

1 Maintenance of Tree Diversity in Tropical Forests

John Terborgh¹, Nigel Pitman¹, Miles Silman²,
Heather Schichter¹ and Percy Núñez V.³

¹Center for Tropical Conservation, Duke University, PO Box 90381, Durham, NC 27708, USA; ²Department of Biology, PO Box 7325, Wake Forest University, Winston-Salem, NC 27109, USA; ³Herbario Vargas, Universidad Nacional San Antonio de Abad de Cusco, Cusco, Peru

Introduction

Many tropical forests contain hundreds of tree species; some contain well over 1000. What are the mechanisms that allow such complex communities to persist over millennia? The question has no simple or agreed-upon answer; the only true answer is that we don't know.

Theoreticians have offered a great many suggestions, ten of which are listed in Table 1.1. The proposed mechanisms are extremely diverse. Some are based on abiotic processes, others on biotic processes. Some operate entirely via chance, whereas others depend on deterministic processes. For all these differences, the ten theories recall the Tower of Babel when considered collectively. Given the irreconcilable differences between some of them, it is highly unlikely that all of them are right. However, it is still possible that many of them contain a grain of truth, so it is best to keep an open mind until each can be tested with appropriate evidence.

To attempt a rigorous test of ten theories in a single chapter would be presumptuous, if not tedious. Here our purpose will be to

present data from a series of empirical studies undertaken in western Amazonian forests at a wide range of spatial scales. We shall then comment briefly on each of the theories in light of the data presented. Some of the results provide direct tests of one or another of the theories, whereas other results may serve to inform new theories as yet unborn.

How do the processes that regulate tree species composition vary with spatial scale, from roughly 1 million square kilometres down to less than 1 m²? We shall begin to answer the question by examining patterns of species composition at the very largest spatial scale and then work down to smaller scales.

Results and Methods

Pattern at the subcontinental scale

A commonly held view of Amazonian forests is that species composition is highly variable, even on spatial scales of a few hectares to a few square kilometres (Gentry, 1988). This idea has been given recent impetus by analyses of false-colour Landsat images, which reveal

Table 1.1. Ten theories of plant diversity.

Theory	Author
Broken stick	MacArthur, 1957
Niche pre-emption	Whittaker, 1965
Escape in space	Janzen, 1970; Connell, 1971
Intermediate disturbance	Connell, 1978
Community drift (non-equilibrium)	Hubbell, 1979
Lottery competition	Chesson and Warner, 1981
Resource limitation	Tilman, 1982, 1988
Spatial heterogeneity	Pacala and Tilman, 1994
Dispersal limitation (winner by default)	Tilman 1994; Hurr and Pacala, 1995
Pathogens	Givnish, 1999

that *terra firme* (upland) forests with distinct reflectance properties form a complex mosaic over great expanses of the Amazon (Tuomisto *et al.*, 1995). Randomly oriented 30 km long transects overlying images of the Peruvian Amazon intersected a median of four distinguishable reflectance patches, suggesting hundreds of distinct *terra firme* forest types within the Peruvian Amazon alone.

To examine this proposition, we shall evaluate results from a series of 1 and 2 ha tree plots in south-eastern Peru and eastern Ecuador. The sites were selected to represent forest patches discernible as distinctive reflectance signals in Landsat images (Pitman *et al.*, 1999). The two regions are 1400 km apart, a vast distance in relation to the scale of patches in the reflectance mosaic revealed by Landsat images. The Peruvian network consisted of nine plots ranging in size from 0.875 to 2 ha and totalling 13.875 ha. The Ecuadorean network consisted of 15 1 ha plots (Pitman, 2000). In both sets of plots, all stems ≥ 10 cm diameter at breast height (dbh) were marked, mapped, measured and identified (or assigned to morphospecies).

In both regions, most tree species showed landscape-scale densities of fewer than one individual per hectare, but most individual trees in both networks belonged to a suite of common species. These common species combine high frequency with high local abundance, to form predictable oligarchic matrices over areas of at least several thousand square kilometres in each region (Pitman, 2000; Pitman *et al.*, 2001). So strong is the pattern that only 15% of the species in each region

comprise >60% of the individual trees in almost every plot.

Not only are the forests within each of the two regions surprisingly homogeneous; they are also remarkably similar to each other. More than two-thirds of the Peruvian species have been collected within the region sampled in Ecuador. Many of the most common species in Peruvian *terra firme* are also very common in Ecuadorean *terra firme*. The same handful of families (*Arecaceae*, *Moraceae*, *Myristicaceae*, *Violaceae*) have more common species than expected in both regions (see Terborgh and Andresen, 1998; ter Steege, 2000). Large-statured tree species are more likely to be common in both forests than small ones.

Notably, tree species recorded in the Peruvian and the Ecuadorean inventories show similar relative abundances in the two regions, even though the sampled areas are separated by 11° of latitude. For the 254 species shared by the two networks, abundance in Ecuador is positively and highly significantly correlated with abundance in Peru ($P < 0.0001$, $r^2 = 0.18$) (Fig. 1.1).

These results paint a surprisingly simple picture of how tree communities may be distributed over the Amazonian landscape. In contrast to the small-scale patches discerned in Landsat images, our inventories suggest that a relatively homogeneous but highly diverse tree community blankets a huge area that extends from Ecuador to south-eastern Peru, and perhaps beyond. A similar large-scale continuity of forest composition has recently been documented in Guyana (ter Steege, 2000).

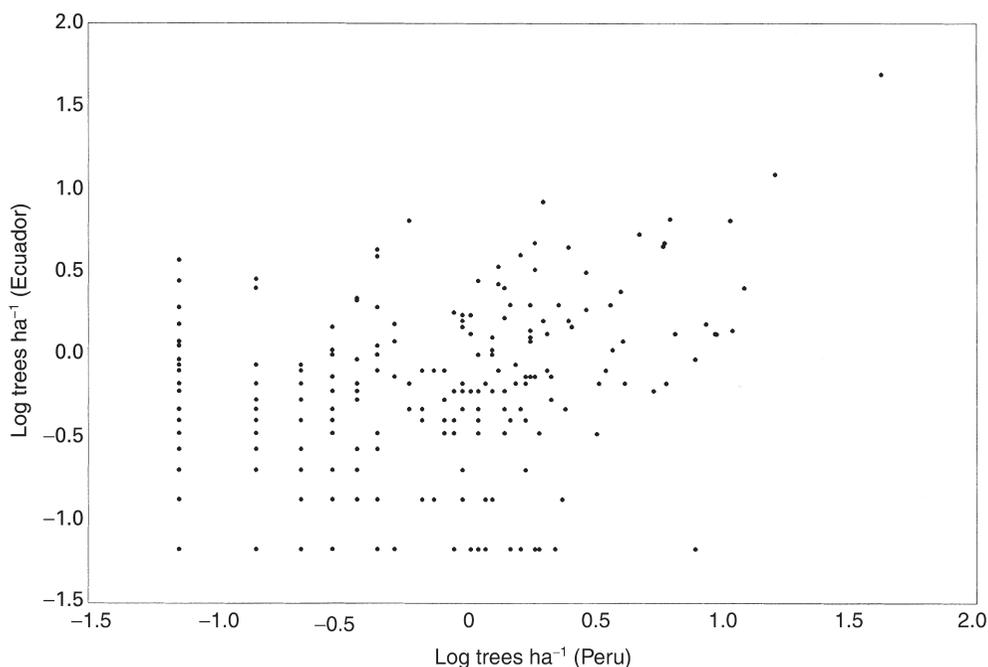


Fig. 1.1. Scattergram showing, for shared tree species, the abundance of each species in eastern Ecuador vs. south-eastern Peru.

Pattern at the regional scale

Just as notably, much of the uniformity observed at very large spatial scales is maintained when the scale is ratcheted down to the regional level. Many authors have emphasized habitat differentiation, especially as generated by edaphic gradients, as crucial to maintaining the diversity of plant communities (Tilman, 1982, 1988; Ashton and Hall, 1992; Tuomisto and Ruokolainen, 1994; Tuomisto *et al.*, 1995). Here we ask how south-west Amazonian trees respond to edaphic gradients. Al Gentry, who wrote extensively about Amazonian forests, was under the impression that beta diversity was characteristically high (Gentry, 1988). For example, two *terra firme* forest plots located only 2 km apart shared only about half their species, a fact he interpreted as supporting this view. But there remains the possibility that the extremely high diversity of these forests results in a sampling variance so great that compositional consistencies are effectively masked in small samples.

To examine this issue more closely, we consider data from 21 plots totalling 36 ha

situated over an area of roughly 400 km² within the Manu Biosphere Reserve in south-eastern Peru. Each plot encompasses 1 or 2 ha, and the whole set of plots totals nearly 20,000 stems ≥ 10 cm dbh. The plots represent four edaphically distinct divisions of the landscape: upland (*terra firme*) forests, mature flood-plain forests, primary successional forests in river meanders and swamp forests (Pitman *et al.*, 1999).

Collectively, the plots contained 829 species and morphospecies. Nearly half of these taxa (45%) occurred in only one of the 21 plots. Little can be concluded about the edaphic requirements of such rare species, if only because many of them were represented by a single stem. If we take the 426 species that occurred in two or more plots, only 26% were confined to a single one of the four major forest types (Fig. 1.2). If we qualify the data even further and consider only the 365 species that occurred in three or more plots, then the proportion restricted to a single forest type drops to 15%. Clearly, if our sample of trees had been 40,000 or 100,000, instead of 20,000, the proportion restricted to a single forest type

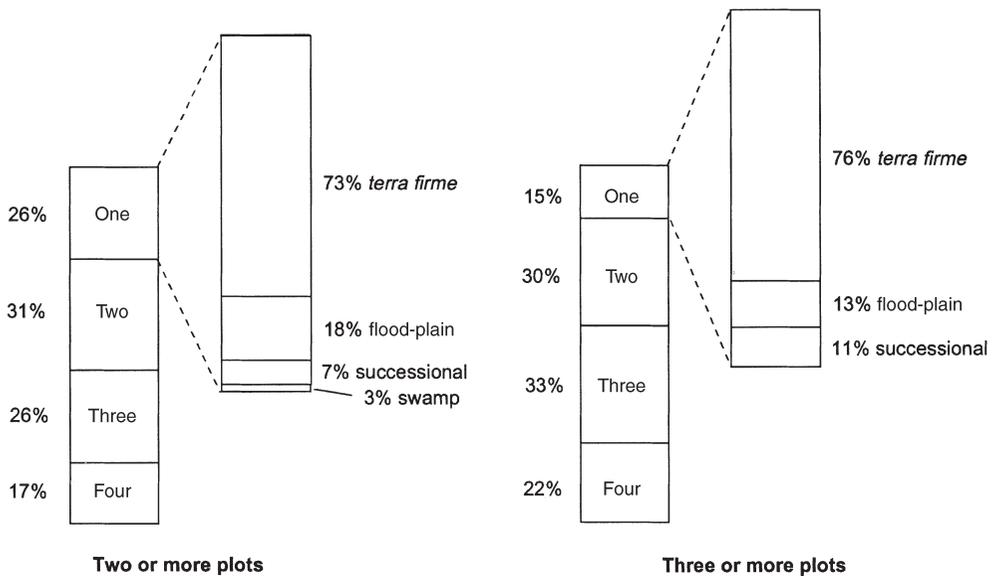


Fig. 1.2. Patterns of occurrence of tree species in 21 plots (36 ha) roughly evenly distributed over four major divisions of the landscape in south-eastern Peru: *terra firme* (uplands), mature flood-plain forest, primary successional forests and swamps. The left diagram includes 462 species and morphospecies that occur in two or more plots; the right diagram includes 365 species that occur in three or more plots. In both diagrams, the left-hand columns show the proportion of species occurring in one, two, three or four forest types; the right-hand columns show the proportions of habitat-restricted species in each of the four forest types. (Reprinted from Pitman *et al.*, 1999, with permission.)

would have dropped even further, probably to less than 10%. Of course, it is possible that the more common species are able to occupy a wider range of edaphic conditions than rare species (Brown, 1995), but, even so, increases in sample size would inevitably lower the fraction of edaphically restricted species. These results are not peculiar to south-eastern Peru. When sampling effort is standardized, data from the Ecuadorean plot network yield very similar results.

Pattern at the subhectare scale

At the spatial scale of a hectare or less, evolutionary–biogeographical influences and variation in physical factors are constrained to a minimum. Instead, we enter the realm of distances over which biotic interactions are presumed to be paramount. One such set of interactions is described by the Janzen–Connell mechanism, which proposes that the

probability of survival of a seed or successful establishment of a seedling increases with distance from its parent tree. Seeds that fall relatively far from the parent enjoy enhanced survival, as they ‘escape in distance’ from predators, herbivores and/or pathogens (Janzen, 1970; Connell, 1971). There have now been dozens of attempts to test and evaluate the Janzen–Connell mechanism, using a variety of tree species and experimental designs (Clark and Clark, 1984).

Although the Janzen–Connell model was proposed 30 years ago, we know of no effort to investigate the consequences of the mechanism, as opposed to the processes driving it. We can do this, as it were, by looking back instead of forward. Rather than beginning with focal trees and studying the fates of seeds around them, we can reverse the process by starting with saplings and then asking how far each is to the nearest potential parent tree. To do this, we mapped all adult trees (defined as stems ≥ 10 cm dbh) in a 2.25 ha plot in mature

flood-plain forest at the Cocha Cashu Biological Station in Peru's Manu National Park. Then we subsampled the nine central $30\text{ m} \times 30\text{ m}$ subplots for small saplings, defined as those $\geq 1\text{ m}$ tall but $< 1\text{ cm}$ dbh (Fig. 1.3). (Effectively, these are saplings ranging from 1 m to about 2.5 m in height.) By considering only those saplings growing in the central portion of the $150\text{ m} \times 150\text{ m}$ adult tree plot, we ensured that all conspecific adults growing within 30 m of any sapling would have a known location. The central subplots were inventoried for saplings in 1996, 1997 and 1998. The locations of saplings were then related to the adult tree stand as it existed in 1990 to allow for the fact

that most saplings were at least several years old at the time they were mapped.

For each sapling representing the 19 most common species in the adult tree stand ($n \geq 10$), we calculated the distance from the nearest conspecific adult that could have been its parent (Fig. 1.4). As predicted by the Janzen–Connell model, there were fewer saplings close to adults than somewhat farther away; the median sapling was 14 m from the nearest conspecific adult. It should be noted that the distances between conspecific adults of these common species were mostly in the range of 20–50 m, so that few saplings could be more than 10–25 m from

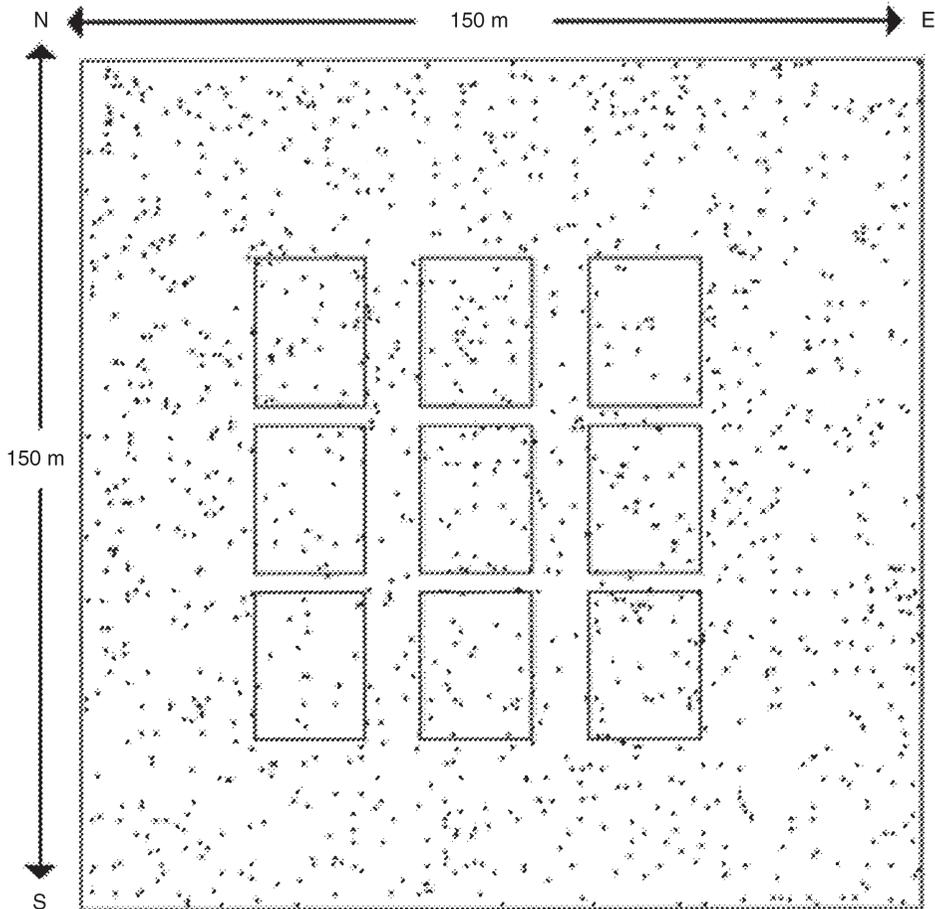


Fig. 1.3. Schematic diagram of the 2.25 ha adult tree plot at Cocha Cashu, Peru. The plot is subdivided into 25 $30\text{ m} \times 30\text{ m}$ subplots. Saplings $\geq 1\text{ m}$ tall and $< 1\text{ cm}$ dbh were sampled in the nine central subplots to ensure that all saplings were $\geq 30\text{ m}$ from the nearest boundary of the adult tree plot.

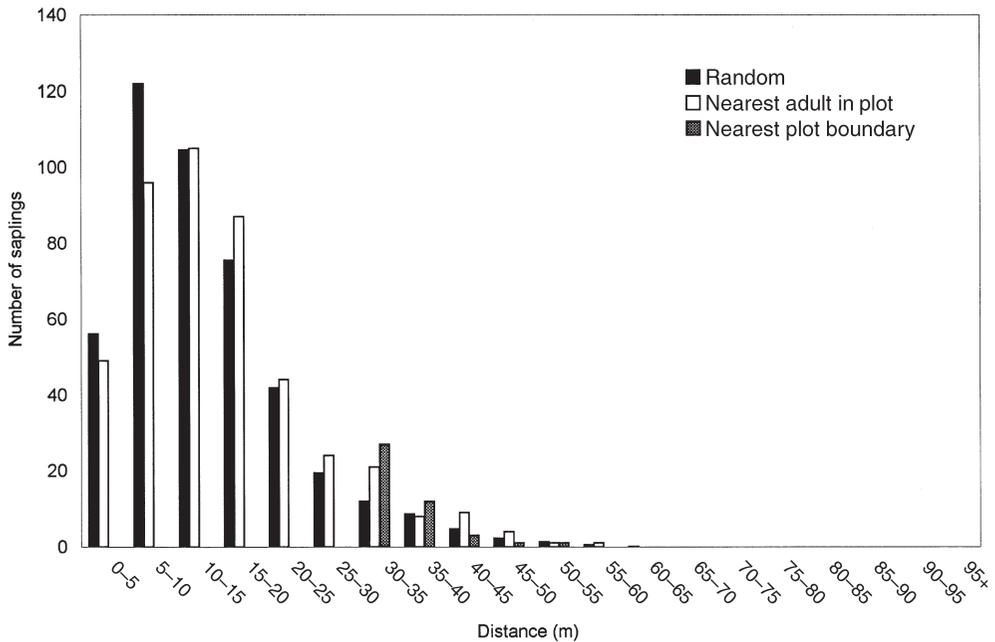


Fig. 1.4. Distribution of distances of saplings ≥ 1 m tall and ≤ 1 cm dbh to nearest conspecific adult for 19 common tree species in the 2.25 ha tree plot at Cocha Cashu, Peru. Black bars show the distribution for the same number of saplings of each species had they been randomly dispersed. White bars represent distances from saplings to the nearest conspecific adult in the plot. The differences between this distribution and randomly arrayed saplings are highly significant ($\chi^2 = 20.34$, $P < 0.01$). (Stippled bars represent distances from saplings to the nearest plot boundary in those cases where a plot boundary was closer than the nearest conspecific adult within the plot.) The species represented in Figs 1.4 and 1.5 were screened to eliminate inhomogeneities in the data set. Specifically, we did not include species that were (i) palms, (ii) small as adults (maturing at dbh < 10 cm) or (iii) considered to be gap pioneers.

the nearest adult, even if all stems were randomly arrayed in space. For perspective, we note that the mean nearest-neighbour distance between adult trees of any species is roughly 4 m.

If equal numbers of saplings of each species had been thrown down at random in the nine central subplots, the distribution of distances to nearest conspecific adults would be as shown by the black bars in Fig. 1.4. Comparison of the random vs. actual distributions reveals that somewhat fewer saplings than expected were close (≤ 10 m) to conspecific adults and somewhat more were further away (≥ 15 m), as would be predicted by the Janzen–Connell mechanism.

Now, we must introduce a complication. Some of the values shown for saplings that were > 30 m from the nearest conspecific adult are overstated, because the nearest conspecific

adult to some saplings was likely to have been outside the adult tree plot and therefore invisible to the analysis. While we cannot eliminate this error, we can bound it by comparing the distance of each sapling from the nearest conspecific adult within the 2.25 ha plot with that of the nearest boundary of the plot, on the very conservative assumption that the nearest conspecific adult lay just outside the nearest boundary (stippled bars). The true values for nearest adults that were ≥ 30 m away therefore lie somewhere between the limits described by these two measures.

Next, we consider a group of 75 species that we shall label as ‘less common’ ($n \geq 1$, < 10). It would not be appropriate to call them ‘rare’, because more than half the tree species in the landscape occur at a density of fewer than one individual per hectare (see above). (The plot contains > 250 species of trees

≥ 10 cm dbh.) Among these less common species, there is a clear tendency to recruit closer to adults than to random points in the forest, although the median distance to nearest conspecific adults was substantially greater than those for common species (32 m) (Fig. 1.5).

If we could accurately measure the seed shadow of each species in the plot, it would be possible to make direct comparisons of the numbers of seeds falling vs. the numbers of saplings at different distances from adult trees. However, measuring dispersal has remained a daunting challenge at the empirical level because of the difficulties inherent in tracking seeds or their dispersers over large expanses of tropical forest (Wenny, 2000). The difficulty of measuring seed shadows is particularly acute in the case of large-seeded trees, because the size of their fruit crops tends to be small (Forget, 1992). Yet, in the forest at Cocha Cashu, large-seeded species predominate in terms of stand basal area (Silman, 1996).

We shall now look at two views of dispersal, one based on the method of using arrays of seed traps, and the other based on finding

where seeds are eventually successful. We shall see that comparing the two approaches proves to be highly enlightening.

Within the same 2.25 ha permanent tree plot described above, Silman set up 40 0.5 m² seed traps at 20 stations arrayed in a rectangular grid, and monitored them for 2 years (Silman, 1996). At each sampling station, there were two traps located 5 m apart to control for small-scale sampling variation. The 20 m² of traps captured >20,000 seeds of 195 species over the 2 years. However, half of the species were represented by only one or two seeds that fell into a single trap. Only 13 of the 195 species reached even 20% of the traps, and these were mostly wind-dispersed lianas (Fig. 1.6).

The surrounding flood-plain forest community is known to contain at least 905 species of trees, shrubs and lianas, of which the vast majority of species (88%) were invisible to the seed traps. Paradoxically, trees from early successional habitats near the river almost 1 km distant dispersed into the plot in surprising numbers: *Alchornea* (*Euphorbiaceae*) 20 seeds, *Sapium aereum* (*Euphorbiaceae*) 14

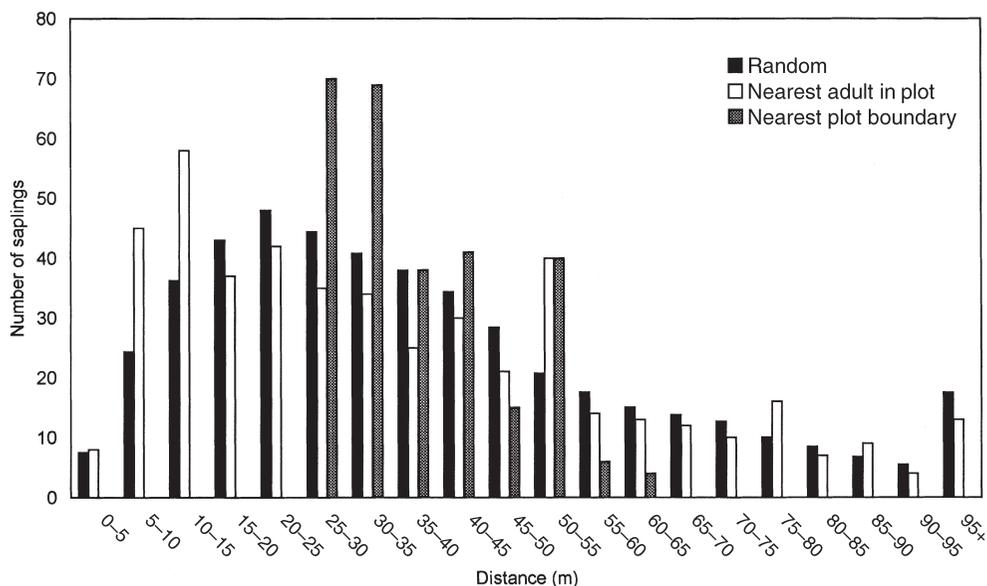


Fig. 1.5. Distribution of distances of saplings ≥ 1 m tall and ≤ 1 cm dbh to nearest conspecific adult for 75 less common tree species in the 2.25 ha tree plot at Cocha Cashu, Peru. Interpretation as in Fig. 1.4. The distribution of distances to nearest adult within the plot (white bars) and that of randomly arrayed saplings are highly significantly different ($\chi^2 = 68.13$, $P < 0.005$).

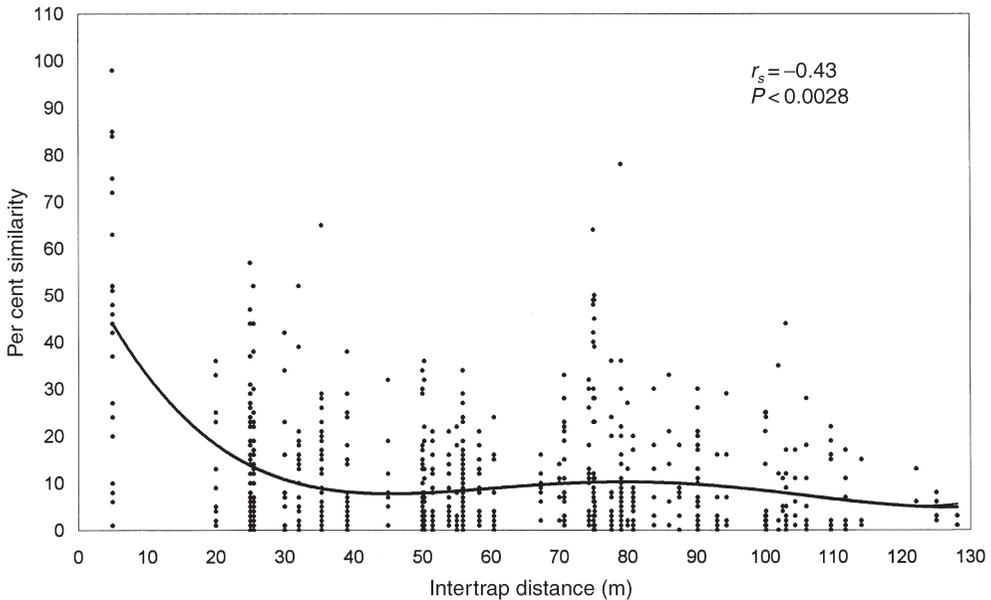


Fig. 1.6. Spatial autocorrelation of composition of seed rain falling into 40 traps arrayed in a grid within the 2.25 ha tree plot at Cocha Cashu, Peru. Spatial correlation drops to background level within approximately 30 m, showing that most seeds fall within 30 m of adults.

seeds, *Sapium ixiamasense* 11 seeds and *Guarea guidonia* (*Meliaceae*) five seeds. These species (all bird-dispersed) contributed to the seed rain, even though no known individuals of any of them occur within 500 m of the plot.

With the exception of the relatively few seeds imported from far outside the plot, the impression given by the results is that most rain-forest trees experience extremely limited dispersal. Similar, but even more extensive measurements made with seed traps on Barro Colorado Island, Panama, convey the same impression (Hubbell *et al.*, 1999). Over a 13-year period, 1.3 million seeds were collected from 200 traps, and yet, on average, seeds of roughly a third of the species with adults in the plot failed to hit any of the traps in a given year (H. Muller-Landau, personal communication). However, all species represented by adults were registered in traps at some time over the 13 years. Results such as these have given rise to the theoretical notion of 'winner by default', which refers to the occupancy of recruitment sites by species other than the best competitor in the community because of dispersal limitation (Hubbell *et al.*, 1999).

But, if dispersal is as limited as seed-trap data seem to imply, many tree species populations should be extremely clumped. It is true that the populations of most tropical tree species are clumped, but not nearly to the degree implied by empirically determined seed shadows. Why not? Undoubtedly, it is because seed traps capture seeds before they are exposed to terrestrial seed predators, whereas saplings represent seeds that escaped seed predators. In addition, so-called secondary dispersal may play a crucial role for some species, and secondary dispersal is invisible to seed traps (Andresen, 1999).

A lot of biology transpires between the moment a seed hits the ground and the time it morphs into a sapling. This is evident when one compares a middle-of-the-road seed-shadow model with the observed distribution of saplings (Clark *et al.*, 1999; Fig. 1.7). If seeds were to fall to the ground in accord with a negative exponential with distance, the expected density of seeds would drop to an undetectable level only a few crown diameters away from a given fruiting adult (Nathan and Muller-Landau, 2000).

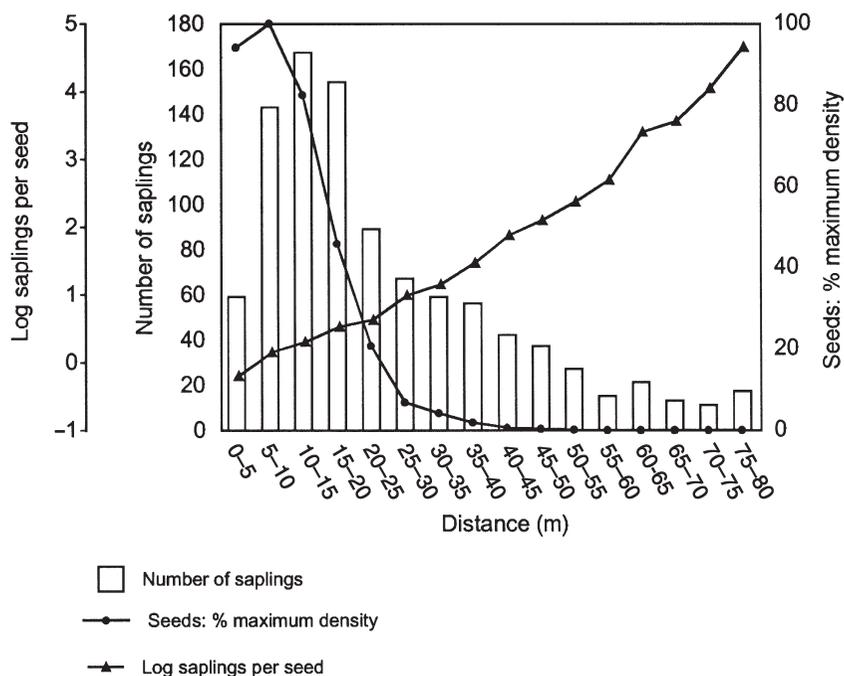


Fig. 1.7. Contrast between a generalized seed shadow that mimics Fig. 1.6 (negative exponential, line marked by solid dots) and the distribution of saplings in respect of the nearest conspecific adults of all 19 'common' and 75 'less common' species combined (white bars). The line marked by triangles represents the hypothetically increasing 'value' of a seed as it is dispersed away from the parent tree. This value is obtained by dividing the distribution of saplings by the distribution of seeds. The result suggests that the 'value' of a seed can increase several orders of magnitude as it is transported away from the parent tree. The scale is arbitrary.

If each seed that fell to the ground had an equal chance of becoming a sapling, the seed and seedling curves would be congruent, but it is obvious that they are dramatically distinct. This can be demonstrated by dividing the distribution of saplings in respect of nearest conspecific adult by the hypothetical seed shadow. The resulting derived curve (Fig. 1.7) gives a crude estimate of the 'value' of a seed dispersed to increasing distances. It is an avowedly rough estimate, because quantitative aspects of seed shadows vary greatly between species and because many years' seed crops may be required to generate a single surviving sapling. Nevertheless, the exercise is informative because it shows that the probability that a given seed will become a sapling increases by perhaps orders of magnitude when that seed is transported away from the parent.

Pattern at the metre scale

Much effort has recently been devoted to searching for density dependence in tropical tree communities (Hubbell and Foster, 1986; Condit *et al.*, 1994; Wills *et al.*, 1997). The fact that density dependence is concentrated at the earliest stages of the life cycle is brought out by what can be termed 'input-output' analysis. Silman (1996) determined that at least 500 seeds fall on to the average square metre of forest floor every year. (Probably the number is much higher, because the mesh used in his seed traps allowed seeds smaller than 1.5 mm in diameter to fall through.) Yet, despite this massive seed rain, the forest floor at Cocha Cashu is occupied by only about 20 plants m^{-2} (tree seedlings, vines and herbs combined, most of which are < 30 cm tall). These plants turn over at a rate of only 20%

year⁻¹, so that roughly four new individuals appear and replace four that have died every year in the average square metre (Terborgh and Wright, 1994). (To put this in perspective, consider the size of a typical starter pot that a gardener would use to raise seedlings prior to transplanting. Such pots typically have an area of *c.* 0.5 dm².) Yet, at 20 m⁻², the average seedling on the forest floor has 5 dm² it can call its own, roughly ten times the area of a seedling pot. Such plants are thus scattered to a degree that suggests interactions between them are relatively weak.

Discussion

Now, let us return briefly to the list of theories of plant diversity to see which ones have withstood the scrutiny of our analyses at multiple spatial scales (see Table 1.1).

Broken stick, niche pre-emption

These are black-box mechanisms that generate species abundance distributions not even remotely approximating the rank abundance curves typical of tropical forest tree communities (May and Stumpf, 2000; Plotkin *et al.*, 2000).

Intermediate disturbance

Connell (1978) proposed that the species diversity of space-limited communities (trees, intertidal organisms, etc.) will be low at high and low rates of disturbance and maximal at some intermediate rate. Phillips *et al.* (1994) have presented evidence suggesting an important role for disturbance in promoting tropical forest tree diversity, but the details of any such relationship are greatly in need of clarification.

Community drift

The community drift or ‘non-equilibrium’ hypothesis of Hubbell (1979) states that all

tree species are adaptively equal, and that community composition will consequently vary over time as described by a random walk. Our findings argue strongly against community drift, which implies uncorrelated species abundances in spatially disjunct forests. Instead, we found that species in a few key families consistently dominate western Amazonian forests located 1400 km apart. Even more notable is the finding that abundance relationships are conserved over this great distance (Fig. 1.1). Such a high degree of spatial coherence of community composition cannot be reconciled by this model (Terborgh *et al.*, 1996). Chance thus fails as a means of accounting for forest homogeneity on such large spatial scales.

Lottery competition

Year-to-year climate fluctuations can have important consequences for tree demography, as abundantly affirmed by the work of Condit *et al.* (1995, 1996) on Barro Colorado Island, Panama. However, the fact that the highest tree diversities occur in regions with the least variable climates suggests that this mechanism makes, at best, only a minor quantitative contribution to the overriding question of how diversity is maintained through time.

Resource limitation

Spatial heterogeneity in the availability of limiting nutrients can generate a corresponding mosaic of species composition. Species turnover occurs on strong edaphic gradients in the tropics as well as elsewhere, but the low beta diversity observed at a landscape scale and the homogeneity of Amazonian forests at medium and large spatial scales seem to preclude an important role for this mechanism as an explanation for alpha diversity.

Dispersal limitation (winner by default)

The notion that dispersal limitation is a powerful force in tropical forest dynamics is partly an

illusion resulting from the fact that the seeds captured in seed traps are nearly all (>99%) destined for failure. If we could magically pick out of the seed rain those seeds that were earmarked for success, an entirely different picture would result because nearly all saplings appear to arise from dispersed seeds (see below).

Spatial heterogeneity

The notion that the forest floor is a complex mosaic of microsites that can enhance or depress the prospects of individual seeds is a powerful one, much in need of further empirical study.

Escape in space (Janzen–Connell), pathogens

These hypotheses are really different aspects of the Janzen–Connell mechanism. Evidence presented here strongly affirms the operation of Janzen–Connell at a broad community level, and further shows that the offspring of rare species are more strongly inhibited by the proximity of conspecific adults than those of common species.

Where are we and where do we go from here?

Perhaps a good place to begin is to point out that, of the ten theories of plant diversity listed in Table 1.1, there is only one that explicitly provides a role for animals. And that, not surprisingly, is Janzen–Connell. And yet how curious, for animals play crucial roles at every step in plant reproduction and recruitment: they pollinate flowers, they prey upon seeds, both before and after dispersal, they disperse both fruits and seeds, they carry out secondary dispersal – a much neglected mechanism – and they destroy or weaken seedlings and saplings through herbivory. So how can one have a theory of plant diversity in which animals play no explicit role? We are at a loss to say, other than to express our astonishment that so many students of plant ecology have overlooked the animals!

Animals are the heart and soul of Janzen–Connell, for they both disperse seeds and destroy them, thereby creating the large disparities we have noted between seed shadows and the distribution of saplings. Our results demonstrate that large numbers of species (in the aggregate) show the expected ‘escape with distance’ pattern anticipated by Janzen and Connell, providing strong affirmation of the postulated mechanism at a broad community level. These observations can be extended to suggest a new interpretation of ‘commonness’ and ‘rarity’ as consequences of interactions underlying the Janzen–Connell mechanism, namely, the events that transpire between dispersal and the successful establishment of seedlings.

On average, the saplings of common species recruit closer to potential parents than those of less common species (see also Condit *et al.*, 1992). Perhaps this is partly a consequence of the fact that common tree species at Cocha Cashu produce larger seeds on average than less common species. Otherwise, we know of no reason why the dispersal biology of the two categories of species should differ in any systematic way. However, other things being equal, it can be presumed that the seed shadows cast by adults of common species would overlap more than those of less common species, thereby elevating the seed rain falling on to the forest floor. Indeed, that is suggested by the fruit-trap data, which show that a small minority of species in the community produce a disproportionately large fraction of seeds captured in traps.

These observations lead us to surmise that what makes a ‘common’ species is the ability to recruit near an adult, as Schupp (1988) found with *Faramaea occidentalis* and Hubbell and Foster (1986) found with *Trichilia tuberculata*, two of the commonest species on Barro Colorado Island, Panama. Conversely, what may make a ‘rare’ species is inability to recruit near a conspecific adult. Indeed, the median distance of saplings of 75 ‘less common’ species to the nearest conspecific adult was 32 m, whereas the median for 19 ‘common’ species was only 14 m. Nevertheless, there is strong evidence that the rarer a tree species is, the more clumped its distribution (Hubbell, 1979; Condit *et al.*, 2000). Statistical clumping is thus

likely to be explained by the scale of the analysis; rare species tend to be clumped at larger scales (e.g. 1 ha), but apparently not at the smaller scales considered here.

Hubbell (1979) was both right and wrong when he maintained that density dependence must be very low, especially in less common species, because few saplings in tropical forests are nearest neighbours of conspecifics. The observation that few saplings of most species are conspecifics of their nearest neighbours is correct, but the inference that consequently there is little or no density dependence is incorrect. Janzen–Connell provides the density dependence in another form – one that is mediated by the actions of seed and seedling predators and pathogens. Comparisons of seed shadows with seedling distributions show density dependence to be very strong, but it operates most stringently before the seedling stage and is manifested as the nearly universal failure of seeds falling near the parent tree.

At Cocha Cashu, an annual input of ≥ 500 seeds m^{-2} results in an output of only four new seedlings. Inescapably, this means that $> 99\%$ of all seeds that fall to the ground fail to produce seedlings that survive even 1 year. Here, then, is where the important biology is happening that determines the future of the forest. The biology operates through both abiotic and biotic processes, which determine which seeds succeed and which fail. Clearly, if the forest is to perpetuate itself, seeds of every species succeed somewhere, but mostly they fail. Learning the ‘rules’ that determine success vs. failure for species having different seed sizes and dispersal modes emerges as a major challenge in tropical plant ecology.

The median adult tree (arbitrarily defined as those ≥ 10 cm dbh) in the forest at Cocha Cashu is 14 m tall. The median crown radius of trees this tall or taller in the flood-plain forest is 4 m (Terborgh and Petren, 1991). If we take this figure to represent the spread of an average adult tree, from Figs 1.4 and 1.5 it can easily be calculated that $> 94\%$ of the saplings of ‘common’ species establish at distances ≥ 4 m from the nearest conspecific adult and for ‘rare’ species the corresponding figure is $> 98\%$.

Looking at this from another perspective, the median distance at which saplings of ‘common’ species establish from the nearest

conspecific adult is 14 m, which is equivalent to 3.5 adult crown radii. In contrast, the median sapling of the 75 ‘less common’ species is 32 m from the nearest conspecific adult, equivalent to eight adult crown radii. These distances describe an ample space around the adults of even common species in which the recruitment of conspecific saplings appears to be inhibited and in which, consequently, recruitment of heterospecifics is favoured. In this manner, ‘rarity’ can help promote diversity, as Janzen (1970) and Connell (1971) so cogently pointed out 30 years ago.

The finding that large numbers of saplings are growing at 20 m, 40 m or even further from the nearest conspecific adult is revealing, because it underscores the importance of dispersal away from parent trees. True dispersal distances are undoubtedly greater than our results suggest, because the parent of a given sapling is not always the nearest adult (Nathan and Muller-Landau, 2000). Indeed, our results make it clear that the vast majority of saplings in the forest originate from seeds dispersed well away from the parent tree. Conversely, undispersed seeds appear to have an extremely low success rate. The hugely increased probability of survival of dispersed seeds thus acts strongly to offset dispersal limitation and helps to explain the oft-cited enigma of isolated individual trees located hundreds of metres from the nearest conspecific.

Some implications of this can be explored in a thought experiment. What if the dispersal and/or seed and seedling predation regimes of a forest were to change as, say, a consequence of seed-disperser populations being decimated by hunting? Such perturbations of the animal community could be expected to alter the optimal recruitment distance for many species, as outlined by Janzen in his original 1970 paper. If this were to happen, the relative abundances of species in the next generation of adult trees would be dramatically modified. In particular, if recruitment distances were to decrease (via reduced dispersal with no concurrent change in seed predation and seedling herbivory), density dependence would increase (i.e. fewer seeds would escape) and diversity would be expected to decrease (see Dirzo and Miranda, 1991). Conversely, if recruitment distances were to increase via intensified seed predation

and/or herbivory with no concurrent change in dispersal, more rare species could participate in the community and diversity should increase. If these imaginary scenarios could be shown to be true, what it would imply is that animals are fundamentally regulating plant diversity. In retrospect, this conclusion seems so obvious, but why have we ecologists so long avoided it?

Janzen (1970) and Connell (1971) (with recent support from Givnish, 1999) got it right, but fully appreciating this gets us only part way to a deeper understanding of the mechanisms that perpetuate tree species diversity through time. The Janzen–Connell mechanism ensures that a few lucky seeds will escape in distance from the largely biotic and deterministic mortality factors that operate near fruiting adults. But, once a seed has escaped these biotic mortality factors, the abiotic properties of the site will determine whether it succeeds or fails – whether it germinates and, if so, whether the conditions of light, moisture, etc. are adequate for the seedling to become vigorously established. Thus, spatial heterogeneity and abiotic processes have a large role to play too, one in which chance is prominent.

What perpetuates diversity, then, is the precise way animal activities (represented by Janzen–Connell) map on to the mosaic of physical microsites on the forest floor. It is therefore the intersection between Janzen–Connell and the abiotic world that should define the frontier of tropical forest ecology for the next generation of theoreticians and empiricists alike.

Chance vs. determinism as a function of scale

Finally, we return to larger spatial scales. A high degree of determinism is required to explain the observed homogeneity of western Amazonian forests at intermediate and large spatial scales. Exactly what the deterministic forces are that bring about the large-scale patterning of tropical tree communities remains to be elucidated, but we can hardly doubt that the structure of the animal community is an important component of the puzzle. At small

scales, more chance enters into the process of tree establishment, as both abiotic and biotic factors (e.g. seed predation) control which seeds among the hundreds that fall in a given microsite survive and prosper. None of the existing theories of plant diversity incorporates this kind of scale-dependent complexity.

Our analysis of tree distribution at the landscape scale comes to a very different conclusion from Gentry's (1988). Beta diversity does not appear to be very high; indeed, it appears to be surprisingly low. A large majority of the tree species in the south-west Amazon, up to 90% or more, appear in two or more edaphically distinct plant communities, albeit at frequently contrasting abundance levels (Pitman *et al.*, 1999). Segregation of species on edaphic gradients does not seem to play a conspicuous role in organizing these communities.

However, this statement should be qualified by placing it in context. The entire landscape of Madre de Dios is an alluvial outwash plain of the Andes, nearly all of it of Pleistocene or Holocene age (Kalliola *et al.*, 1993). None of it is influenced by local bedrock, which, in any case, is buried under thousands of metres of sediment. The 'edaphically distinct' elements of this landscape that define its principal vegetation formations (*terra firme* forest, swamps, successional stands, etc.) are all constructed of the same or similar substrate but differ in such factors as hydrology, time of exposure to weathering and pH (Terborgh *et al.*, 1996). The region's floristic homogeneity thus reflects its geological homogeneity. In contrast, geologically complex tropical regions tend to display much greater floristic heterogeneity (Ashton and Hall, 1992; ter Steege, 2000).

The *terra firme* forests of eastern Ecuador and south-eastern Peru, although 1400 km apart, share hundreds of tree species, many of which occur in the two regions at similar relative abundances. Geographically, what ties the two regions together is that both lie in the Andean foreland region, which is built on recent alluvial sediments originating in the Andes (Salo *et al.*, 1986; Kalliola *et al.*, 1993). Perhaps this is what lies behind the strong floristic similarity of the two regions, notwithstanding the fact that eastern Ecuador

is non-seasonal and receives 4000 mm of rain annually, whereas south-eastern Peru is markedly seasonal and receives only half as much precipitation (Pitman, 2000). The fact that 70% of the tree species recorded from south-eastern Peru also occur in eastern Ecuador (Pitman, 2000) argues against a prominent role of climate as a determinant of the floristic composition of the respective regions (see Condit *et al.*, 1995).

Another test of the role of climate can be found by comparing the flora of eastern Ecuador with that of the Iquitos region in north-eastern Peru. The Iquitos flora is markedly distinct from that of eastern Ecuador, even though Iquitos is only half as distant as south-eastern Peru (*c.* 650 km) and lies in the same non-seasonal climate zone (Vásquez, 1997). The difference is that Iquitos is much further from the Andes and lies in a Tertiary basin containing weathered sediments derived from a variety of sources, including the Guiana Shield (Kalliola *et al.*, 1993; Räsänen *et al.*, 1995).

We argue that these patterns call for a sea change in the way ecologists think about tropical forests. The traditional view of small-scale vegetational mosaics must yield to a new picture of very large areas dominated by predictable species associations, not unlike the situation in temperate forests.

Conclusions

- We examined community-level patterns in western Amazonian tree communities at spatial scales ranging from subcontinental to 1 m² as a means of evaluating ten prominent theories of plant diversity.
- More than 70% of tree species in south-eastern Peru are also found in eastern Ecuador, 1400 km distant. Abundances of shared species are positively correlated in the two regions.
- Within each region, a set of approximately 150 common tree species predominates in both abundance and frequency. These regional forests are thus dominated by an ‘oligarchy’ of species, much as temperate forests.
- Within south-eastern Peru, more than 85% of all tree species are found in two or more major habitats (*terra firme*, flood-plain, successional stands, swamps), indicating that beta diversity is very low at the regional scale.
- At the hectare scale, we report that > 95% of saplings appear outside the projected crown radius of the nearest conspecific adult, implying that nearly all saplings originate from dispersed seeds.
- The median sapling of 19 ‘common’ tree species was 14 m from the nearest conspecific adult, whereas the corresponding distance for saplings of 75 ‘less common’ species was 32 m. These distances indicate that saplings typically appear at distances equivalent to several crown radii from potential parents, thereby leaving ample space in the neighbourhood for heterospecific recruitment, as postulated by Janzen (1970) and Connell (1971).
- These results lead to the suggestion that ‘common’ tree species are those that are able to recruit near conspecific adults, whereas ‘less common’ species are those that are unable to do so.
- ‘Input–output’ analysis of the seed rain at Cocha Cashu in Peru indicated that > 500 seeds fall on to each square metre of forest floor every year and yet give rise to only four new plants. We suggest that density dependence operates in this community mainly at the seed and early seedling stages, thereby explaining the difficulty investigators have had in demonstrating strong density dependence at later ontogenetic stages.
- The intersection between the Janzen–Connell mechanism and the abiotic world is what should define the frontier of tropical forest ecology for the next generation of theoreticians and empiricists, alike.

Conservation relevance and avenues for future research

- The tree communities of western Amazonia are composed largely of

species with broad geographical distributions, which display a wide range of tolerance of local edaphic gradients.

- The pre-eminence of alpha over beta diversity at the regional scale implies that randomly situated conservation areas will capture most tree species inhabiting the region.
- The importance of animals as dispersal agents in tropical forests is underscored by the observation that >95% of all saplings in the understorey of a Peruvian forest arose from seeds that had been transported away from the nearest potential parent.
- Consequently, the widespread decimation of dispersers by overhunting can be predicted to have devastating long-term consequences for the maintenance of tree species diversity in tropical forests.

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