At 50, Janzen–Connell Has Come of Age

JOHN TERBORGH

Fifty years ago, Janzen (1970) and Connell (1971) independently published a revolutionary idea to explain the hyperdiverse tree communities of the tropics. The essential observations were that seedfall is concentrated in the vicinity of fruiting trees, whereas saplings recruit at a distance from reproductive conspecifics. These observations were encapsulated in a simple focal-tree model constructed of intersecting curves for seedfall and escape from host-specific enemies postulated to attack propagules (seeds and seedlings) in the vicinity of reproductive conspecifics. In conflict with the thinking of the times, the mechanism operates from the top down rather than from the bottom up. A deterrent to broad acceptance has been the giant intuitive leap required to generalize the focal tree model to an entire forest community. Recent theoretical and empirical results have succeeded in bridging the gap between the focal tree model and its community-level implications. With these new findings, Janzen–Connell has come of age.

Keywords: distance dependence, escape from enemies, Janzen–Connell, tree recruitment, seed dispersal, top down, tropical forest

It is fitting that we celebrate the 50th anniversary of the Janzen–Connell hypothesis (JCH), because the revolutionary idea of these two brilliant ecologists is finally gaining the high ground. For decades, the insights of Janzen (1970) and Connell (1971) remained one of many unproven hypotheses proposed to account for the extraordinary tree diversity of many tropical forests (Chave et al. 2001, Wright 2002). Only recently and mostly in the last decade have investigators begun to delve more deeply into the predictions and workings of the Janzen–Connell model with consistent affirmations. For this investigator at least, it is time to say that the JCH has come of age.

What is the JCH? It is a deduction derived from the empirical observations of two field ecologists, one, Janzen (1970), in Central America and the other, Connell (1971), in tropical Australia. Both observed that seedfall was most concentrated around fruiting trees, whereas sapling recruitment failed close to parent trees and succeeded at a distance. Their model consists of two intersecting curves, one that describes the seed shadow of a focal tree and a second that describes a sharply rising per-capita probability of seed success as a function of distance away from the focal tree. Seeds falling close to fruiting conspecifics fail to succeed because host-specific agents, bruchid beetles in many of Janzen's examples, kill virtually 100% of the seeds within what we shall call the "exclusion zone" (Janzen 1971a, 1971b). The hypothesis puts much weight on the importance of seed dispersal because seeds dispersed away from the parent tree have a greatly enhanced possibility of developing into adults.

Although generalist seed predators and herbivores, such as rodents and ungulates, may consume many of the seeds or seedlings of a given species of tree, they do not generate the necessary distance dependence that lies at the core of the hypothesis (Molofsky and Fisher 1993, Terborgh et al. 1993, reviewed by Hammond and Brown 1996). Distance dependence results from the actions of host-specific pests and pathogens that are postulated to complete their life cycles in or around fruiting individuals of host species (Janzen 1970, 1980). It is therefore the spatially restricted occurrence of seed or seedling mortality agents that generates distance-dependent mortality, which is the signal feature of the Janzen–Connell mechanism.

Why now after 50 years has the JCH not been decisively refuted or fully accepted? I think there are three main reasons that skepticism has persisted. First, 1970 fell in the heyday of niche-based thinking about diversity, propounded first by Lotka and Volterra and then by a succession of distinguished followers including Gauss, Lindeman, Hutchinson, MacArthur and many more. Janzen–Connell did not incorporate essential features of niche-based models, such as carrying capacity, limiting similarity and density dependence and, therefore, did not conform to contemporary thinking. Indeed, it challenged that thinking, so that coming to terms with its mechanism would have required a major overturning of prevailing opinion. So what is it? In fact, it is a top-down theory, the antithesis of a bottom-up approach.

Second, reported tests of the JCH produced a bewildering array of results. Augspurger (1983), Clark and Clark (1984),

BioScience 70: 1082–1092.
doi:10.1093/biosci/biaa110

Howe and colleagues (1985), Schupp (1988) and others did exemplary and largely confirmatory experimental work in the 1980s, but it did not go beyond testing the focal tree model. Attention then turned to other approaches, including Hubbell's (1979) Neutral Theory and frequency-dependent effects, now referred to as conspecific negative density dependence (Wills et al. 2006). Reported tests of the focal tree model have resulted in both affirmations and refutations. The absence of a clear and consistent signal emerging from empirical studies led to persistent doubt (Hyatt and colleagues (2003), but see Comita and colleagues (2014) for a more positive perspective). There are good reasons for why the experiments, as they were conducted, produced inconsistent results.

With notable exceptions, some of which are mentioned above, many focal tree experiments have been initiated with little knowledge of the natural history of the target species. A relevant issue is whether the distance-dependent mortality agents that prevent recruitment near fruiting conspecifics act at the seed or seedling stage. A majority of species (80%–85% in the community at Cocha Cashu in Perú) are limited at the seed stage, but in the remaining 15%–20% the bottleneck is at the seedling stage. If one guesses wrong, the experiment will fail. But this error in constructing tests of the focal tree model pales next to the misleading results that emerge from terminating experiments too soon. In experiments conducted at Cocha Cashu, we have typically run seed presentation trials for at least 1 year and up to several years (Terborgh et al. 1993, Cintra 1997, Paine and Beck 2007, Paine et al. 2016) and seedling trials for 3 to 4 years (Swamy and Terborgh 2010, Alvarez and Terborgh 2011). Seeds typically yield clear results in a few weeks or months whereas seedlings often take much longer to die under conspecific adults, up to several years. The report by Murphy and colleagues (2017), which followed a cohort of seedlings for 12 years, is a refreshing exception. Failure of many attempts to test the hypothesis of distance dependence can be attributed to premature termination of the experiments.

Another reason many experiments have failed to demonstrate clear distance effects is that they employed cages to exclude mammalian seed predators, but did not include a treatment to exclude arthropods. However, Janzen himself stressed the fundamental role of nonmammalian host-specific agents as drivers of distance effects. Moreover, in experiments that took pains to distinguish mammalian from nonmammalian agents in the generation of distance effects, nonmammalian agents were clearly implicated whereas mammals were not (Molofsky and Fisher 1993, Terborgh et al. 1993, reviewed by Hammond and Brown 1996). Therefore, failure to demonstrate distance effects in past experiments was more often because of inappropriate experimental design than to any weakness in the Janzen–Connell model.

The final and most crucial of my points is that broad acceptance of the JCH was stifled because it required a huge intuitive leap from the basic focal tree model to its postulated community-wide effects, namely, that the existence of exclusion zones around fruiting adults could somehow explain tropical tree diversity. The idea was challenged by Hubbell (1980) who published a theoretical model based on exclusion zones that could sustain, at most, barely a handful of species, not the hundreds that would be required to provide a convincing representation of nature. We have recently shown through simulations that Hubbell's result is a special case that does not reflect the situation in nature. In fact, the Janzen–Connell mechanism can sustain up to 1000 species in a finite community (Levi et al. 2019).

Although the JCH is now 50 years old, this synthesis could not have been written even 10 years ago because the conceptual gap between the focal tree model and community diversity had not then been breached at either the empirical or theoretical levels. But the last 10 years have seen a flourishing of new approaches to an old idea and these have succeeded in bridging the gap.

What now follows should be read more as an essay than as a traditional review of literature. For reviews, the reader can refer to Hammond and Brown (1996), Carson and colleagues (2008), Terborgh (2012), and Comita and colleagues (2014). Instead, the story line will be based on 30 years of research on Janzen–Connell at Cocha Cashu in Perú. True, the perspective will be that gained from work at just one site, but all long journeys start with a single step. The products of these 30 years have fleshed out a fuller perspective on the Janzen–Connell mechanism and its workings than has yet to emerge from other sites. My purpose in the present article is not to put Janzen–Connell to rest but to encourage further research, because many questions remain unanswered, as will be made explicit in the final section.

As explained above, the basic focal tree model contains two components, a seed shadow and an escape curve. I will begin by detailing evidence related to the escape curve, the most critical and distinctive component of the hypothesis. In the second section, I will present evidence related to the seed shadow component of the model. Dispersal is critical to the operation of the Janzen–Connell mechanism but has properties in hyperdiverse tropical forests that are not yet widely appreciated. Finally, I will attempt to combine what we know about the escape process with that derived from studies of dispersal and show that there are important questions about the relative strengths of the two processes that have yet to be resolved.

The escape curve. Research conducted at Cocha Cashu has provided both visual and statistical evidence pertaining to the strength and spatial extent of what we have called *exclusion zones*, the radius around fruiting trees within which propagule success is zero or near zero. I shall start with the visual evidence, because it is thoroughly convincing and suggests topics for further investigation.

But first, some comments on our methods. Our research was conducted in a 4-hectare (ha) tree plot in which all trees

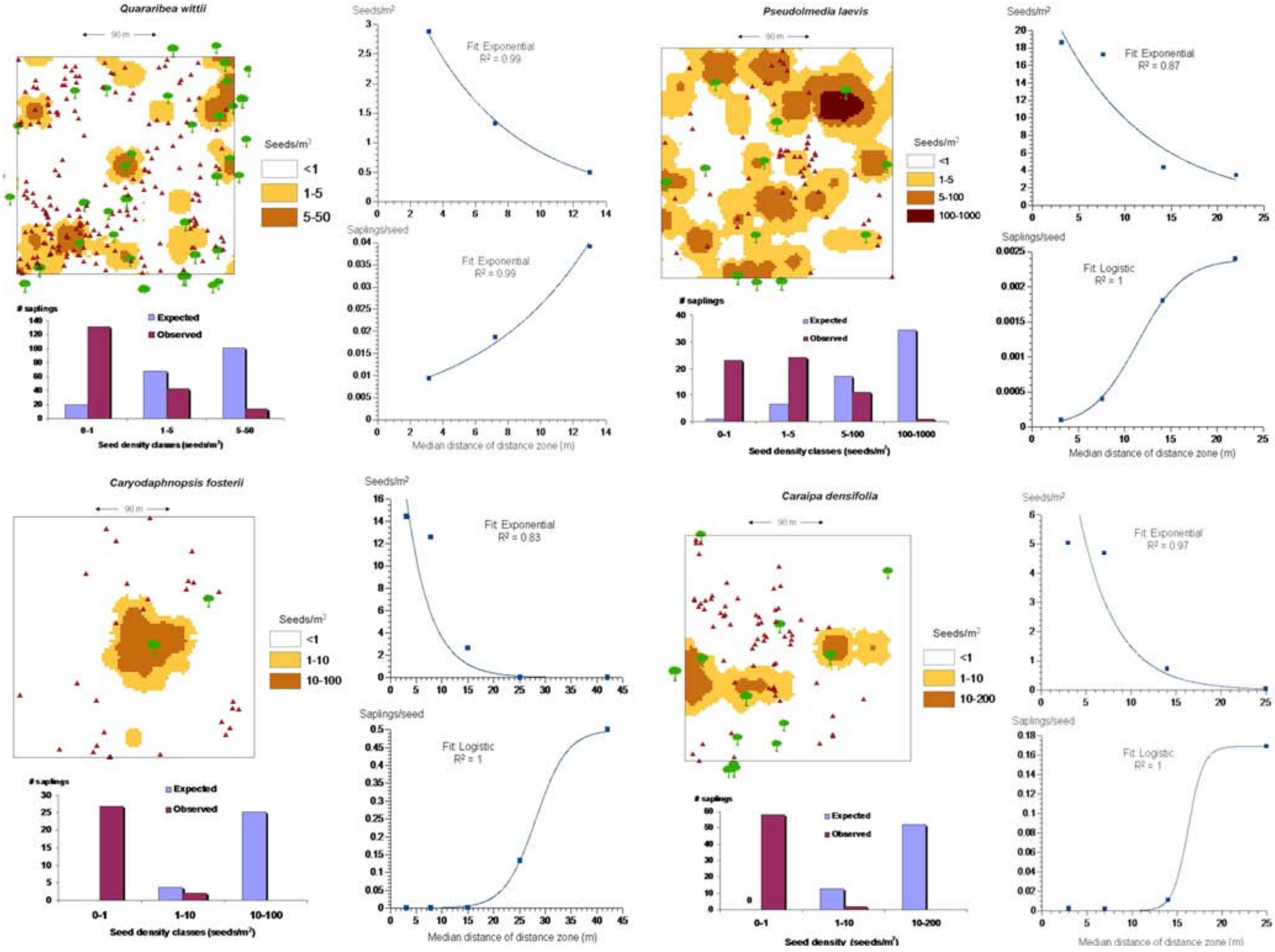

Figure 1. Stand maps for four representative species with bar graphs representing observed and expected sapling occurrences on the assumption that all seeds are equal. To the right of each map are the corresponding Janzen–Connell seed shadow and escape curves calculated from the data. Green tree symbols represent trees greater than 10 cm dbh with size scaled according to dbh. Red triangles represent small saplings (stems at least 1 m tall, less than 1 cm diameter). Seed density classes (seeds per m^2) are shaded from white to dark brown, representing regions of lowest to highest recorded seedfall, respectively. The figure illustrates results for species dispersed mainly by small and medium primates (Q. wittii), medium and large primates and large birds (P. laevis), birds (C. fosteri), and wind (C. densifolia). Source: Reprinted from Swamy and Terborgh (2011) with permission.

at least 10 centimeters (cm) diameter at breast height (dbh) are tagged, identified, mapped, and measured. The plot was initiated in 1974–1975 and was subsequently enlarged several times, most recently from 2.25 ha to 4.0 ha in 2002. A single hectare located in the center of the plot was inventoried and monitored for large saplings (at least 1 cm but less than 10 cm dbh) beginning in 1993, and small saplings (at least 1 meter [m] tall and less than 1 cm dbh) beginning in 1997–1998. Then, in 2002, we initiated a program of seed trapping with 289, 0.5 square meter (m^2) traps set 7.5 m apart in a 17 × 17 array covering 1.44 ha centered over the sapling monitoring portion of the encompassing tree plot. The traps were monitored biweekly for 8.4 years until January 2011; trees and saplings were monitored until 2015. Therefore, we have a long-term record of seedfall onto the central subplot within which we monitored sapling recruitment with known X, Y coordinates for all traps and qualifying stems.

Suppressed sapling recruitment around fruiting conspecifics is obvious when trees, saplings and seedfall are all concurrently mapped (figure 1). In all of the four cases illustrated, most saplings are found in zones of barely detectable to unmeasurable seedfall. Assuming a null hypothesis in which all seeds are equal, we found the highest values for observed and expected sapling density at opposite poles of the seed density scale. Results of the same character were obtained for all 101 species that could be adequately represented by data. Seed success increases, often by more than 100-fold, away from seed-bearing conspecifics and

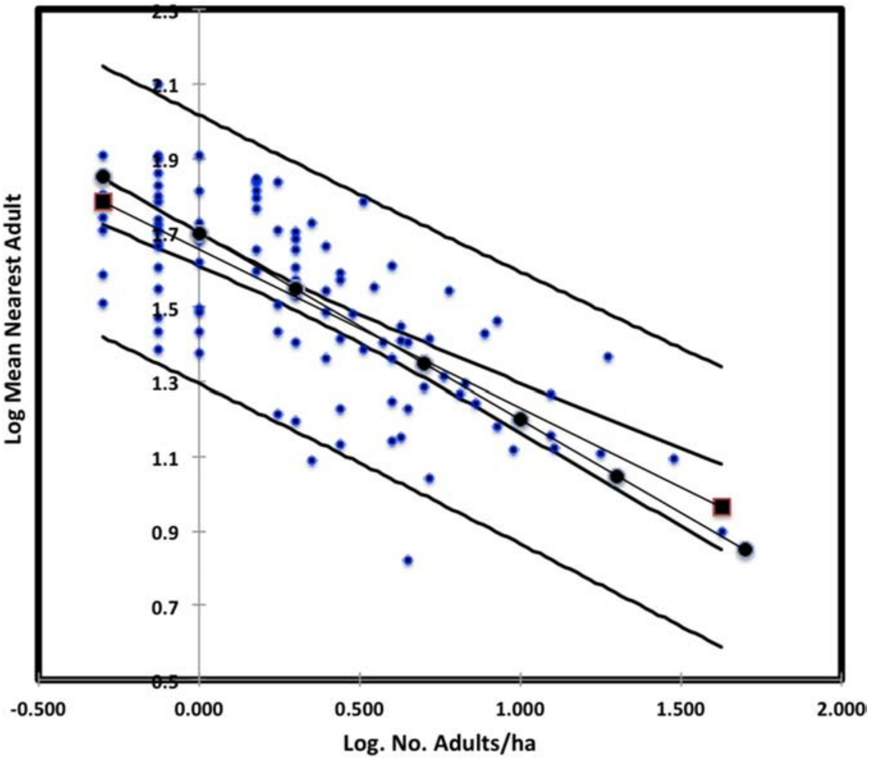

Figure 2. The regression of the log mean recruitment distance as a function of the log of the number of conspecific trees per ha for 101 species of common to moderately common trees at Cocha Cashu (the square symbols). A closely parallel line (the dots) shows the expected regression line calculated from the formula 1 ÷ (2 × the square root of density), which portrays the expected nearest-neighbor distance of randomly arrayed points as a function of their density. The envelopes represent, respectively, the 95% confidence limits of the regression (inner) and points (outer). Note that the calculated expected line is within the 95% confidence limits of the regression through the points. Clumped populations would plot below the expected line and hyperdispersed populations above it. The symmetry of the residuals around the regression line suggests that the deviations are normal sampling and measurement errors, not evidence of conflict with the model. Note that the mean recruitment distances represented by small diamonds in the figure represent distances to the nearest conspecific tree at least 10 cm dbh, not to the nearest confirmed seed producing conspecific. The distances based on seed bearing trees would have been ideal, but the task of identifying every fruiting tree in 4 ha was beyond our capacity. Source: Adapted from Terborgh and colleagues (2008) with permission.

is maximal at seedfall densities that were often too low to measure (Swamy and Terborgh 2011). Seeds falling near fruiting conspecifics had zero or near-zero success in generating saplings.

The same data can be used to construct Janzen–Connell seed shadow and escape curves (figure 1). Note that the escape curves do not rise at the same distance from the nearest adult. One, *Quararibea wittii*, the commonest tree in the forest, recruits at distances less than 10 meters, whereas the escape curve of *Caryodaphnopsis*, an uncommon species, does not reach a point of inflection until approximately 28 meters. The other two species are both of intermediate abundance and their escape curves rise at intermediate distances. The association of escape distance with abundance is a broad feature of our data that can be visualized more comprehensively in a different representation (to follow below).

Knowing the locations of all trees at least 10 cm dbh in the 4.0 ha encompassing plot and the locations of all saplings in a centrally situated subplot allows calculation of the distances of every sapling of a species to the nearest conspecific tree for all conspecific trees out to 55 m, the horizon for this scheme. The horizon is set by the distance from the outer boundary of the central sapling subplot to the outer perimeter of the encompassing 4.0 ha tree plot. Therefore, our data set is limited to species of sufficient abundance that a conspecific tree is within 55 m of every sapling in the central subplot.

We can test the hypothesis that saplings occur at random (or other) distances from conspecific trees using a simple formula NND = 1 ÷ (2 × the square root of the density), which describes the nearest neighbor distances (NNDs) of points in a plane as a function of the density of points. The formula yields a straight line on a double log plot. To represent values for species instead of individuals, we calculated the minimum distance of each sapling of 101 species to the nearest conspecific tree and then averaged these minimum distances to obtain an estimate for what I shall call the mean recruitment distance for the species. The log of these distances is then plotted against the log of the density of conspecific trees.

What emerges (figure 2) is a tight regression (R^2 = .51) that is indistinguishable from the line of randomness. The points, representing species, are closely associated with the trend and there are only three points that lie outside the 95% confidence limits, fewer than expected. Therefore, with a sample of 101 species, there is no evidence of establishment bias toward conspecific trees. If there were, those species would cluster more and more tightly through generations, but this clearly does not happen when recruitment occurs at random distances from established conspecifics. Most importantly, there was not one species among the 101 that deviated from the pattern, suggesting that all species in the community are subject to Janzen–Connell regulation.

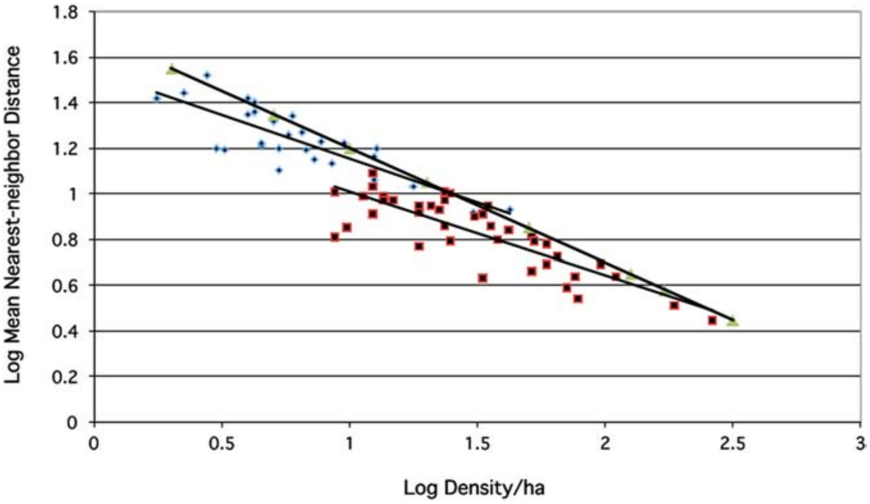

Figure 3. Similar log–log plots showing nearest-neighbor distances between conspecific trees (squares) and between conspecific saplings (diamonds) against their respective abundances in the stand. The line marked with triangles is the line of randomness.

Clustering of stems does occur, however, in both saplings and trees at least 10 cm dbh (figure 3). Divergence of the sapling versus sapling and tree versus tree regressions below the line of randomness indicates that clumping becomes more pronounced for less common species, as was also noted by Condit and colleagues (2000). Because saplings tend to be clustered *inter se*, but occur at random distances from mature conspecifics, clustering cannot result from weak dispersal but arises instead through the process of dispersal itself, when several dispersed seeds are successful in a small area, perhaps a gap or under a bird, bat, or primate roost (Russo and Augspurger 2004). Clusters of saplings will then give rise to clusters of adults (Fragoso et al. 2003).

Propagule mortality near reproducing conspecifics may be conditional in certain circumstances (e.g., in gaps versus under the canopy), but the issue has been rarely investigated (Hammond and Brown 1996, Alvarez-Loayza et al. 2011, Deniau et al. 2018).

What are the mortality agents that generate distance effects? Janzen himself wrote extensively on this question in the 1970s in a series of rarely cited papers (e.g., Janzen 1971a, 1971b). His main emphasis was seed predation. The mortality agents were mostly bruchid beetles that incubate their larvae inside seeds with lethal consequences for the seed (summarized in Janzen 1980). The most essential attribute of these beetles is that they carry out their entire life cycle in association with the host species. Therefore, they are not everywhere in the forest except perhaps as rare dispersing individuals. They occur in abundance only around host trees that produce the required substrate for their larvae. It is the close spatial association between pest and host that creates exclusion zones and distance dependence. Furthermore, research by Wright (1983), Fragoso and colleagues (2003), and others on palm seeds have largely supported Janzen's results.

Without knowledge of a tree's natural history, there is no certainty as to whether it's host-specific mortality agents act at the seed or seedling stage. At Cashu we have been studying the tree community for more than 40 years, so which tree species produce seedling carpets is well known. A seedling carpet, as it is defined in the present article, is a dense aggregation of seedlings under a reproducing conspecific, mostly arising from undispersed seeds. Seedling carpets appear under certain species after each fruiting episode and the seedlings may persist for months or even years.

To study this phenomenon, we selected fruiting individuals of four species that generate seedling carpets for close observation. Seedling carpets resulting from a known fruiting episode were monitored periodically for up to 37 months. Also monitored were heterospecific seedlings growing among the conspecific seedlings. The purpose was to determine how each seedling died, with the specific goal of identifying the mortality agent. For conspecific seedlings, this was challenging because several of the agents proved to be tiny arthropods—stem borers, root borers, leaf miners—that we isolated by placing infected seedlings in plastic bags and waiting until the adult insect emerged. In no case did we recover any of these insects from heterospecific seedlings (figure 4). Fungi were also implicated as mortality agents, as had been shown earlier (Packer and Clay 2000, Klironomos 2002, Pringle et al. 2007, Mangan et al. 2010). At the end of the monitoring period, at least 90% of conspecific seedlings had died, whereas half or more of the initial crop of heterospecific seedlings survived (figure 5; Alvarez-Loayza and Terborgh 2011). To evaluate whether conspecific seedlings ever survive, we surveyed the areas under the crowns of all focal trees for conspecific saplings at least 1m tall and found none. We therefore concluded that mortality of conspecific seedlings under reproducing adults is normally 100%.

Our data clearly show that most species can establish anywhere in the plot, which is flat and rests on recently deposited alluvium (entisol), so contains minimal spatial heterogeneity. Apart from seedling carpets, which are infrequent and local, tree seedlings are scattered and mixed with liana seedlings and herbs, including ferns, which are particularly numerous at our site.

Small plants (less than 30 cm tall), including all groups mentioned above average about 20 per m^2 (Terborgh and Wright 1994), a value that lies well below the density at which crowding effects set in (approximately 100 per m^2; Wiener 1995). To address the question of whether tree seedlings experience competition from other small plants, Paine

Calatola microcarpa: stems bored by a lepidopteran larva that destroys the vascular system and ultimately causes the death of the seedling. The damage progresses from the top of the stem downwards, following a characteristic spiral pattern.	
Clarisia racemosa: damage produced by a coleopteran larva that attacks the root and lower stem of young and old seedlings. It causes wilting, whereupon the fungus *Colletotrichum* sp. invades (or becomes pathogenic from its endophytic phase), the wounds causing dark spots inside the stem. Eventually the seedling dies.	
Matisia cordata: first leaf of a young seedling invaded by a leaf miner (lepidoptera) enabling a secondary fungal infection (brown sunken lesions near the mines) that eventually kills the plant.	
Sorocea pileata: seedling infested with a fungal pathogen, *Phoma* sp. Leaf veins become brown and release black spores. The seedling eventually wilts and dies.	

Figure 4. Host-restricted arthropod or fungal mortality agents affecting conspecific seedlings of four tree species at Cocha Cashu, Perú. Source: Reprinted from Alvarez-Loayza and Terborgh (2011) with permission.

and colleagues (2008) removed up to 90% of small plants in experimental plots at Cocha Cashu and assessed the effects on those that remained. They found no discernible effects, either on growth or survival and concluded that competition was minimal as a process influencing species diversity at the seedling stage. Much stronger is the asymmetric competition of trees on seedlings (Lewis and Tanner 2000, Freckleton and Watkinson 2001). Trees absorb most of the sunlight entering forests and have pervasive root systems that absorb water and nutrients everywhere in the forest. Therefore, in general, saplings are less likely to be affected by one another than by the trees growing over them.

Dispersal. A majority of the tree species in the hyperdiverse forests of the central tropics occur at low to very low densities. The tree species of median abundance at Cocha Cashu, for example, is represented by less than one individual per thousand trees at least 10 cm dbh. Moreover, many of these scattered individuals are juveniles or males that do not produce fruit. Consequently, the seed rain of many species is so scant as to be scarcely detectable.

Dispersal limitation is defined as the failure of seeds of a given species to arrive at a given establishment site (Clark, Macklin and Wood 1998). To quantify dispersal limitation at Cocha Cashu, we monitored 0.5 m^2 seed traps for 8.4 years. The seeds of 60% of the species captured (not counting those that were not captured) fell into less than 1% of the 289 traps every year (Terborgh et al. 2019). Only 4 of 104 common species produced enough seeds to reach even 10% of the traps. Therefore, establishment sites, which we will define for convenience as including an area of 0.5 m^2 (equal to that of seed traps), receive seeds of only three or four tree species in a given year, or less than 1% of the forest's diversity. The failure of the seeds of most species to arrive at even 1% of the available sites in a given year implicated fecundity as the principal cause of dispersal limitation (Terborgh et al. 2011). The circumstances conform to Hurtt and Pacala's (1995) "winner by forfeit" paradigm, in which the best competitor in the community fails to contest the site.

Species accumulation curves generated by the 289 individual seed traps are essentially linear, not leveling off even after 8.4 years of monitoring (Terborgh et al. 2019). Some show a sharp rise in the first year, reflecting fruit or seeds falling from overhanging trees. Subsequently, similar numbers of new species, representing dispersed seeds from a pool of hundreds of species, add to the total every year to maintain the linear trend. Differences between the traps in the rate of species accumulation result in part from greatly reduced seedfall in gaps (Terborgh et al. 2017) and in part from low overhanging branches and vines that may deflect falling seeds. High rates of species accumulation can be expected under bird, bat, and primate roosts (Russo and Augspurger 2004).

To relate sapling recruitment to the rain of dispersed seeds, we calculated two independent sets of distance measurements, one for dispersed seeds captured in seed traps and the other for saplings recruiting in the surrounding plot, referring them to the nearest seed-bearing conspecifics for 17 species for which adequate data were available (figure 6). The two sets of distances did not differ significantly, implying that the distribution of dispersed seeds, like that of recruiting saplings (cf. figure 2), is random in relation to reproductive conspecifics.

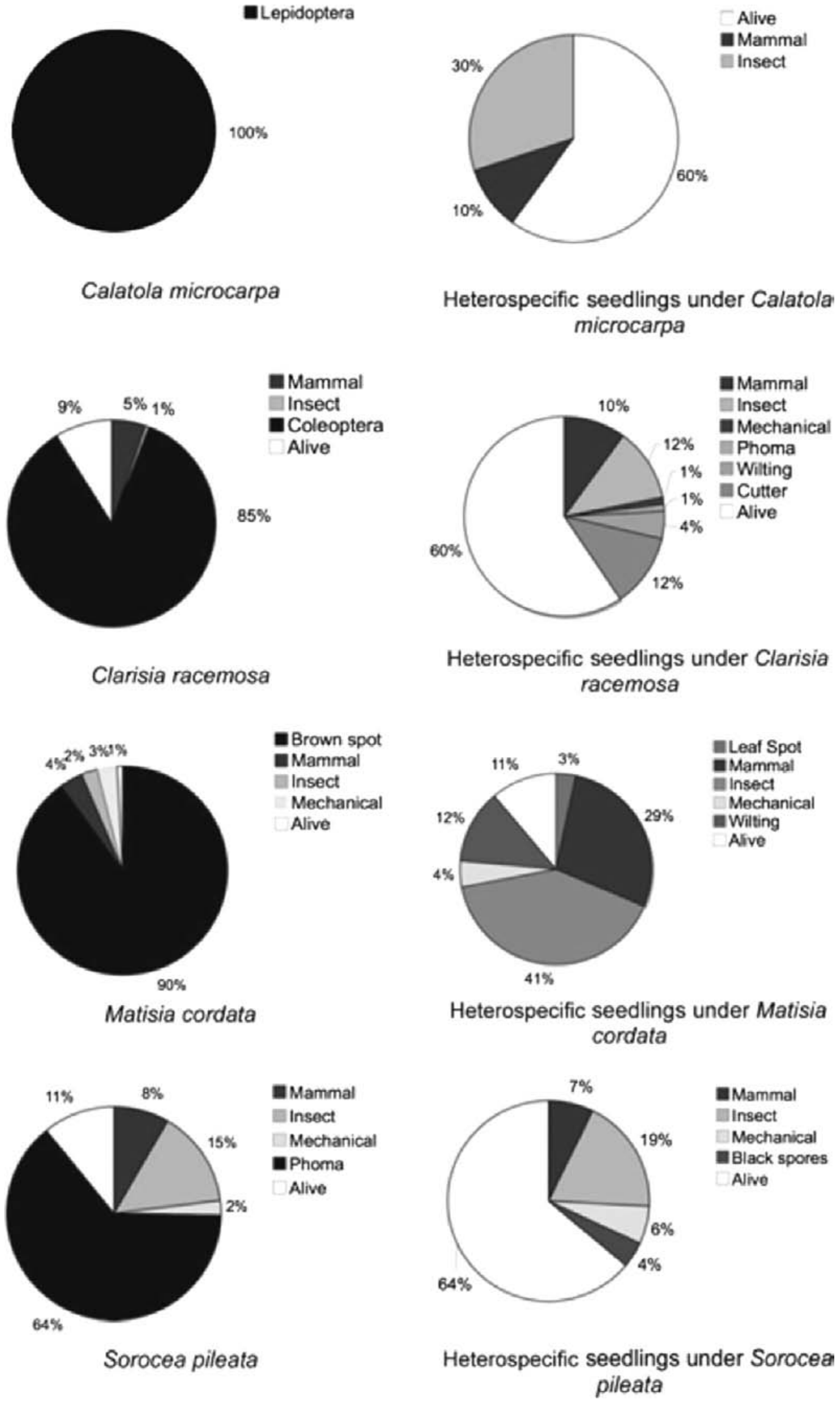

Figure 5. Pie diagrams representing percentage mortality, by cause, for conspecific (left) and heterospecific seedlings (right) in seedling carpets of the indicated species. Source: Reprinted from Alvarez-Loayza and Terborgh (2011) with permission.

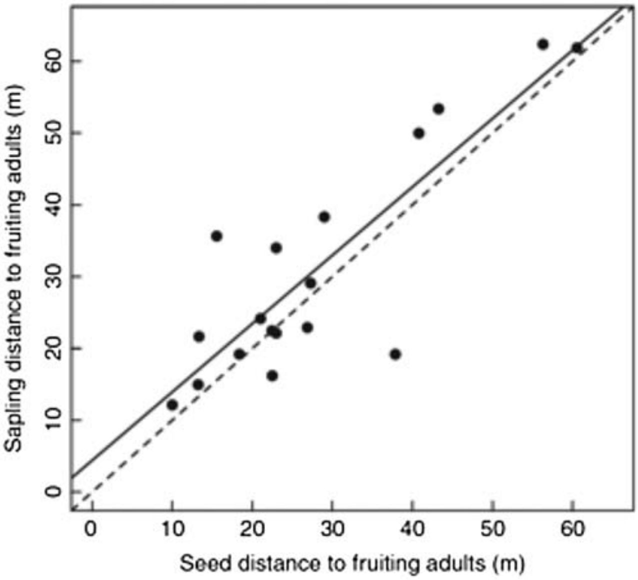

Figure 6. Median distance of recruited saplings versus median distances of dispersed seeds of 17 tree species at Cocha Cashu to the nearest seed-producing conspecific. The observed, best-fit linear relationship is shown (solid line) is indistinguishable from a 1:1 linear relationship (dashed line). Fewer species are included in this figure because distances are calculated to the nearest fruiting conspecifics rather than any conspecific stem at least 10 cm dbh. Source: Reprinted from Terborgh and colleagues (2011) with permission.

This result bears on one feature of Janzen's (1970) focal tree model, which shows a population recruitment curve nested under the seed shadow and escape curves, a feature that may have given rise to misunderstandings. Tropical dispersers, whether birds, bats, primates or the wind, are capable of carrying seeds hundreds of meters, or even kilometers, distances that far exceed the distances between the nearest neighboring fruiting conspecifics (Holbrook and Smith 2000, Hardesty et al. 2006). In our experience, sapling recruitment does not occur in a circumscribed band around fruiting trees; it occurs at low densities throughout the forest. Therefore, it appears that the seed shadows of fruiting conspecific trees broadly overlap, implying that the seeds of most species are distributed broadly but in scant numbers.

Efforts to model the seed shadows of tropical forest trees have frequently employed the assumption that all seeds are equal and have calculated steeply concave dispersal kernels that are heavily influenced by undispersed seeds (Muller-Landau et al. 2008, Marchand et al. 2020). Where disperser communities remain intact, as they are at Cocha Cashu, dispersed seeds fall at random in the forest although this may not be true of defaunated forests lacking important dispersers (Terborgh et al. 2008, Bagchi et al. 2018). Studies of seedling parentage have revealed that the nearest adult tree is seldom a parent of a given seedling (Hardesty et al. 2006, Moran and Clark 2011). Dispersal beyond the distance of the nearest neighboring conspecific trees is probably routine, ensuring that the seed shadows of dispersed seeds are broadly overlapping and relatively flat (Terborgh et al. 2019).

Unsettled questions. Fifty years of research has produced hundreds of publications on the JCH, and has seen a great deal of progress, but there remain many important questions to be resolved, some of which go to the very heart of the diversity issue. Obsessive preoccupation with the focal tree model has blinded investigators to many aspects of the Janzen–Connell mechanism that have the potential to yield new insights and important results. I shall now offer comments on some of these outstanding issues.

Nearly all the empirical research into the Janzen–Connell mechanism has examined large canopy trees (reviewed by Carson et al. 2008), but the tropical forest isn't composed only of canopy trees; most of its plants are small (Spicer et al. 2020). How far down the size scale does Janzen–Connell operate?

We uncovered evidence pertaining to the issue of plant size and Janzen–Connell in pursuing another question: *How many seeds does it take to make a sapling?* (Terborgh et al. 2014). Canopy level trees may produce hundreds or thousands of fruits, whereas understory treelets may produce scarcely a dozen or so a year. How is it that trees and treelets, on average, have the same mean lifetime reproductive success? An analysis of the seed production and sapling recruitment rates of 48 species of trees and treelets found, after removing effects of seed size, dispersal mode, and sapling mortality rates (a surrogate for light dependence), that tree height accounted for a 13-fold difference between trees and treelets in the number of seeds required to generate a sapling.

How can the potential of a treelet seed be 13 times greater than that of an otherwise equivalent tree seed? Is it better germination? Better dispersal? Fewer enemies? All these possibilities are valid. However, the last of them relates directly to the Janzen–Connell mechanism. A treelet that produces only a handful of fruits a year may not generate enough resources (seeds or seedlings) to encourage the evolution of host-specific pests. Related to this is the fact that many treelets exhibit a fruiting schedule very different from that of canopy trees, many of which offer ripe fruit for a few days to a few weeks and then drop any that are not harvested by consumers. In contrast, many treelets ripen fruits one or a few at a time and may continue for many weeks to display any that are not promptly harvested, a trait that promotes eventual dispersal (Terborgh 1983). Whether or not the seeds or seedlings of treelets attract host-specific mortality agents is currently unknown but it is a question that can readily be answered.

How host specific are Janzen–Connell mortality agents? Trees may have many pests. Is there redundancy among them? That is, if one pest is absent, can another host-specific pest create a similar exclusion zone? What if host specificity is relaxed so that pests are able to attack multiple species? The community-level effects are probably small because a given pest species is unlikely to be equally lethal for each of several host species (Augspurger and Wilkinson 2007, Alvarez and Terborgh 2011).

What is the relation between the size of the exclusion zone and a species' abundance in the community? In our simulations of the Janzen–Connell model, broadening exclusion zones to two or three crown diameters from a focal tree increased the number of species that could be sustained in the community, implying that, on average, each species was less common (Levi et al. 2019). If one generalizes the result, it suggests that variation in the size of exclusion zones could regulate species' abundances. This is an intriguing possibility that begs to be investigated.

Another fundamental question that remains to be answered is how to reconcile what we know about the dimensions of exclusion zones versus recruitment distances (the mean distance of recruiting saplings to the nearest conspecific that is at least 10 cm dbh). For many species, recruitment distances exceed 50 m. The data presented in figure 1 show that the escape distance (taken as the point of inflection of empirically constructed escape curves) for four species ranged from less than 10 m for the most abundant tree in the forest to 28 m for an uncommon species. The recruitment distances of the four species illustrated in figure 1 and their respective escape distances are as follows from most to least abundant: *Q. wittii*, recruitment distance = 7.9, escape distance = 9 m; *P. laevis*, recruitment distance = 14.4 m, escape distance = 12 m; *C. densifolia*, recruitment distance = 11.0 m, escape distance = 17 m; *C. fosteri*, recruitment distance = 31.5 m, escape distance = 28 m. Although they were calculated in different ways, the numbers are in rough agreement. However, the escape distances refer to the distances from zones of high seedfall, whereas the recruitment distances refer to the nearest conspecific tree of at least 10 cm dbh without regard to its reproductive status. If recruitment distances had been referenced to seed-bearing conspecifics, the values would have been greater. Does this mean that recruitment distances are in general greater than escape distances? This is another question that awaits resolution.

How is one to interpret data on escape and recruitment distances? Do elevated densities of host-specific pests extend out to 30 m or more from host trees? Possibly so. Howe and colleagues (1985) found that experimental seeds and seedlings of *Virola surinamensis* showed improved survivorship out to 45 m from fruiting focal conspecifics. Augspurger (1984), working with transplanted seedlings of nine species of wind-dispersed trees, found that the escape distances of three of the species ranged between 30 and 60 m. (By the inflection point criterion used in the present article, the escape distances of the three species were closer to 25 m.) The relation between recruitment distances and escape distances remains to be clarified.

Is there a role of dispersal in determining recruitment distances? Because the seeds of a large majority of the tree species in the community fail to reach even 1% of establishment sites in a given year, establishment may occur at a considerable distance from parent trees just by chance. Further investigation will be required to resolve this matter as well.

Has enough evidence accumulated to elevate Janzen–Connell to the status of a mature theory, one that has enough credibility to be put to use in science, management, conservation and restoration (Terborgh 2013)? The answer will continue to be a matter of debate, because ecologists are notoriously slow to accept the broad validity of a theory. Arguing against this native skepticism are credible reports implicating the Janzen–Connell mechanism in temperate forests (Packer and Clay 2000, Yamazaki et al. 2009), temperate grasslands (Petermann et al. 2008) and coral reefs (Marhaver et al. 2013). The astute observations of Janzen and Connell have, like Robert Paine's (1966) experiment with starfish, been thought of as perhaps true but nevertheless mere idiosyncrasies of the particular environment from which they were described. We now know that Paine discovered a general principle of nature that extends to virtually all ecosystems (Estes et al. 2011, Terborgh 2015). If the reports of Janzen–Connell operating in diverse ecosystems around the world prove robust, we ecologists will be in possession of another powerful principle that can serve the needs of science and nature in a rapidly changing world.

Acknowledgments

We are grateful to the managers of Perú's Manu National Park (SERNANP and, previously, INRENA and DGFF) for annually issuing us permits to conduct research at Cocha Cashu for more than 40 years. Patricia Alvarez-Loayza and Fernando Cornejo V. have my special gratitude for their invaluable collaboration over more than two decades. I am grateful to three anonymous reviewers and the editors of *BioScience* for suggesting many ways to improve the manuscript. Research assistants, far too numerous to name, contributed indispensable support in data gathering and data transcription. Financial support of the Andrew Mellon Foundation and National Science Foundation (grant no. DEB0742830) is gratefully acknowledged.

References cited

Alvarez-Loayza P, Terborgh J. 2011. Fates of seedling carpets in an Amazonian floodplain forest. Journal of Ecology 99: 1045–1054.

Alvarez-Loayza P, White JF Jr, Torres MS, Balslev H, Christiansen T, Svenning J-C, Gil N. 2011. Light coverts endosymbiotic fungus to pathogen influencing seedling survival and niche-space filling of a common tropical tree, *Iriartea deltoidea*. PLOS ONE 6: e16386. https://doi.org/10.1371/journal.pone.0016386.

Augspurger CK. 1983. Seed dispersal distance of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. Journal of Ecology 71: 759–771.

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

Augspurger CK, Wilkinson HT. 2007. Host-specificity of pathogenic *Pythium* species: Implications for tree species diversity. Biotropica 39: 702–708.

Bagchi R, Swamy V, Farfan J-PL, Terborgh J, Vela CIA, Pitman NCA, Sanchez WG. 2018. Defaunation increases the spatial clustering of lowland Western Amazonian tree communities. Journal of Ecology 106: 1470–1482.

Carson WP, Anderson JT, Leigh EG Jr, Schnitzer SA. 2008. Challenges associated with testing and falsifying the Janzen–Connell hypothesis: A review and critique. Pages 210–241 in Carson WA, Schnitzer SA, eds. Tropical Forest Community Ecology. Wiley-Blackwell.

Chave J, Muller-Landau HC, Levin SA. 2001. Comparing classical community models: Theoretical consequences for patterns of diversity. American Naturalist 159: 1–23.

Cintra R. 1997. A test of the Janzen–Connell model with two common tree species in Amazonian forest. Journal of Tropical Ecology 13: 641–658.

Clark DA, Clark DB. 1984. Spacing dynamics of a tropical rain forest tree: Evaluation of the Janzen–Connell model. American Naturalist 124: 769–788.

Clark JS, Macklin E, Wood L. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecological Monographs 68: 213–235.

Comita LS, Queenborough SA, Murphy SJ, Eck JL, Xu K, Krishnadas M, Beckman N, Zhu Y. 2014. Testing predictions of the Janzen–Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. Journal of Ecology 102: 845–856.

Condit R, et al. 2000. Spatial patterns in the distribution of tropical tree species. Science 288: 1414–1418.

Connell JH. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–310 in den Boer PJ, Gradwell GR, eds. Dynamics of Populations. Centre for Agricultural Publications and Documentation. Wageningen, The Netherlands.

Deniau M, Jung V, Le Lann C, Kellner H, Béchade B, Morra T, Prinzing A. 2018. Janzen–Connell patterns can be induced by fungal-driven decomposition and offset by ectomycorrhizal fungi accumulated under a closely related canopy. Functional Ecology 32: 785–798.

Estes JA, et al. 2011. Trophic downgrading of planet Earth. Science 333: 301–306.

Fragoso JMV, Silvius KM, Correa JA. 2003. Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. Ecology 84: 1998–2006.

Freckleton RP, Watkinson AR. 2001. Asymmetric competition between plant species. Functional Ecology 15: 615–623.

Hammond, DS, Brown VK. 1996. Disturbance, phenology and life history characteristics: Factors influencing distance/density-dependent attack on tropical seeds and seedlings. Pages 51–78 in Newbery DM, Prins HHT, Brown ND, eds. Dynamics of tropical communities: The 37th symposium of the British Ecological Society Cambridge University. Blackwell Scientific.

Hardesty BD, Hubbell SP, Birmingham E. 2006. Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. Ecology Letters 9: 516–525.

Holbrook KM, Smith TB. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical forest. Oecologia 125: 249–257.

Howe HF, Schupp EW, Westley LC. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). Ecology 66: 781–791.

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.

Hurt GC, Pacala S. 1995. The consequences of recruitment limitation: Reconciling chance, history and competitive differences between plants. Journal of Theoretical Biology 176: 1–12.

Hyatt LA, et al. 2003. The distance dependence prediction of the Janzen–Connell hypothesis: A meta-analysis. Oikos 103: 590–602.

Janzen DH. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501–528.

Janzen DH. 1971a. Escape of juvenile *Dioclea megacarpa* (Leguminosae) vines from predators in a deciduous tropical forest. American Naturalist 105: 97–112.

Janzen DH. 1971b. Escape of *Cassia grandis* L. beans from predators in time and space. Ecology 52: 964–979.

Janzen DH. 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. Journal of Ecology 68: 929–952.

Klironomos JN. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417: 67–70.

Levi T, Barfield M, Barrantes S, Sullivan C, Holt RD, Terborgh J. 2019. Tropical forests can maintain hyperdiversity because of enemies. Proceedings of the National Academy of Science 116: 581–586.

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

Mangan SA, Herre EA, Bever JD. 2010. Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant–soil feedback. Ecology 91: 2594–2603.

Marchand P, Comita LS, Wright SJ, Condit R, Hubbell SP, Beckman NG. 2020. Seed-to-seedling transitions exhibit distance-dependent mortality but no strong spacing effects in a Neotropical forest. Ecology 101: e02926.

Marhaver KL, Vermeij MJA, Rohwer F, Sandin SA. 2013. Janzen–Connell effects in a broadcast-spawning Caribbean coral: Distance-dependent survival of larvae and settlers. Ecology 94: 146–160.

Molofsky J, Fisher BL. 1993. Habitat and predation effects on seedling survival and growth in shade-tolerant tropical trees. Ecology 71: 261–265.

Moran EV, Clark JS. 2011. Estimating seed and pollen movement in a monoecious plant: A hierarchical Bayesian approach integrating genetic and ecological data. Molecular Ecology 20: 1248–1262.

Muller-Landau HC, Wright SJ, Calderón O, Condit R, Hubbell SP. 2008. Interspecific variation in primary seed dispersal in a tropical forest. Journal of Ecology 96: 653–667.

Murphy SJ, Wiegand T, Comita LS. 2017. Distance-dependent seedling mortality and long-term spacing dynamics in a neotropical forest community. Ecology Letters 20: 1469–1478.

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

Paine CET, Beck H. 2007. Seed predation by neotropical rain forest mammals increases diversity in seedling recruitment. Ecology 88: 3176–3187.

Paine CET, Harms, KE, Schnitzer SA, Carson WP. 2008. Weak competition among tropical tree seedlings: Implications for species coexistence. Biotropica 40: 432–440.

Paine CET, Beck H, Terborgh J. 2016. How mammalian predation contributes to tropical tree community structure. Ecology 97: 3326–3336.

Paine RT 1966. Food web complexity and species diversity. American Naturalist 100: 65–75.

Petermann JS, Fergus AJF, Turnbull LA, Schmid B. 2008. Janzen–Connell effects are widespread and strong enough to maintain diversity in grasslands. Ecology 89: 2399–2406.

Pringle EG, Alvarez-Loayza P, Terborgh J. 2007. Seed characteristics and susceptibility to pathogen attack in tree seeds of the Peruvian Amazon. Plant Ecology 193: 211–222.

Russo SE, Augspurger CK. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecology Letters 7: 1058–1067.

Schupp EW. 1988. Seed and early seed predation in the forest understory and in treefall gaps. Oikos 51: 71–78.

Spicer ME, Mellor H, Carson WP. 2020. Seeing beyond the trees: A comparison of tropical and temperate plant growth forms and their vertical distribution. Ecology 101: e02974.

Swamy V, Terborgh J. 2010. Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. Journal of Ecology 98: 1096–1107.

Swamy V, Terborgh JW. 2011. Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest. Ecology Letters 14: 195–201.

Terborgh J. 1983. Five New World Primates. Princeton University Press.

Terborgh J. 2012. Enemies maintain hyperdiverse tropical forests. American Naturalist 179: 303–314.

Terborgh J. 2013. Using Janzen–Connell to predict the consequences of defaunation and other disturbances of tropical forests. Biological Conservation 163: 7–12.

Terborgh JW. 2015. Toward a trophic theory of species diversity. Proceedings of the National Academy of Sciences 112: 11415–11422.

Terborgh J, Losos E, Riley MP, Bolaños Riley M. 1993. Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. Vegetatio 107: 375–386.

Terborgh J, Wright SJ. 1994. Effects of mammalian herbivores on seedling recruitment and survivorship in two neotropical forests. Ecology 75: 1829–1833.

Terborgh J, Pitman N, Silman M, Schichter H, Nuñez PV. 2002. Maintenance of tree diversity in tropical forests. Pages 1–17 in Levey DJ, Silva WR, Galetti M, eds. Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation. CABI.

Terborgh J, Nuñez-Iturri G, Pitman NCA, Cornejo Valverde FH, Alvarez P, Swamy V, Pringle EG, Paine CET. 2008. Tree recruitment in an empty forest. Ecology 89: 1757–1768.

Terborgh J, Alvarez-Loayza P, Dexter K, Cornejo F, Carrasco CR. 2011. Decomposing dispersal limitation: Limits on fecundity or seed distribution? Journal of Ecology 99: 935–944.

Terborgh J, Zhu K, Alvarez-Loayza P, Cornejo F. 2014. How many seeds does it take to make a sapling? Ecology 95: 991–999.

Terborgh J, Huanca Nuñez N, Alvarez Loayza P, Cornejo FV. 2017. Gaps contribute tree diversity to a tropical floodplain forest. Ecology 98: 2895–2903.

Terborgh J, Zhu K, Alvarez-Loayza P, Cornejo FV. 2019. Seed limitation in an Amazonian floodplain forest. Ecology 100: e02642.

Wiener J. 1995. Following the growth of individuals in crowded plant populations. Trends in Ecology and Systematics 10: 389–390.

Wills C, et al. 2006. Non-random processes maintain diversity in tropical forests. Science 311: 527–531.

Wright SJ. 1983. The dispersion of eggs by a bruchid beetle among *Scheelea* palm seeds. Ecology 64: 1016–1021.

Wright SJ. 2002. Plant diversity in tropical forests: A review of mechanisms of species coexistence. Oecologia 130: 1–14.

Yamazaki M, Iwamoto S, Seiwa K. 2009. Distance- and density-dependent seedling mortality caused by several diseases in eight tree species co-occurring in a temperate forest. Plant Ecology 201: 181–196.

John Terborgh (manu@duke.edu) is affiliated with the Department of Biology and with the Florida Museum of Natural History at the University of Florida, in Gainesville and with the College of Science and Engineering at James Cook University, in Cairns, Queensland, Australia.