The Monte Carlo simulation held tree locations constant and swapped d.b.h. and status (recruited, survived, or died) for two censuses for large numbers of randomly selected pairs of conspecifics. Let N equal the number of conspecifics observed in a particular subplot in the two censuses. Then $N=R+S+D$, where R recruits first appeared in the second census, S survivors were present in both censuses, and D individuals died between censuses. The Monte Carlo simulations maintained N but allowed R, S, and D to vary. The final response variables were correlation coefficients. Each 50-ha plot was divided into contiguous subplots and correlation coefficients were calculated among subplots for pairs of metrics derived from observed or simulated R, S, D, and d.b.h.. The choice of correlation coefficients is critical. Correlation coefficients vary from –1 to 1 and squared correlation coefficients (or coefficients of determination) vary with the proportion of variation in one variable explained by variation in the second variable (Sokal and Rohlf 1995, p 564).

Consider the expected values of the simulated correlation coefficients. Wills et al. (1997) simulated correlation coefficients between per capita recruitment (R/A) and conspecific basal area (BA) for 84 species from BCI. Adults (A) were larger than a species-specific d.b.h. in the first census. Subplots without an adult were excluded to insure that per capita recruitment was defined. The expected value of simulated correlation coefficients is zero because the expected value for each simulated R/A is $\Sigma R/\Sigma A$, where sums are over all subplots. Wills and Condit (1999) simulated correlation coefficients between R and $S+D$ (or BA) for 100 species from BCI and 100 species from Pasoh, Malaysia. The expected simulated slope of the relationship between R and $S+D$ equals $\Sigma R \div \Sigma(S+D)$ because expected simulated values of R equal $N\times(\Sigma R \div \Sigma N)$ and expected simulated values of $S+D$ equal $N\times[\Sigma(S+D)\div\Sigma N]$, where sums are again over all subplots. Expected simulated correlation coefficients are positive because expected simulated slopes are positive. Similar logic applies to the relationship between R and BA. Evidence for negative density dependence occurred when observed correlation coefficients were smaller than 2.5% of the simulated correlation coefficients.

Now consider how biological phenomena affect observed correlation coefficients. Any phenomenon that concentrated recruits where $S+D$ or BA was low will reduce the slope of relationships between R/A and BA or between R and $S+D$ (or BA). If the slope becomes negative, the correlation coefficient also becomes negative. In addition, any phenomenon that tended to aggregate recruitment independently of $S+D$ or BA would also reduce observed correlation coefficients. Negative density dependence would concentrate recruits where $S+D$ and BA were low. Unfortunately, recruitment in treefall gaps or low canopy sites, where $S+D$ and BA are always small, would also have this effect. Recruits were significantly aggregated in low canopy sites for 70 of 155 BCI tree species (Welden et al. 1991). A number of additional phenomena cause spatial aggregation of recruitment. These phenomena include spatial heterogeneity in resource availability, localized seed dispersal, and aggregated mortality due to wind, lightning, or pest outbreaks (Hamill and Wright 1986). Given that Condit et al. (1992) demonstrated that recruits were concentrated near conspecific adults for many BCI species, it is probable that the analyses of Wills and associates detected nearly ubiquitous spatial aggregation of recruitment rather than negative density dependent recruitment.

References

Aide TM (1987) Limbfalls: a major cause of sapling mortality for tropical forest plants. Biotropica 19:284–285

Alvarez-Buylla ER (1994) Density dependence and patch dynamics in tropical rain forests: matrix models and applications to a tree species. Am Nat 143:155–191

Alvarez-Buylla ER, García-Barrios R, Lara-Moreno C, Martínez-Ramos M (1996) Demographic and genetic models in conservation biology: applications and perspectives for tropical rain forest tree species. Annu Rev Ecol Syst 27:387–421

Armstrong RA (1989) Competition, seed predation, and species coexistence. J Theor Biol 141:191–195

Ashton PS (1993) Species richness in plant communities. In Fiedler PL, Jain SK (eds) Conservation biology. Chapman and Hall, New York, pp 4–22

Ashton PS, Givnish TJ, Appanah S (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am Nat 132:44–66

Aubréville A (1938) La foret de la Cote d'Ivoire. Bull Com Afr Occie Franc 15:205–261

Augspurger CK (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. Ecology 65:1705–1712

Bawa KS (1990) Plant-pollinator interactions in tropical rain forests. Annu Rev Ecol Syst 21:399–422

Bawa KS, Bullock SH, Perry DR, Coville RE, Grayum MH (1985) Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. Am J Bot 72:346–356

Becker P, Lee LW, Rothman ED, Hamilton WD (1985) Seed predation and the coexistence of tree species: Hubbell's models revisited. Oikos 44:382–390

Brokaw N (1987) Gap-phase regeneration of three pioneer tree species in a tropical forest. J Ecol 75:9–19

Brown ND, Jennings S (1998) Gap-size niche differentiation by tropical rainforest trees: a testable hypothesis or a broken-down bandwagon. In: Newbery DM, Prins HHT, Brown ND (eds) Dynamics of tropical communities. Blackwell, Oxford, pp 79–94

Brown ND, Whitmore TC (1992) Do dipterocarp seedlings really partition tropical rain forest gaps? Philos Trans R Soc Lond B 335:369–378

Brown ND, Press M, Bebber D (1999) Growth and survivorship of dipterocarp seedlings: differences in shade persistence create a special case of dispersal limitation. Philos Trans R Soc Lond B 354:1847–1855

Burnham RJ, Graham A (1999) The history of neotropical vegetation: new developments and status. Ann Missouri Bot Gard 86:546–589

Burslem DFRP, Whitmore TC, Brown GC (2000) Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. J Ecol 88:1063–1078

Canham CD, Denslow JS, Platt WJ, Runkle JR, Spies TA, White PS (1990) Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can J For Res 20:620–631

Chazdon RL, Pearcy RW (1991) The importance of sunflecks for forest understory plants. BioScience 41:760–766

Chesson P, Huntly N (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am Nat 150:519–553

Clark DA, Clark DB (1994) Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rainforest. J Ecol 82:865–872

Clark DB, Clark DA (1989) The role of physical damage in the seedling mortality regime of a neotropical rain forest. Oikos 55:225–230

Clark DB, Clark DA, Read JM (1998) Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. J Ecol 86:101–112

Clark DB, Palmer MW, Clark DA (1999) Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology 80:2662–2675

Comins HN, Noble IR (1985) Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. Am Nat 126:706–723

Condit R, Hubbell SP, Foster RB (1992) Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. Am Nat 140:261–286

Condit R, Hubbell SP, Foster RB (1994) Density dependence in two understory tree species in a neotropical forest. Ecology 75:671–680

Condit R, Hubbell SP, Foster RB (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. Ecol Monogr 65:419–439

Condit R, Hubbell SP, Foster RB (1996) Changes in tree species abundance in a neotropical forest: impact of climate change. J Trop Ecol 12:231–256

Condit R, Ashton PS, Manokaran N, LaFrankie JV, Hubbell SP, Foster RB (1999) Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. Philos Trans R Soc Lond B 354:1739–1748.

Coomes DA, Grubb PJ (1998) Responses of juvenile trees to above- and belowground competition in nutrient-starved Amazonian rainforest. Ecology 79:768–782

Coomes DA, Grubb PJ (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol Monogr 70:171–207

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pp 298–313

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1309

Connell JH, Tracey JG, Webb LJ (1984) Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. Ecol Monogr 54:141–164

Croat TB (1978) Flora of Barro Colorado Island. Stanford University Press, Stanford, Calif. USA

Denslow JS (1980) Gap partitioning among tropical rainforest trees. Biotropica [Suppl] 12:47–55

Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annu Rev Ecol Syst 18:431–451

Dirzo R, Miranda A (1991) Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. In: Price PW, Lewinsohn PW, Fernandes GW, Benson WW (eds) Plant-animal interactions: evolutionary ecology in tropical and temperate regions. Wiley, New York, pp 273–287

Federov AA (1966) The structure of the tropical rain forest and speciation in the humid tropics. J Ecol 54:1–11

Feinsinger P (1983) Coevolution and pollination. In: Futuyma DJ, Slatkin M (eds) Coevolution. Sinauer, Sunderland, Mass. pp 282–310

Fraver S, Brokaw NVL, Smith AP (1998) Delimiting the gap phase in the growth cycle of a Panamanian forest. J Trop Ecol 14:673–681

Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann Mo Bot Gard 75:1–34

Gentry AH, Dodson C (1987) Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19:149–156

Gilbert GS, DeSteven D (1996) A canker disease of seedlings and saplings of *Tetragastris panamensis* (Burseraceae) caused by *Botryosphaeria dothidea* in a lowland tropical forest. Plant Dis 80:684–687

Gilbert GS, Hubbell SP, Foster RB (1994) Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. Oecologia 98:100–108

Givnish TJ (1999) On the causes of gradients in tropical tree diversity. J Ecol 87:193–210

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107–145

Grubb PJ (1996) Rainforest dynamics: the need for new paradigms. In: Edwards DS (ed) Tropical rainforest research – current issues. Kluwer, Dordrecht, pp 215–233

Hamill DN, Wright SJ (1986) Testing the dispersion of juveniles relative to adults: a new analytic method. Ecology 67:952–957

Hammond DS, Brown VK (1998) Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. In: Newbery DM, Prins HHT, Brown ND (eds) Dynamics of tropical communities. Blackwell, Oxford, pp 51–78

Harms KE, Wright SJ, Calderón O, Hernández A, Herre EA (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493–495

He F, Legendre P, LaFrankie JV (1997) Distribution patterns of tree species in a Malaysian tropical rain forest. J Veg Sci 8:105–114

Horvitz CC, Schemske DW (1990) Spatio-temporal variation in insect mutualists of a neotropical herb. Ecology 71:1085–1097

Howe HF (1990) Survival and growth of juvenile *Virola surinamensis* in Panama: effects of herbivory and canopy closure. J Trop Ecol 6:259–280

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annu Rev Ecol Syst 13:201–228

Hubbell SP (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203:1299–1309

Hubbell SP (1980) Seed predation and the coexistence of tree species in tropical forests. Oikos 35:214–229

Hubbell SP (1997) A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral Reefs 16:S9-S21

Hubbell SP, Foster RB (1986) Biology, chance, and history and the structure of tropical rain forest tree communities. In: Diamond J, Case TJ (eds) Community ecology. Harper and Row, New York, pp 314–329

Hubbell SP, Foster RB (1992) Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. Oikos 63:48–61

Hubbell SP, Condit R, Foster RB (1990) Presence and absence of density dependence in a neotropical tree community. Philos Trans R Soc Lond B 330:269–281

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Weschler B, Wright SJ, Loo de Lao S (1999) Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554–557

Hurtt GC, Pacala SW (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. J Theor Biol 176:1–12

Huston MA (1994) Biological diversity. Cambridge University Press, Cambridge

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528

Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98:419–428

Kress WJ, Beach JH (1994) Flowering plant reproductive systems. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (eds) La Selva, ecology and natural history of a tropical rain forest. University of Chicago Press, Chicago, Ill. pp 161–182

LaFrankie J (1996) Initial findings from Lambir: trees, soils and community dynamics. Cent Trop For Sci 1995:5

Latham RE, Ricklefs, RE (1993) Continental comparisons of temperate-zone tree species diversity. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities. University of Chicago Press, Chicago, pp 294–314

Lewis SL, Tanner EVJ (2000) Effects of aboveground and belowground competition on growth and survival of rain forest tree seedlings. Ecology 81:2525–2538

Lieberman M, Lieberman D, Peralta R, Hartshorn GS (1995) Canopy closure and the distribution of tropical forest trees at La Selva, Costa Rica. J Trop Ecol 11:161–177

Lord J, Westoby M, Leishman M (1995) Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. Am Nat 146:349–364

Marquis RJ, Young HJ, Braker HE (1986) The influence of understory vegetation cover on germination and seeding establishment in a tropical lowland wet forest. Biotropica 18:273–278

Martínez-Ramos M, Sarukhán JK, Piñero DD (1988) The demography of tropical trees in the context of forest gap dynamics: the case of *Astrocaryum mexicanum* at Los Tuxtlas tropical rain forest. In: Davy DJ, Hutchings MJ, Watkinson AR (eds) Plant population ecology. Blackwell, Oxford, pp 293–313

Molofsky J, Fisher BL (1993) Habitat and predation effects on seedling survival and growth in shade-tolerant tropical trees. Ecology 74:261–265

Momose K, Yumoto T, Nagamitsu T, Kato M, Nagamasu H, Sakai S, Harrison RD, Itioka T, Hamid AA, Inoue T (1998) Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. Am J Bot 85:1477–1501

Morley RJ (2000) Origin and evolution of tropical rainforests. Wiley, New York

Muller-Landau M, Wright SJ, Calderon O, Hubbell SP, Foster RB (in press) Assessing recruitment limitation: concepts, methods, and case studies from a tropical forest. In: Levey DJ, Silva WR, Galetti M (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, Oxford

Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol Evol 15:278–285

O'Brien ST, Hubbell SP, Spiro P, Condit R, Foster RB (1995) Diameter, height, crown, and age relationships in eight Neotropical tree species. Ecology 76:1926–1939

Oliveira AA de, Mori SA (1999) A central Amazonian terra firme forest. I. High tree species richness on poor soils. Biodivers Conserv 8:1219–1244

Orians GH (1982) The influence of tree-falls in tropical forests in tree species richness. Trop Ecol 23:255–279

Osunkoya OO, Ash JE, Hopkins MS, Graham AW (1992) Factors affecting survival of tree seedlings in North Queensland rainforests. Oecologia 91:569–578

Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol Monogr 66:1–43

Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404:278–281

Palmer MW (1994) Variation in species richness: towards a unification of hypotheses. Folia Geobot Phytotaxon 29:511–530

Phillips OL, Hall P, Gentry AH, Sawyer SA, Váquez R (1994) Dynamics and species richness of tropical rain forests. Proc Natl Acad Sci USA 91:2905–2809

Poulin B, Wright SJ, Lefebvre G, Calderón O (1999) Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. J Trop Ecol 15:213–227

Prance GT (1977) Floristic inventory of the tropics: where do we stand? Ann Mo Bot Gard 64:659–684

Ricklefs RE (1977) Environmental heterogeneity and plant species diversity: a hypothesis. Am Nat 111:376–381

Roubik DW (1992) Loose niches in tropical communities: why are there so few bees and so many trees? In: Hunter MD, Ohgushi T, Price PW (eds) Effects of resource distribution on animal-plant interactions. Academic Press, San Diego, pp 327–354

Schupp EW (1992) The Janzen-Connell model for tropical tree diversity: population implications and the importance of spatial scale. Am Nat 140:526–530

Sagers CL, Coley PD (1995) Benefits and costs of defense in a neotropical shrub. Ecology 76:1835–1843

Silva Matos DM, Freckleton RP, Watkinson AR (1999) The role of density dependence in the population dynamics of a tropical palm. Ecology 80:2635–2650

Snow DW (1965) A possible selective factor in the evolution of fruiting seasons in tropical forest. Oikos 15:274–281

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Sollins P (1998) Factors influencing species composition in tropical lowland rain forest: does soil matter? Ecology 79:23–30

Stevens GC (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. Am Nat 140:893–911

Stiles FG (1977) Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. Science 198:1177–1178

Svenning J-C (1999) Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. J Ecol 87:55–65

Svenning J-C (2001) On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). Bot Rev 67:1–53

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

Terborgh J, Wright SJ (1994) Effects of mammalian herbivores on plant recruitment in two neotropical forests. Ecology 75:1829–1833

Ter Steege H (1994) Flooding and drought tolerance of two Mora species segregated along a soil hydrological gradient in the tropical rain forest of Guyana. Oecologia 100:356–367

Ter Steege H, Sabatier D, Castellanos H, Van Andel T, Duivenvoorden J, Oliveira AA de, EK R, Lilwah R, Maas P, Mori S (2000) An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. J Trop Ecol 16:801–828

Tilman D (1994) Competition and biodiversity in spatially structured habitats. Ecology 75:2–16

Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities. University of Chicago Press, Chicago, pp 13–25

Uhl C, Clark K, Dezzeo N, Maquirino P (1988) Vegetation dynamics in Amazonian treefall gaps. Ecology 69:751–763

Valencia R, Balslev H, Paz y Miño G (1994) High tree alpha-diversity in Amazonian Ecuador. Biodivers Conserv 3:21–28

Van Steenis CGGJ (1969) Plant speciation in Malesia, with special reference to the theory of non-adaptive saltatory evolution. Biol J Linn Soc 1:97–133

Webb CO, Peart DR (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. Ecology 80: 2006–2017

Welden CW, Hewett SW, Hubbell SP, Foster RB (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. Ecology 72:35–50

Whitmore TC, Brown ND (1996) Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. Philos Trans R Soc Lond B 351:1195–1203

Whitmore TC, Burslem DFRP (1998) Major disturbances in tropical rain forests. In: Newbery DM, Prins HHT, Brown ND (eds) Dynamics of tropical communities. Blackwell, Oxford, pp 549–565

Wills C, Condit R (1999) Similar non-random processes maintain diversity in two tropical rainforests. Proc R Soc Lond B 266: 1445–1452

Wills C, Condit R, Foster RB, Hubbell SP (1997) Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. Proc Natl Acad Sci USA 94: 1252–1257

Wright SJ (1999) Plant diversity in tropical forests. In: Pugnaire FI, Valladares F (eds) Handbook of functional plant ecology. Dekker, New York, pp 449–472

Wright SJ, Calderón O (1995) Phylogenetic constraints on tropical flowering phenologies. J Ecol 83:937–948

Wright SJ, Machado JL, Mulkey S, Smith AP (1992) Drought acclimation among tropical forest shrubs (*Psychotria*, Rubiaceae). Oecologia 89:457–463

Wright SJ, Carrasco C, Calderón O, Paton S (1999) The El Niño Southern Oscillation, variable fruit production and famine in a tropical forest. Ecology 80:1632–1647

Wu X, McCormick JF, Busing RT (1999) Growth pattern of *Picea rubens* prior to canopy recruitment. Plant Ecol 140:245–253

Yavitt JB, Wright SJ (in press) Seasonal drought and irrigation effects on fine root dynamics in a tropical moist forest on Barro Colorado Island, Panama. Biotropica

Yu DW, Terborgh JW, Potts MD (1998) Can high tree species richness be explained by Hubbell’s null model? Ecol Lett 1:193–199

Zhang D, Lin K (1997) The effects of competitive asymmetry on the rate of competitive displacement: how robust is Hubbell’s community drift model? J Theor Biol 188:361–367