Tree Dispersion, Abundance, and Diversity in a Tropical Dry Forest

Stephen P. Hubbell

SCIENCE

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That tropical trees are clumped, not spaced,
alters conceptions of the organization and dynamics.

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A widely held generalization about tropical tree species is that most occur at very low adult densities and are of relatively uniform dispersion, such that adult individuals of the tree species are thinly and evenly distributed in space. If true, this generalization has potentially profound consequences for the reproductive biology, population structure, and evolution of tropical tree species (*1*). In this article the adequacy of this generalization is judged with respect to a particular tropical forest, a large tract of which has been mapped in detail (*2*).

The origins of this generalization can be traced back at least to Wallace (*3*), who stated the following concerning his impressions of species densities in Malaysian forests:

If the traveller notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions, and colours are around him, but he rarely sees any one of them repeated. Time after time he goes toward a tree which looks like the one he seeks, but a closer examination proves it to be distinct. He may at length, perhaps, meet with a second specimen half a mile off, or may fail altogether, til on another occasion he stumbles on one by accident.

Dobzhansky and co-workers (*4*) enumerated the species in several 1-hectare stands of Amazonian rain forest, and concluded that "the population density of a half or more of the tree species in Amazonian forests is likely to be less

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than one individual per hectare." One or both parts of this generalization (low density, uniform dispersion) now appear in most ecology texts (*5*), and theories have been proposed to explain both the causes and consequences of low density and uniform dispersion of adult tropical trees. Janzen (*6*) and Connell (*7*) independently proposed theories to explain low density and spacing between adults. Janzen focused attention on the effects of host-specific herbivores that attack

ber of seeds arriving at that point" (*6*, p. 501).

Connell, in his earlier rain-forest studies, focused more attention on the dispersion and survival of young tree seedlings. In experimental studies of the fate of seedlings in an Australian rain forest, Connell, Tracy, and Webb (*8*) showed that survival was better in seedlings planted under adults of different species than under adults of the same species. They did not identify the causes of the differential mortality, but did suggest that herbivores attracted by adjacent adults would more often tend to defoliate and kill nearby seedlings rather than distant seedlings. Janzen and Connell both argued that such host-specific attack by herbivores would reduce the local density of any given species, open up habitat to invasion by additional species, and thereby maintain high species diversity (*9*).

Many explanations have been offered for the high species diversity in tropical forests, and these have been classified into equilibrium and nonequilibrium hypotheses by Connell (*10*), who now believes that high diversity is only maintained because of frequent disturbance.

Summary. Patterns of tree abundance and dispersion in a tropical deciduous (dry) forest are summarized. The generalization that tropical trees have spaced adults did not hold. All species were either clumped or randomly dispersed, with rare species more clumped than common species. Breeding system was unrelated to species abundance or dispersion, but clumping was related to mode of seed dispersal. Juvenile densities decreased approximately exponentially away from adults. Rare species gave evidence of poor reproductive performance compared with their performance when common in nearby forests. Patterns of relative species abundance in the dry forest are compared with patterns in other forests, and are explained by a simple stochastic model based on random-walk immigration and extinction set in motion by periodic community disturbance.

seeds. He noted that a high proportion of seeds falling under the parent tree are killed by such seed "predators," so called because the death of the seed is virtually assured; and he suggested that only those viable seeds transported some distance away from the parent would escape discovery and manage to germinate. The predicted result: "most adults of a given tree species appear to be more regularly distributed than if the probability of a new adult appearing at a point in the forest were proportional to the num-

Potential consequences of a low-density uniform dispersion of adult trees in tropical species might include lower outcrossing success, reduction in deme size, and requirements for long-distance pollination. Thus, the generalization that adults of tropical tree species are widely spaced has also spawned a number of hypotheses about unusual breeding systems in tropical trees (*11*), or special pollinator movements over long distances (*12*). It now appears that the majority of tropical tree species is facultatively or

obligately outcrossed; and the frequency of dioecy in tropical trees is very high by temperate zone standards (*13, 14*). Animals rather than wind, in most cases, are the agents of cross-pollination.

Characteristics of the Dry Forest

Many of the ideas about low density and uniform tree dispersion developed from observations in the rain forest. Therefore, the major results of this study are presented with the caveat that they may apply better to deciduous tropical forests or monsoon forests than to rain forests. Nonetheless the patterns found in the dry forest appear to be fully consistent with the available information on rain forests, with the exception that the dry forest has only a third to half the number of tree species. Conclusions about forest dynamics are necessarily tentative because they are based on the circumstantial evidence provided by one census at a single point in time.

The dry forest results were obtained from a detailed map of 13.44 hectares of forest in Guanacaste Province, Costa Rica, in which all woody plants with stem diameters at breast height (dbh) ≥ 2 centimeters were located to the nearest meter. A separate map of the population of each species was drawn by computer, with each plant marked by a letter to indicate position and dbh, and whether it was juvenile or adult. Maps were then analyzed in an attempt to answer, in part or in whole, the following questions about each of the tree species: (i) Is the dispersion of the adult tree population uniform? (ii) Are adult trees less clumped than the juveniles, or than the population as a whole? (iii) How do the densities of adult and juvenile trees change with greater distance from a given adult in the population? (iv) Is there evidence that spacing from a given adult to other trees increases from the juvenile to the adult tree classes? (v) How distant is the nearest adult, and how many adults can be expected within m meters of a given adult? (vi) What, if any, is the relationship between rarity of a tree species and its dispersion pattern or its population (size, age) structure? (vii) Does mode of seed dispersal or breeding system relate to abundance or dispersion pattern? (viii) Is there any evidence for density dependence in the per capita reproductive performance of adult trees? Questions of interest about the dry-forest community in general include: (ix) What tentative conclusions can be drawn about the equilibrium or nonequilibrium status of the forest? (x) What are the pat-
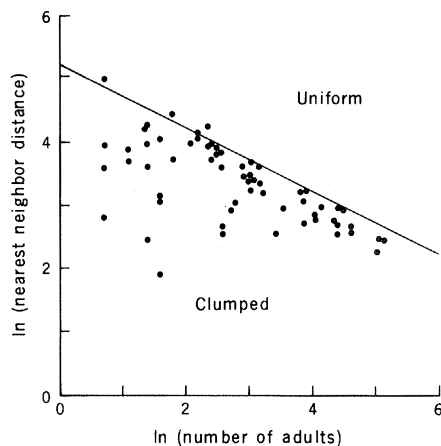

Fig. 1. Clumping in 61 tropical dry-forest tree species, as measured by mean nearest neighbor distance in meters. Diagonal line is the expected nearest neighbor distance for randomly dispersed populations [see (*37*)].

terns of relative species abundance in the dry forest, and how do they compare with the patterns in forests at other latitudes? Are the patterns of similar mechanistic origin?

Questions (i) through (iv) are of importance in evaluating the Janzen-Connell hypothesis. Question (v) is concerned with the minimum distance that a potential pollinator must fly to encounter another conspecific adult, and relates to the general question of deme size in tropical dry forest tree species. The answer to question (vi) is relevant to a discussion of the minimal density at which adult outcrossed trees of a species are capable of self-replacement. One way that a rare species can persist, in theory at least, even in the absence of long-distance pollination, would be through a higher degree of adult clumping than found in common species (*15*). Answers to questions (v) and (vi) may also suggest which of several alternative explanations of tree rarity is most probable (*16*).

The answer to question (vii) should reveal whether there are systematic differences in the adult or juvenile dispersion patterns of small-seeded species with wind or bird dispersal and large-seeded species with water or mammal dispersal. It should also reveal whether dioecious species differ systematically in density or dispersion pattern from self-compatible or hermaphroditic species. Janzen (*6*) and Bawa and Opler (*14*) hypothesized that, given similar pollination systems, the average interadult distance might be less in dioecious species because deme size would be roughly halved from that of an equally abundant hermaphroditic species. Skewed sex ratios, to the extent that they occur (*17*), should exacerbate the problem for the locally more abundant sex.

Question (viii) addresses the issue of what regulates the population size of tropical tree species. Does the number of nearby conspecific adults have a measurable influence on the reproductive performance of a given adult tree? The Janzen-Connell hypothesis would lead us to expect greater losses per adult in seeds and seedlings when adults are closer together, provided the per capita attractiveness of adult trees to herbivores is greater when the adults are in groups. Grouped adults may also compete more strongly for pollinator attention (*14, 18*) and encounter root and crown competition if they are actually adjacent to one another (*19*). Alternatively, there may be no detectable effect of adult density on per capita reproductive success (*20*).

Question (ix) relates to questions (vi) and (viii) and the reproductive success of rare trees. If the forest and its component species are in equilibrium, there should be found evidence that the rare species as well as the common species are self-replacing. In equilibrium theory, each species is presumed to be competitively superior at exploiting a particular microhabitat (*10*), with relative species abundance determined by the relative abundance of the microhabitat types. However, if the forest is in a nonequilibrium state, there should be evidence that some species are increasing in numbers while others, most likely the currently rare species, are declining.

Finally, question (x) asks whether the patterns of dominance and diversity in tropical, temperate, and boreal forests reveal any similarities that might suggest similar underlying control mechanisms. Using a simple stochastic model, I show that it is relatively easy to generate the patterns of relative species abundance in natural forest communities along a disturbance gradient. The model adds to the current theory of island biogeography a new statistical explanation for the relative abundance of species in arbitrarily defined habitat "islands" (*21*).

Study Site

The tract of mapped forest in Guanacaste Province, Costa Rica, lies approximately 8 kilometers west of Bagaces and 2 kilometers south of the Pan American Highway (*22*). The tract has been the site of studies of the pollinator community (*23*), and of the breeding systems and seasonal phenology of a number of tree species (*14, 18*). As a result of these and other studies (*24*), the pollination biology and the phenological cycles of leafing,

shedding, flowering, and fruiting are known for many of the deciduous forest tree species. Most species are obligately outcrossed by insects, birds, or bats. The climate of the Dry Forest Life Zone has also been described (25).

A total of 135 species of woody plants with stem diameters $\geq$ 2 cm dbh were found in the mapped area. These include 87 overstory and understory trees, 38 shrubs, and 10 vine species (26). About two-thirds of the tree species are deciduous through part or all of the dry season (December to May). The canopy is somewhat broken (15 to 25 meters high), and consists primarily of trees with medium-length boles and spreading crowns. Canopy cover is approximately 87 percent; the remainder consists of light gaps made by recent tree falls, and a narrow

grassland corridor through the center of the site (7 percent of the mapped area). The understory consists of a diverse array of tree seedlings and shrubs (27). Vines are common, but epiphytes are infrequent. Insect flower visitors, especially bees, are abundant, as are night pollinators such as bats and hawkmoths. Several types of vertebrate seed dispersers are common (28), and there is evidence of heavy insect and vertebrate seed predation in a number of tree species (29).

The mapped forest tract was a rectangular area, 420 m by 320 m, gridded into 336 quadrats 20 m on a side. All woody plants $\geq$ 2 cm dbh were identified to species (30), measured for diameter, and mapped to within $\pm$ 1 m of their true position within each quadrat (31). Sepa-

rate data were taken on the dbh of trees and shrubs in flower or fruit to establish a lower bound on the diameter of reproductive individuals (adults) for each species (32). The data for each quadrat were transcribed to computer cards; programs sorted individuals to species and recomputed the coordinates of each plant from its local quadrat to its coordinates in the study area as a whole. Maps were then drawn by a Calcomp plotter for each species (33).

Juvenile and adult dispersion patterns were examined over a range of quadrat sizes from 4 m² to 38,416 m² (196 m on a side), by Morisita's index of dispersion, I_δ (34). Determining juvenile and adult densities at different distances from each adult tree in the population was done from the Calcomp maps. Average den-
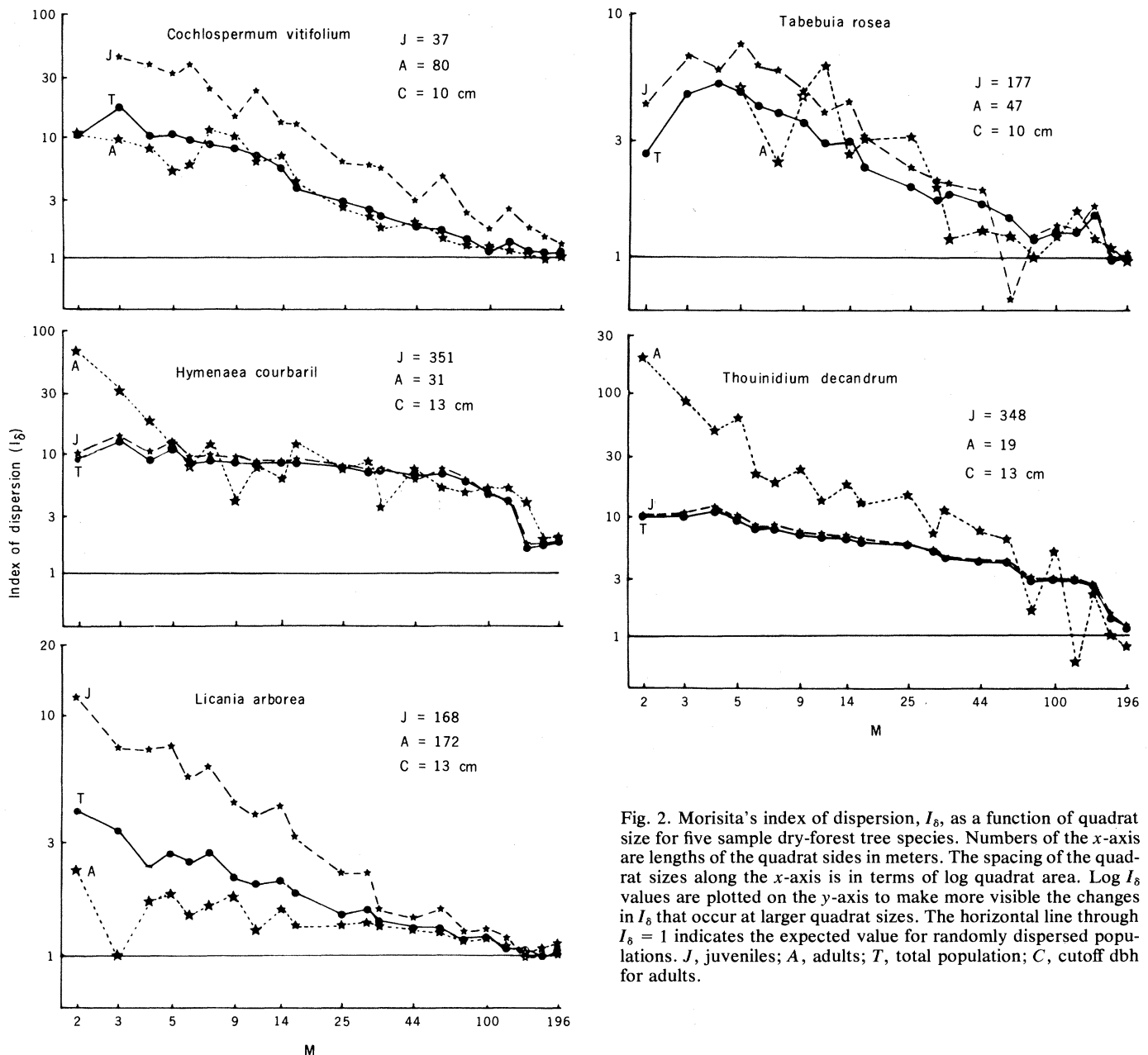
Fig. 2. Morisita's index of dispersion, I_δ, as a function of quadrat size for five sample dry-forest tree species. Numbers of the x-axis are lengths of the quadrat sides in meters. The spacing of the quadrat sizes along the x-axis is in terms of log quadrat area. Log I_δ values are plotted on the y-axis to make more visible the changes in I_δ that occur at larger quadrat sizes. The horizontal line through $I_\delta = 1$ indicates the expected value for randomly dispersed populations. J, juveniles; A, adults; T, total population; C, cutoff dbh for adults.

sities were computed for increments of 5 m out to a distance of 100 m (35). The maps were also analyzed to obtain the distribution of nearest neighbor distances between adults.

Tests for density dependence in per capita reproductive performance were made on 30 of the most abundant species. The gridded area was divided into 80 subplots of equal area, and the densities of adult and juvenile trees were noted for each subplot. The ratio of juveniles to adults was plotted as a function of adult density. Significant departures of slopes from zero were determined by regression analysis of variance. A necessary assumption of this test is that the adults counted in a subplot are the parents of the juveniles in the same subplot. Validity of this assumption varies with tree species and mode of seed dispersal (36).

Adult and Juvenile Dispersion Patterns

The adults of tropical dry-forest tree species are not uniformly dispersed in the forest, as shown in Fig. 1 for the 61 species on which information could be obtained on threshold adult diameter. The diagonal line in Fig. 1 is the expected nearest neighbor distance for randomly dispersed adults at the given mean density (37). Of these species, 44 (72 percent) exhibit significant adult clumping ($P < .05$, F test). The remaining 17 species (28 percent) have adult dispersion patterns which cannot be distinguished from random. No species has a significantly uniform adult dispersion.

When the dispersion of both adults and juveniles together is considered, the clumping is again pronounced. Of the 114 identified tree, shrub, and vine species having at least two individuals in the mapped area (38), fully 102 species exhibited significant clumping ($P < .05$, F test) in quadrats < 196 m on a side. As many as 95 species still showed significant clumping even in quadrats as small as 14 m on a side. No species showed a significantly uniform pattern of dispersion of its total population.

The pattern of change in Morisita's index of dispersion as quadrat size is increased from 2 to 196 m on a side, is shown (Fig. 2) for five species chosen at random from the 30 most common species (39). The dispersion indices for juveniles, adults, and total population are plotted separately. In all cases, including the species not illustrated, the dispersion index, I_δ, drops from its highest values in the smaller quadrat sizes irregularly downward toward unity as quadrat size

increases. Such I_δ patterns are typical of populations having "point sources" of relatively high population density, surrounded by more diffuse clouds of individuals diminishing in density away from the centers (32). Small quadrats may contain the high-density centers, thereby producing large I_δ values, whereas large

quadrats tend to have lower I_δ values because they average the density of the concentrated centers with the density of the more sparsely populated surroundings.

Question (ii) asks if the adults are less clumped than the population as whole, as would be expected from the Janzen-Connell hypothesis (6, p. 522). At a quadrat size of 14 m on a side and for the 30 most common tree species, adults are less clumped than juveniles and than the population as a whole in 16 species, equally clumped in nine species, and more clumped in five species. The results change somewhat depending on quadrat size and the scale of pattern resolution as well. Of the five species (Fig. 2), two species (Cochlospermum and Licania) show more clumping in juveniles than in adults at small quadrat sizes, two species (Hymenaea and Thouinidium) show more clumping in adults at small quadrat sizes, and one species (Tabebuia) shows approximately equal clumping in adults and juveniles.

Because of such clumping many species appear to be quite rare (less than one individual per hectare) when half or more of the study area is considered, but they turn out to be quite common when the rest of the study area is included. These patchy tree distributions help to explain data on tree species densities for relatively small plots of tropical forest (1 or 2 hectares) (40).

Demographic Neighborhood of the Average Adult

The "demographic neighborhood" of a tree may be defined as the population of adults and juveniles of the same species occurring within a specified radius of the tree. The "average adult" may be considered for the purposes of this article as one that exhibits the expected demographic neighborhood for an adult of the given species.

Question (iii) asks how the densities of adults and juveniles change with increasing distance from the average adult in the population. If the Janzen-Connell hypothesis is correct, densities should be lower near the adult than at some intermediate distance. What constitutes an
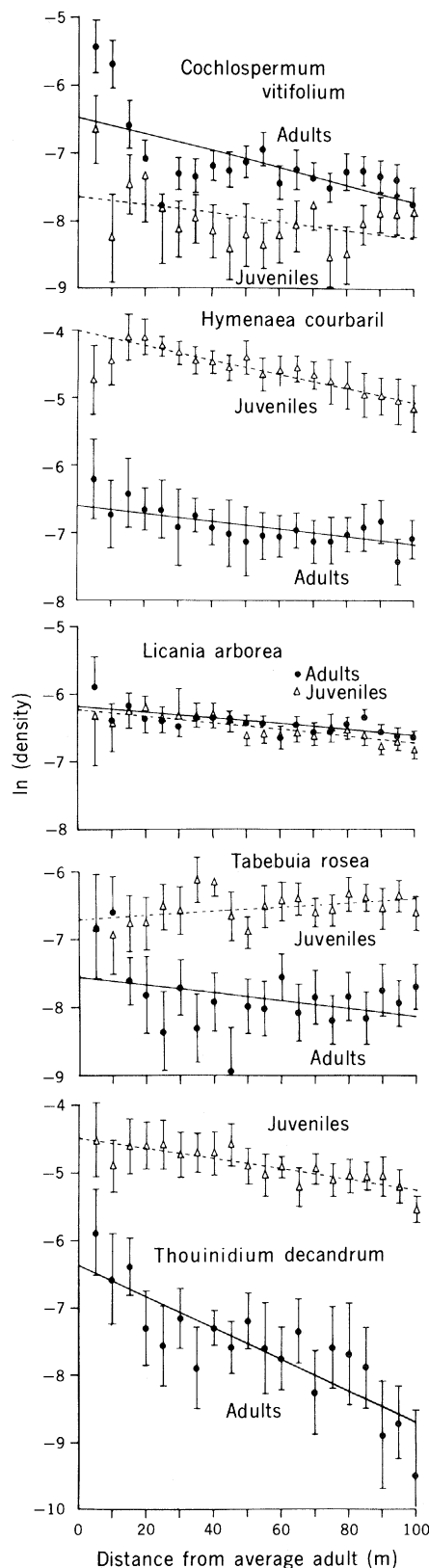
Fig. 3. Adult and juvenile densities (natural logarithm of numbers per square meter) at various distances from the average adult in the population, showing the negative slopes away from the average adult (the slope in Tabebuia rosea for juveniles is not different from zero) in the five sample species. The bars are 95 percent confidence limits for the means.

Table 1. Relative adult (A) and juvenile (J) densities in 5-m distance intervals away from the average adult, in the five sample species. Relative densities within adult and juvenile classes have been normalized to a sum of 100 percent for ease of visual comparison. In each distance interval, χ^2 tests were performed on the numbers of juveniles and adults counted.

Species		Relative densities at distance interval in meters:									
		0 to 4.9	5 to 9.9	10 to 14.9	15 to 19.9	20 to 24.9	25 to 29.9	30 to 34.9	35 to 39.9	40 to 44.9	45 to 49.9
Cochlospermum vitifolium	J	27.43	5.72	12.34	14.62	8.89	6.36	7.71	6.12	4.82	5.99
	A*	31.11	24.59	9.92	5.93	3.03	4.71	4.57	5.36	5.06	5.72
Hymenaea courbaril	J	7.23	9.30	12.77	12.15	11.45	10.36	9.44	9.29	8.21	9.80
	A†	16.41	9.90	13.19	10.35	10.69	8.06	9.75	7.93	7.09	6.63
Licania arborea	J	10.17	9.18	10.93	11.60	9.64	10.13	10.33	10.76	9.42	7.84
	A†	15.44	9.47	11.79	9.63	9.35	8.53	10.02	9.83	9.75	6.19
Tabebuia rosea	J	7.74	7.12	8.14	8.35	10.35	9.99	15.90	15.68	9.06	7.67
	A*	21.24	26.61	9.81	7.92	4.44	8.82	4.90	7.12	2.54	6.60
Thouinidium decandrum	J	11.44	7.98	10.78	10.86	11.02	9.50	9.72	9.89	11.08	7.73
	A*	26.94	13.48	16.84	6.74	5.25	7.86	3.60	6.57	5.18	7.54

*Significant difference ($P < .05$).   †Not significant ($P > .05$).

"intermediate distance" will depend on the tree species, but clearly it should not exceed the mean nearest neighbor distance between adults. The 30 most common species were analyzed, and the results do not support the Janzen-Connell expectation. Either adult and juvenile densities decline approximately exponentially away from the average adult, or densities remained unchanged, to and beyond the intermediate distances appropriate for the species. In 67 percent of the species, there were negative slopes for the log-transformed juvenile densities as a function of distance; and the slopes in all remaining species were not distinguishable from zero (41). An even greater percentage (90 percent) of these species also showed negative slopes for adult densities, and there were no positive slopes. Thus, at least for the 30 most common species, the average adult is clearly found in a clump with other adults and juveniles.

The adult and juvenile density curves for the five sample species (Fig. 3) reveal that the densities after log-transformation generally exhibited equal variance at all distances. In 15 of the 30 most common species, the highest mean juvenile density occurred in the 0 to 5-m annulus, closest to the adult. In ten additional species with horizontal density curves, mean juvenile density was no lower in the annulus closest to the adult than in other annuli. However, in the five remaining species, maximal juvenile density was achieved between 5 and 15 m from the adult. Hymenaea is one of these species in which there was a notable scarcity of juveniles immediately under the adult canopy. This species suffers heavy losses of seeds to predators (such as specialized insects and generalized vertebrates), but in spite of these losses, the maximum recruitment of juveniles is still quite close to the adult (15 m), only a

few meters beyond the crown perimeter (42).

It is possible that the distance at which the density of juveniles is maximal is not the distance with the highest probability of producing an adult. If juveniles die more often when they are growing close to an adult, there should be an increase in the mean distance between an adult and successively older cohorts of neighboring trees [question (iv)]. Alternatively, if mortality is a random thinning process regardless of distance from adult trees, there should be no significant change with increasing cohort age in the proportion of cohort individuals at a given distance. Seeds, seedlings, and saplings < 2 cm dbh—stages in which most of the mortality occurs—were not mapped. However, whatever the postulated mortality patterns in seeds and seedlings, the greatest density of surviving juveniles that remain after this mortality has taken its toll is nevertheless usually in the annulus closest to the adult. Therefore, if appreciable spacing is occurring, it must occur as a result of differential mortality among censused cohorts of juveniles ≥ 2 cm dbh.

Relative densities in juvenile and adult cohorts were computed to a distance of 50 m in the five sample species (Table 1). Two species (Hymenaea and Licania) do not show significant differences in the distributions of relative adult and juvenile densities, and for these species the null hypothesis of random thinning cannot be rejected. In the three remaining species, adult relative densities are shifted significantly closer to the average adult than are juvenile relative densities. This suggests that, contrary to prediction, the more distant juveniles suffer greater losses in these species (43). One explanation for such a result could be that adults are already growing in the sites most favorable to the species, with

outlying areas generally of lower microhabitat suitability. This pattern is repeated in the 30 most common tree species (including the five discussed above), of which 13 species have relative adult densities shifted closer to the average adult than relative juvenile densities. In the remaining 17 species the null hypothesis of random thinning could not be rejected. No species showed the predicted shift in relative adult densities to greater distances.

Question (v) concerns tree spacing from the point of view of pollinator movement. Although adults generally occur in clumps with other adults and juveniles, it is more specifically the absolute distance from one adult to the next that is important to pollination success. For the 30 most common species, the mean nearest neighbor distances are within 20 m in 16 species, and within 40 m in all species (44). These 30 species average 5.6 ± 1.3 adults within 50 m of a given adult, and 12.7 ± 2.7 adults within 100 m. A fourfold increase in area produces, on average, only a 2.3-fold increase in the number of adults, a further indication of adult clumping (Fig. 4).

The demographic neighborhood of the average adult is a composite of all the adults and juveniles in the population. Therefore, the density curves away from the average adult cannot be equated to the seed shadows of single adult trees since the curves result from the superposition of several overlapping shadows of neighboring adults. Nevertheless, the approximately negative exponential character of the composite density curves away from the average adult constitutes strong circumstantial evidence that relatively simple physical and biological mechanisms govern seed dispersal in these species.

One might expect that the effects of different seed sizes and modes of dis-

persal would be reflected in the slopes of these density curves [question (vii)]. In log transformation the slopes of the exponential density curves conveniently become independent of the absolute abundance and seed production of the species, permitting cross-species comparisons. Comparison of the slopes for adult and juvenile log density as a function of distance, in mammal-, wind-, and bird- or bat-dispersed species, is shown in Fig. 5. Mammal-dispersed species show the steepest slopes; shallower slopes are found in wind-dispersed species; and the shallowest slopes, on average, characterize the bird- and bat-dispersed species. All three pairwise contrasts of juvenile slopes are significantly different, and two of three adult slopes (except wind compared to bird) are significantly different ($P < .05$, Mann-Whitney U test).

Early work on dispersal by Dobzhansky and Wright (45) suggested that a bivariate normal might typically describe dispersal patterns. However, dispersal is frequently strongly leptokurtic, with a pronounced peak near the point of propagule origin (46). These results for dry-forest tree species suggest that seed dispersal as well as juvenile survival are much more leptokurtic in distribution in mammal-dispersed species than in either wind- or bird-dispersed species.

Dispersion, Abundance, and Density Dependence

In the preceding discussion I have dealt primarily with the most common third of the tree species. What is the dispersion of rare species? If individuals of rare species were dispersed at random, or spaced uniformly, nearest neighbor distances should increase with decreased density as fast or faster than the inverse square root of mean density (37); but this is not the case in adults (Fig. 1). When total population size is considered, the trend is toward increased clumping with decreased abundance (Fig. 6). A few species (outliers) do not conform to the general species sequence. I believe that these nonconforming species are probably "accidentals" or last survivors of once more abundant species (see below). Greater clumping in rare species has also been reported by Hairston (47) in old-field communities of soil arthropods.

The second part of question (vii), whether differences in breeding system explain any of the variation in dispersion, independently of population size, is answered in Fig. 6 (48). Self-compatible species are not overrepresented among rare species, nor are dioecious species more clumped for their abundance than hermaphrodite species. That most rare species are highly clumped might suggest that they are at least locally successful (reproducing themselves) when their microhabitat requirements are satisfied. However, the data on size (dbh) class suggest that per capita reproduction in rare species is considerably less per unit time than in common species. The coefficient of skewness of the dbh distribution about the midpoint diameter for each species was computed
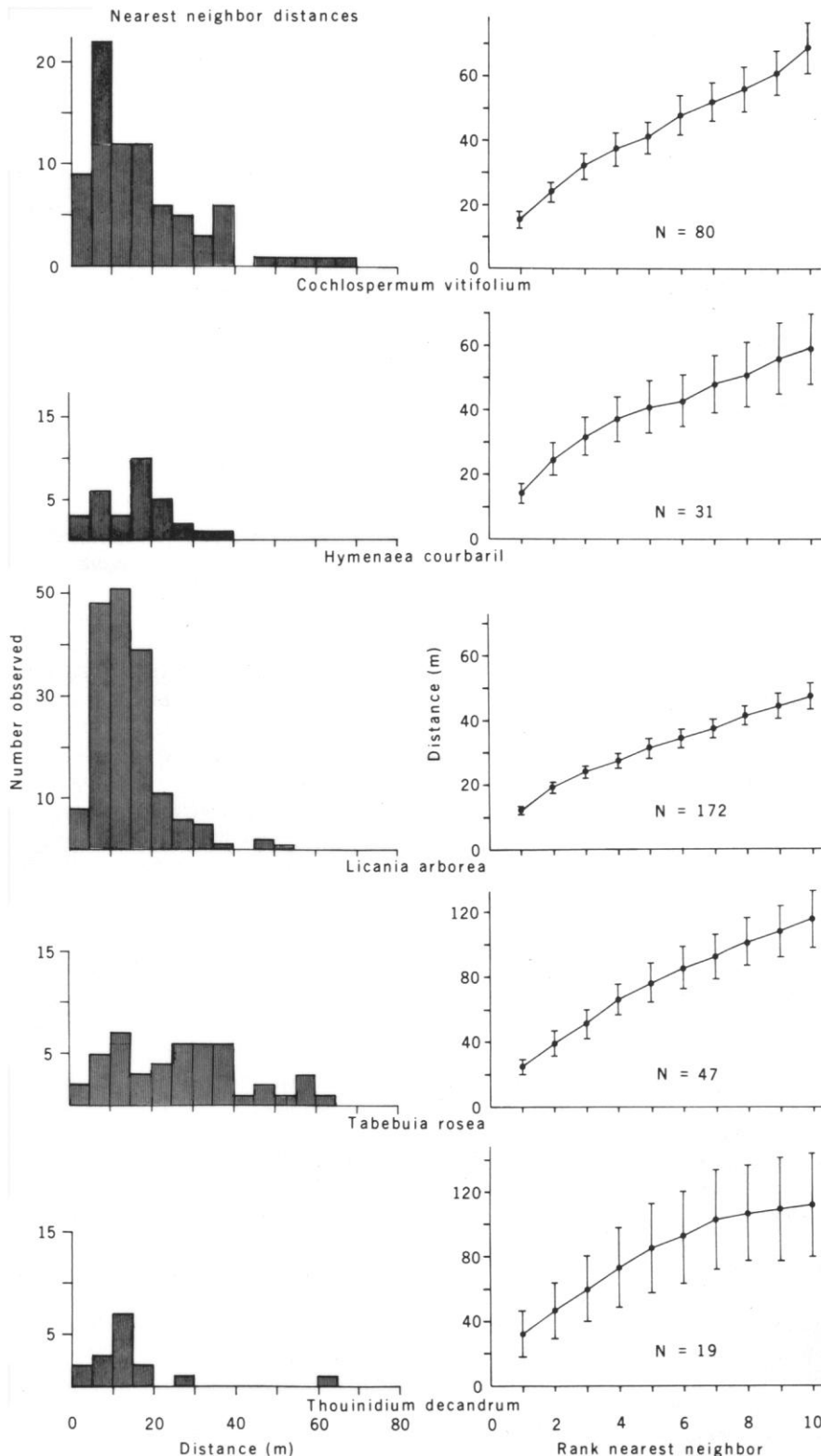

Fig. 4. (Left) The distribution of all first nearest neighbor distances for all adults, showing the closeness of the nearest adult, as well as the tendency to skew near (mode < mean). (Right) The mean distances, and their 95 percent confidence limits, to the first ten nearest neighbor adults, in the five sample species.

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(49); species having an excess of large adults show positive or zero skewing, and species with an excess of juveniles show negative skewing.

Rare species exhibit positive or zero skewing about the midpoint dbh, whereas common species exhibit negative skewing (Fig. 7). No biology is needed to explain negative skewing in common species because it would be physically impossible to fit so many trees into the available space if all were large adults. However, skewing in rare species is not constrained in either direction, yet no rare species is negatively skewed. This pattern does not prove that the rare species are failing to reproduce themselves—for example, successful reproduction might be extremely episodic (16)—but it is clear evidence for a much slower per capita rate of juvenile establishment in rare species than in common species (50).

Some of the rare species in the forest may be last survivors of species once more common in earlier successional stages, and some may be accidentals that became established through good fortune outside the habitat to which they are optimally adapted. All seven of the outlier species (Fig. 6) may be such accidentals because they are represented solely by very large, randomly scattered adults (51). These and other rare species are common on sites elsewhere in Guanacaste Province (52), and, where common, they exhibit strong negative dbh class skewing, as would be expected. Unless one is prepared to accept radically different life history strategies in adjacent plant populations of the same species, these results point to reproductive failure in the rare species in the tract of forest described here (53). Thus, the available circumstantial evidence suggests that the forest is in a nonequilibrium state (question ix).

Rare species might persist longer in a given forest stand than otherwise if the abundance of common tree species is limited, short of complete space monopoly, by density-responsive herbivory or seed predation, or by other density-dependent processes. There is no question that seed predation by specialized herbivores is intense and results in considerable thinning. Even if seed and seedling predation is a random thinning process in relation to distance from the average adult, it is still quite possible that seed predation can lower the per capita reproductive performance of whole clumps of adults compared to more isolated adults.

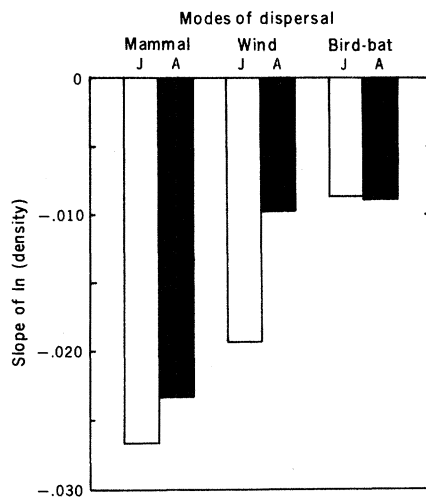Density dependence can be detected in the tree species [question (viii)]. Of

Fig. 5. Relation between the mode of seed dispersal and the steepness of the slope with which the natural log of the density (numbers per square meter) in adult (A) and juveniles (J) decreases with distance (meters) from the average adult in the population, showing the steeper slopes found in the heavier seeded, mammal-dispersed species. Sample sizes: 9 mammal-dispersed species; 12 wind-dispersed species; 9 bird- or bat-dispersed species.

the 30 most common species, 17 species (57 percent) exhibited significantly negative slopes in the regression of juveniles per adult on adult density. All 13 remaining species also showed a negative slope, but the null hypothesis of zero slope could not be rejected ($P > .05$). Density dependence was detected more frequently in species producing a large number of small seeds (generally the wind- and bird-dispersed species) as compared to species producing a smaller number of large seeds (mammal-dispersed species). Two-thirds of the wind- and bird-dispersed species exhibited density dependence, whereas only one-third of the mammal-dispersed species did (54).

What is the source of this apparent

density dependence? If it is primarily density-responsive seed and seedling predation, one might expect that the species attacked most heavily would in general be those exhibiting the strongest density dependence. However, in general, the large-seeded species are more frequently attacked by host-specific seed predators (commonly bruchid weevils) than are the smaller seeded species. An alternative hypothesis is that the density dependence is occurring via reduced per capita seed output in crowded adults, perhaps because of competition for pollinator attention or root and crown competition. It is also possible that some of these intraspecific effects are more apparent than real. The apparently greater frequency of density dependence among wind- and bird- dispersed tree species may be spurious (36). Moreover, if the adults of several species are positively associated in space, the shade and root competition they collectively produce would result in "diffuse" competition against the seedlings of all species growing beneath them (55).

Dominance-Diversity Relationships

Although it has long been clear that tropical land plant communities are far richer in species number than their temperate or boreal counterparts, sufficiently large data sets from which to make quantitative comparisons of relative species abundance have become available only in the last 25 years. When the species of a plant community are arranged in a sequence of importance (using a measure such as standing crop, basal area, or annual net production) from most to least important, they form a smooth progression without major discontinuities from the common to the rare

Fig. 6. Relation between total abundance (juveniles and adults in 13.44 hectares) and dispersion pattern for 87 tree and 8 large shrub species, showing the increased clumping in rare species. The y-axis is log I_δ for a quadrat size of 14 m on a side. Solid circles are outcrossed hermaphroditic species; open circles are self-compatible hermaphroditic species; and stars are dioecious species. The seven outlier species (inside dotted line) are not significantly clumped and are represented solely by very large adults.
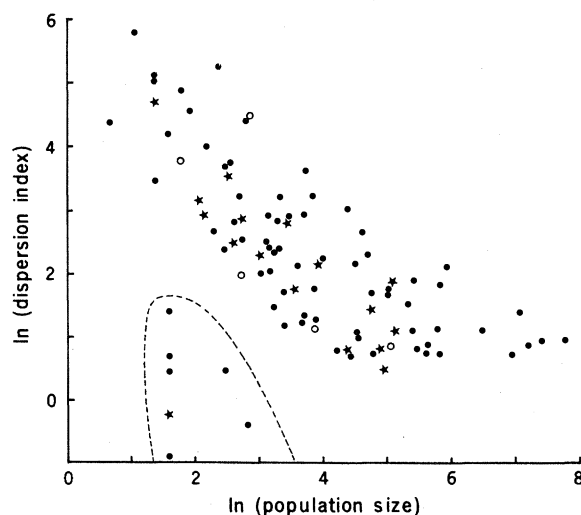
species. Different plant communities produce characteristic "dominance-diversity" curves when the importance values are log-transformed and plotted against the rank of the species in importance. Simple communities with few species generally yield almost straight ("geometric") lines on these semilog plots, whereas species-rich communities characteristically exhibit S-shaped ("lognormal") progressions (56).

Figure 8 compares the dominance-diversity curve for the tropical dry forest at 10°N (this study) with the curves for an equatorial (Amazonian) forest (57), for a rich temperate forest, and for a species-poor temperate montane forest similar to boreal forest (56). A number of factors distort the quantitative differences between the temperate and tropical dominance-diversity curves (58), but the qualitative pattern is clear: tropical forests exhibit the same general lognormal curve characteristic of rich temperate forests, but the distributions differ in location (mean) and scale (variance).

The rank-1 species in the dry forest has an importance value of 11 percent, compared with only 4.7 percent in the Amazonian forest. At 35°N, the rank-1 species in rich temperate forest has an importance value of 36 percent, which increases to about 65 percent in the montane spruce-fir forest. If the latter dominance-diversity pattern is comparable to patterns in the boreal coniferous forest at 50° to 60°N, then, as a general rule, the importance value of the dominant species in neotropical and neoarctic forests increases by approximately one percentage point for every latitudinal degree of northward movement, starting from a base of a few percent at the equator. Factors such as topographic diversity, elevation, the frequency and magnitude of disturbance, and physical harshness will likely cause local deviations from this general pattern (59).

Relative Species Abundance in Nonequilibrium Communities

The qualitative similarity between the dominance-diversity curves for temperate and tropical forests suggests that similar processes control the relative abundance of tree species in the two regions (question x). May (60) has cautioned against reading too much significance into lognormal species abundance patterns, noting that lognormal distributions may be expected when many random variables compound multiplicatively, given the "nature of the equations of population growth" and the central limit theorem. Recently, Caswell (61) built several "neutral" models of community organization and relative species abundance, based on neutral-allele models in population genetics; but lognormal relative abundance patterns were not obtained from any of them.

Another line of reasoning, however, does generate lognormal relative abundance patterns under one set of circumstances, as well as geometric patterns under other circumstances. The model is essentially a dynamic version of MacArthur's "broken stick" hypothesis (62), and is based on a nonequilibrium interpretation of community organization. Suppose that forests are saturated with trees, each of which individually controls a unit of canopy space in the forest and resists invasion by other trees until it is damaged or killed. Let the forest be saturated when it has K individual trees, regardless of species. Now suppose that the forest is disturbed by a wind storm, landslide, or the like, and some trees are killed. Let D trees be killed, and assume that this mortality is randomly distributed across species, with the expectation that the losses of each species are strictly proportional to its current relative abundance (63). Next let D new trees grow up, exactly replacing the D "vacancies" in the canopy created by the disturbance, so that the community is restored to its predisturbance saturation until the next disturbance comes along (64). Let the expected proportion of the replacement trees contributed by each species be given by the proportional abundance of the species in the community after the disturbance (65). Finally, repeat this cycle of disturbance and resaturation over and over again.

In the absence of immigration of new species into the community, or of the recolonization of species formerly present but lost through local extinction, this simple stochastic model leads in the long run to complete dominance by one species. In the short run, however, the model leads to lognormal relative abundance patterns, and to geometric patterns in the intermediate run. The magnitude of the disturbance mortality, D, relative to community size, K, controls the rate at which the species diversity is reduced by local extinction: the larger D is relative to K, the shorter the time until extinction of any given species, and the faster the relative abundance patterns assume an approximately geometric distribution (66).

The random differentiation of relative species abundance in a 40-species community closed to immigration is illustrated in Fig. 9 (67). Given equal abundances at the start, after 25 disturbances the species form the set of approximately lognormal dominance-diversity curves;

Fig. 7 (left). Coefficient of skewness of dbh distribution about midpoint dbh, as a function of total species abundance. Rare species are positively skewed toward large dbh, suggesting infrequent or highly episodic reproduction.   Fig. 8 (right). Comparison of the dominance-diversity curves for two tropical forests and two temperate forests. Importance values for the temperate forests are based on annual net production; importance values for the dry forest in Costa Rica are from basal area (cross-sectional area of all stems of a given species); importance values in the Amazonian forest are based on above-ground biomass [see (58) for additional comments].
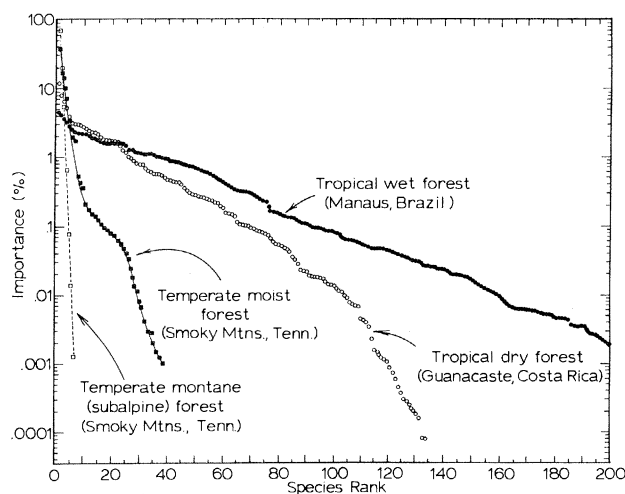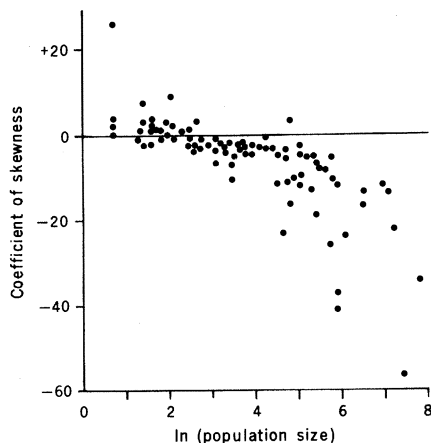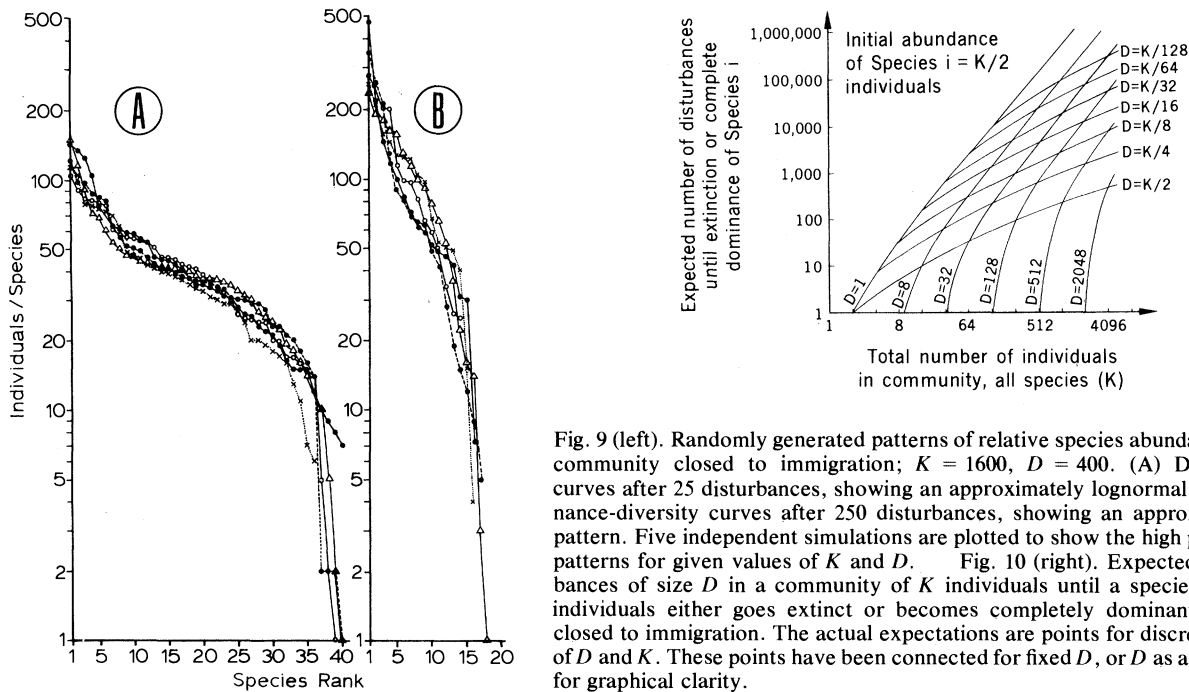
Fig. 9 (left). Randomly generated patterns of relative species abundance in a 40-species community closed to immigration; $K = 1600$, $D = 400$. (A) Dominance-diversity curves after 25 disturbances, showing an approximately lognormal pattern. (B) Dominance-diversity curves after 250 disturbances, showing an approximately geometric pattern. Five independent simulations are plotted to show the high predictability of the patterns for given values of K and D.   Fig. 10 (right). Expected number of disturbances of size D in a community of K individuals until a species starting with $K/2$ individuals either goes extinct or becomes completely dominant, in a community closed to immigration. The actual expectations are points for discrete (integral) values of D and K. These points have been connected for fixed D, or D as a fixed fraction of K, for graphical clarity.

whereas after 250 disturbances with no immigration, the species have formed the set of approximately geometric curves. These transient distributions are not perfectly lognormal or geometric, but exhibit a "tailoff" phenomenon in the abundances of rare species. Rare species are somewhat less common than would be expected from the symmetric lognormal distribution, resulting from the continual attrition of rare species through local extinction. The large data set for the dry forest reveals this same rare-species tailoff in the dominance-diversity curve (Fig. 8).

If total community size is expanded (K larger), the number of disturbances to extinction of any given species gets rapidly larger for any fixed disturbance size, D (Fig. 10) (68). If D is small and K is moderate-sized to large, time to extinction or complete dominance can be very long. For example, if eight trees are killed with each disturbance out of a community total of 512, it will on average take about 90,000 such disturbances to remove or "fix" a species which begins with 256 individuals (69).

When immigration of new or old species is allowed, however, eventual complete dominance by one species is precluded; and a stochastic equilibrium is established between species immigration and local species extinction. The resulting relative abundance patterns can be either more nearly lognormal or more nearly geometric, depending on the relative importance of immigration in replenishing species diversity reduced by dis-

turbance. If local extinctions outpace immigrations, local relative abundance patterns become increasingly geometric with time. As the rarer species drop out, the remaining species fill the gaps and grow more abundant, and thereby become less prone to extinction per unit time for a given level of disturbance. This causes the local extinction rate to drop into balance with the immigration rate. In contrast, if species immigrations outpace local extinctions, species must accumulate in the community, and local relative abundance patterns become more lognormal with time. Since more and more species are being packed into a finite space of size K, however, some species inevitably random walk to such rarity that they have a high risk of local extinction per time as compared with common species (70). A point is reached when sufficient numbers of species are rare and locally going extinct per unit time that the immigration rate is balanced, and the number of species in the community stops increasing.

Observed latitudinal changes in dominance-diversity patterns of local forest communities are predicted by the model provided that there are (i) fewer species in the source pool of potential immigrants, and (ii) more frequent or severe disturbances (or both) in boreal and temperate forests than in tropical forests. Whether these conditions are met is not yet clear. Persistently lower species richness in boreal and temperate forests may be due to elevated rates of extinction during the Pleistocene (71). In

historical times boreal and temperate forests have been disturbed frequently by fires, plagues, and strong winds (72). On somewhat longer time scales, paleo-ecological evidence reveals that interglacial periods have been too brief for equilibria to be achieved in temperate deciduous forests before glacial periods set in again (73).

Disturbance in equatorial forests tends to be a localized, rather than a large-scale phenomenon, with blowdowns generally involving only a few trees at a time (74). Indeed, the observed clumped dispersion pattern of dry-forest tree species is just what one would expect if the forest is essentially a palimpsest of small, regenerating light gaps of different ages. However, stability of tropical climates over Pleistocene times is not certain, in view of mounting evidence of long dry periods during full-glacial and mid-Holocene times in equatorial regions (75).

Obviously this model is an oversimplified representation of the dynamics of natural communities (76), but it does provide a number of important lessons. First, we may expect to observe substantial differentiation of the relative abundance of species in natural communities as a result of purely random-walk processes—a kind of "community drift" phenomenon. Second, we cannot necessarily conclude that, just because a species is of rank-1 importance in a community, its current success is due to competitive dominance or "niche pre-emption" (56), stemming from some superior

adaptation to the local environment. Because such a simple model generates the basic patterns of relative species abundance in natural plant communities, it would perhaps be preferable to use departures from the lognormal or geometric distributions as evidence for competitive dominance. Finally, whether or not forest communities are at equilibrium, our understanding of community organization would profit from more study of processes of disturbance, immigration, and local extinction, in conjunction with the more traditional studies of the biotic interactions of species (such as competition, niche differentiation, and seed predation).

References and Notes

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5. P. A. Colinvaux, *Introduction to Ecology* (Wiley, New York, 1973), p. 477ff.; J. M. Emlen, *Ecology: An Evolutionary Approach* (Addison-Wesley, New York, 1973), p. 400; C. J. Krebs, *Ecology: The Experimental Analysis of Distribution and Abundance* (Harper & Row, New York, 1972), p. 520; R. H. MacArthur and J. H. Connell, *The Biology of Populations* (Wiley, New York, 1967), p. 37; R. H. MacArthur, *Geographical Ecology* (Harper & Row, New York, 1972), p. 191; E. R. Pianka, *Evolutionary Ecology* (Harper & Row, New York, ed. 2, 1978), p. 296; P. Price, *Insect Ecology* (Wiley Interscience, New York, 1975), p. 49; J. L. Richardson, *Dimensions of Ecology* (Williams & Wilkins, Baltimore, 1977), p. 219; R. E. Ricklefs, *Ecology* (Chiron, Portland, 1973), p. 721. Most texts present several of the competing theories to explain the low density of tropical tree species.
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7. J. H. Connell, in *Dynamics of Populations*, P. J. den Boer and G. R. Gradwell, Eds. (PUDOC, Wageningen, Netherlands, 1970), pp. 298–312.
8. J. H. Connell, J. G. Tracy, O. O. Webb, unpublished result cited in (7).
9. D. H. Janzen, in *Taxonomy and Ecology*, V. H. Heywood, Ed. (Systematics Association, special volume No. 5), (Academic Press, New York, 1973), chap. 10; *Annu. Rev. Ecol. Syst.* **2**, 465 (1971).
10. J. H. Connell, *Science* **199**, 1302 (1978).
11. H. G. Baker, *Cold Spring Harbor Symp. Quant. Biol.* **24**, 177 (1959); A. A. Fedorov, *J. Ecol.* **54**, 1 (1966); A. Kaur, C. O. Ha, K. Jong, V. E. Sands, H. T. Chan, E. Soepadmo, P. S. Ashton, *Nature (London)* **271**, 440 (1978).
12. D. H. Janzen, *Science* **171**, 203 (1971); G. W. Frankie, in *Tropical Trees: Variation, Breeding, and Conservation*, J. Burley and B. T. Styles, Eds. (Linnean Society Symposium Series No. 2, 1976), pp. 151–159.
13. K. S. Bawa, *Evolution* **28**, 85 (1974).
14. ____ and P. A. Opler, *ibid.* **29**, 167 (1975).
15. I do not mean to suggest that clumping is any sort of evolved adaptation to rarity.
16. For example, if a rare species occurs only as widely scattered, very large adults, we may suspect that the population is a relict of an earlier successional episode when the species was once more abundant. Alternatively, if a rare species is locally abundant with a high proportion of juveniles, it may be self-replacing and may be rare only because its microhabitat is local and rare. This sort of evidence is only circumstantial, at best, since it is always possible to construct a life table for any observed age distribution consistent with population growth, constancy, or decline. However, the reasonableness of some life tables necessary to balance some age distributions may be questionable. For example, to balance a population consisting only of extremely old individuals requires (i) highly episodic reproduction so that there is very little overlap of generations, (ii) extremely delayed age at maturity, (iii) high survival from seed to adult, or else extremely high adult fecundities, and (iv) synchronous fruiting, at long intervals, corresponding to (i). [Also see (53).]
17. K. S. Bawa and P. A. Opler (*14*), and M. N. Melampy and H. F. Howe [*Evolution* **32**, 867 (1978)] have reported that, although sex ratios may be skewed from 1:1, the staminate and pistillate plants are distributed at random with respect to one another in the species they studied. Determining what "sex ratio" means in plants can be difficult at times, particularly if there is temporal variation in the number of staminate and pistillate flowers offered by individual plants. See also R. W. Cruden and S. W. Hermann-Parker [*ibid.* **31**, 863 (1977)] and K. S. Bawa (*ibid.*, p. 52).
18. G. W. Frankie, H. G. Baker, P. A. Opler, *J. Ecol.* **62**, 881 (1974).
19. Information on the effects of root and crown competition and thinning on the growth of plantation stands is available in references on tropical trees [T. C. Whitmore, *Tropical Rainforests of the Far East* (Clarendon, Oxford, 1975)].
20. Potentially positive effects of density on reproductive success are also possible, within certain density ranges. For example, if pollinators are limiting seed set, a group of adult trees might exhibit greater per capita seed set than isolated adults if per capita rates of pollinator visitation were greater in the group.
21. The mathematical model is similar in aspects to verbal models developed by J. H. Connell (*10*) and J. Terborgh [*Am. Nat.* **107**, 956 (1973)].
22. The site is a nearly level plain at 100 m elevation, 10°32′N, 85°18′W. Soils are uniform, pale orange-brown silty clays derived from low bluffs of rhyolitic tuff, and exposed basaltic flows 200 to 600 m north of the site. Soils are 1.4 to 2.2 m deep, underlain by basaltic flows. Because the forest is seasonally dry for 6 months, a shallow layer of leaf litter (A-0) and humus (A-1) persists all year. A small seasonal creek flows through the site in a channel cut to the basaltic bedrock.
23. E. R. Heithaus, *Ann. Mo. Bot. Gard.* **61**, 675 (1974); L. K. Johnson and S. P. Hubbell, *Ecology* **56**, 1398 (1975); S. P. Hubbell and L. K. Johnson, *ibid.* **58**, 949 (1977); *ibid*, in press.
24. D. H. Janzen, *Evolution* **21**, 620 (1967); R. Daubenmire, *J. Ecol.* **60**, 147 (1972).
25. L. R. Holdridge, *Life Zone Ecology* (Tropical Science Center, San José, Costa Rica, 1967); J. O. Sawyer and A. A. Lindsey, *Vegetation of the Life Zones of Costa Rica* (Indiana Academy of Sciences, Indianapolis, 1971); C. E. Schnell, Ed., *O. T. S. Handbook* (Organization for Tropical Studies, San José, Costa Rica, 1971).
26. This total represents approximately a third of all woody species reaching a size of 2 cm dbh or larger in the Dry Forest Life Zone of Costa Rica.
27. Cattle enter the forest on occasion and cause some damage to the shrub understory by trampling and browsing. This disturbance is discussed in relation to the dispersion patterns found (*2*); cattle disturbance cannot have produced the clumped dispersion patterns of adult trees, nor the concentrations of juveniles around adults found in nearly all species (*2*).
28. Potential mammalian seed dispersers common in the forest include deer, howler monkeys, variegated squirrels, and agoutis. Visits by white-faced monkeys, spider monkeys, tapirs, peccaries, and pacas have also been recorded. Other mammals include armadillos, coatimundis, and kinkajous. Frugivorous birds are also common.
29. It is difficult to find intact seeds of species such as *Hymenaea courbaril*, *Enterolobium cyclocarpum*, *Cassia* spp., and many others that have not been attacked by weevils.
30. Many of the unknown plants were identified in the field by P. A. Opler and confirmed by voucher specimens sent to W. Burger (Field Museum, Chicago) or R. Leisner (Missouri Botanical Gardens, St. Louis). A few specimens could not be identified to species because they lacked reproductive structures.
31. Individual maps for each quadrat were drawn on graph paper (scale 2 m/cm) in the field. Plants within 5 m of the quadrat perimeter were mapped first; plants inside the inner square (10 by 10 m) were added afterward, the perimeter plants being the reference points. Independent checks of the accuracy of mapping showed that two people could locate most plants to within 1 m of each other, and of the plant's true position. Mapping took two people 3 months. Gross forest structure, by dbh class, is as follows: 2.0 to 4.9 cm, 9788 stems; 5.0 to 9.9 cm, 2606 stems; 10.0 to 14.9 cm, 1359 stems; 15.0 to 19.9 cm, 650 stems; 20.0 to 29.9 cm, 768 stems; 30.0 to 39.9 cm, 411 stems; 40.0 to 49.9 cm, 117 stems; 50.0 to 99.9 cm, 163 stems; > 100 cm, 27 stems.
32. It was not possible to check the reproductive capacity of every tree or species. Information was obtained on 61 tree species. The somewhat arbitrary rule of setting the lower limit for adult size at the smallest-sized individual of the species in flower or fruit was used. In general, this rule means that we probably have virtually all of the adults in the "adult" class. By the same token, however, some nonreproductive subadults are probably included with the adults. For purposes of this study, it was better to risk overestimating the number of adults since, in general, there were many more juveniles than adults.
33. Maps were drawn to a scale of 1:450. Locations of individual plants were marked by a letter. The letter A represented plants < 2.5 cm dbh; B represented plants between 2.5 and 5.0 cm dbh; and thereafter, letters represented 5 cm dbh increments.
34. M. Morisita, *Mem. Fac. Sci. Kyushi Univ. Ser. E* **2**, 215 (1959). Morisita's dispersion index is a ratio of the observed probability of drawing two individuals randomly without replacement from the same quadrat (over q quadrats), to the expected probability of the same event for individuals randomly dispersed over the quadrats. The index is unity when individuals are randomly dispersed, regardless of quadrat size or the mean density of individuals per quadrat. Values greater than unity indicate clumping, and values between 0 and 1 indicate uniformity. An F statistic can be computed to test for significant departure of the index (symbolized by I_δ) from unity (randomness).
35. Circular, clear plastic overlays with concentric rings drawn to scale every 5 m were made by a Thermofax copier. These overlays were centered in turn over each adult tree on the map, and the numbers of adults and juveniles were counted in each successive 5-m annulus, out to 100 m. Density was computed by dividing the number of counts by the area of the annulus in question.
36. Small-seeded species with wind, bird, or bat dispersal should exhibit greater dispersal distance than large-seeded species dispersed by ground mammals. The greater dispersal distance expected in small-seeded species should tend (i) to obscure the local difference in seed production by both crowded and scattered adults and (ii) to increase the apparent per capita reproduction of scattered versus crowded adults. Consider, for example, the limiting case in which regional averaging of juvenile production is so complete that all quadrats have an equal density of juveniles. Then quadrats that have a small number of adults will show a high ratio of juveniles to adults, whereas quadrats that have many adults will show a low ratio, regardless of any density dependence.
37. The expected nearest neighbor distance, d, is given by $d = 1/(2\sqrt{\rho})$, where ρ is the mean density in number of adults per square meter [P. Clark and F. C. Evans, *Ecology* **35**, 445 (1954)].
38. Of the 21 remaining species of trees, shrubs, or vines represented by one individual, eight species could not be identified from our vegetative samples.
39. *Cochlospermum vitifolium* Spreng. (Cochlospermaceae) is a deciduous species found in large light gaps. It grows rapidly and has wood of low density. Its large dry-season flowers (see cover) are pollinated by big anthophorid bees, and its seeds are wind-dispersed. *Hymenaea courbaril* L. (Leguminosae) is a slow-growing, evergreen species commonly found in riparian areas, and it has dense wood. It has fairly large flowers which are bat-pollinated. Its seeds are large and encased in a thick, woody pod, are attacked on the tree before dispersal by bruchid weevils, and are food for a number of mammals [D. H. Janzen, *Science* **189**, 145 (1975)]. *Licania arborea* Seem. (Rosaceae) is a slow-growing, evergreen, high-canopy species of the mature dry forest, with very dense wood. It has small, bee-pollinated flowers, and its seeds are dispersed by bats, birds, and monkeys. *Tabebuia rosea* DC (Bignoniaceae) is a tree of intermediate stature characteristic of forest edge and large light gaps. It is relatively fast growing, with wood of intermediate density. It is deciduous and produces a showy display of large flowers in the dry season. Pollination is by large anthophorid bees. Its pods are straplike, containing numerous small, flat, winged, wind-dispersed seeds. *Thouinidium decandrum* Radlk. (Sapindaceae) is a medium-sized, deciduous tree of mature forest, with a moderate growth rate and medium to dense wood; its seeds are wind-dispersed.

40. P. S. Ashton (*1*) and M. E. D. Poore [*J. Ecol.* **56**, 143 (1968)] also report clumping in rain-forest tree species in Malaysian dipterocarp forests. Their large rain forest maps cannot be used very effectively to test the Janzen-Connell hypothesis since only trees with a circumference ≥ 30 cm were mapped, and they did not distinguish between adult and juvenile trees.

41. Because the demographic neighborhoods of adjacent adults are not completely independent (some juveniles are counted in the neighborhoods of more than one adult), compensation for this partial nonindependence should be made by a downward adjustment of the degrees of freedom of the regression analysis of variance. Accordingly, the average redundancy of juvenile counts was determined by the ratio of apparent number of juveniles in the neighborhoods of all adults to the actual number of juveniles in the union of all adult neighborhoods. The number of degrees of freedom was reduced by dividing the number of adults by the mean juvenile redundancy. This procedure results in a conservative estimate of the true degrees of freedom (R. Lenth, Department of Statistics, Univ. of Iowa, personal communication), and corresponds to the case of completely dependent demographic neighborhoods. For example, suppose that there are only three coincident adults in the population, which consequently have completely identical demographic neighborhoods in which every juvenile is counted three times. Therefore, mean juvenile redundancy is 3, and the number of independent data sets is found by dividing the number of adults by 3, giving one degree of freedom. A similar procedure was followed in testing the slopes of the adult density curves, with mean adult redundancy being used to adjust the degrees of freedom. However, even without the downward adjustment of degrees of freedom, the significance tests are conservative since individual trees counting in the neighborhoods of more than one adult should always bias the slopes in the positive, not in the negative, direction. The slopes found were all negative or zero.

42. Fifteen meters away from the parent tree might be enough to permit the seeds to escape from discovery by seed predators. However, D. E. Wilson and D. H. Janzen [*Ecology* **53**, 954 (1972)] found that in *Scheelea* palm there was no reduction in the percentage of seeds attacked under the palm and at a distance of 8 m, when seed density was held constant.

43. This analysis, of course, is analogous to constructing a vertical life table, which assumes that the population size has been approximately stationary for some time. While the conclusions are not necessarily invalid if the population is increasing, their validity cannot be confirmed.

44. In the 30 most common tree species, immediately adjacent adults with touching crowns are not infrequent.

45. Th. Dobzhansky and S. Wright, *Genetics* **28**, 304 (1943).

46. J. A. Endler, *Geographic Variation, Speciation, and Clines* (Princeton Univ. Press, Princeton, N.J., 1977).

47. N. G. Hairston, *Ecology* **40**, 404 (1959).

48. The self-compatible species may do little if any selfing (R. Cruden, personal communication). K. S. Bawa (personal communication) has shown that most of the hermaphroditic species in the dry forest he has studied are self-incompatible. Therefore, in Fig. 6, hermaphroditic species for which self-compatibility data are lacking are pooled with the obligately outcrossed hermaphrodites.

49. I chose the midpoint of the dbh range as the pivotal size in order to be conservative in my estimate of the number of species showing positive skewness. This means that, when positive skewing is detected, it is actually very pronounced.

50. Similar patterns of skewing have been reported in rare species by Connell (*10*) and by D. H.

Knight [in *Tropical Ecological Systems* (Ecology Series No. 11), F. B. Golley and E. Medina, Eds. (Springer-Verlag, New York, 1975), pp. 53–59]. Knight studied late second-growth stands of semi-evergreen forest on Barro Colorado Island, Panama.

51. In 7 years of work at the study site, I have seen no juveniles produced by these species in spite of repeated flowering (seed set was not observed).

52. Of the 59 species in the forest studied, which occur with an average density (ignoring dispersion) of greater than one individual per hectare, I know of at least 42 species that occur locally in much higher densities elsewhere in Guanacaste; and I expect the same is true for most of the remaining species.

53. The most parsimonious explanation for the data on rare species in the dry-forest stand described here is general reproductive failure. However, undoubtedly there are some rare species in the forest that are replacing themselves, and there are probably some species that are everywhere rare. G. S. Hartshorn [in *Tropical Trees as Living Systems*, P. B. Tomlinson and M. H. Zimmerman, Eds. (Cambridge Univ. Press, New York, 1978)] has suggested that "nonregenerating" rare species may simply require particular types of light gaps in order to regenerate, and that rarity is due to the infrequency of creation of such gaps.

54. Of 21 wind- or bird-dispersed species, 14 showed density dependence, but of nine mammal-dispersed species, only three showed density dependence.

55. Diffuse competition is a term coined by R. H. MacArthur [*Geographical Ecology* (Harper & Row, New York, 1972)]. It refers to the sum of competition from all interspecific competitors in the community acting on a given species. I have not yet analyzed the association of species to check this possibility.

56. R. H. Whittaker, *Science* **147**, 250 (1965).

57. Data of H. Klinge, as was reported by E. F. Brunig [*Amazoniana* **4**, 293 (1973)].

58. The curves for the Smoky Mountains are derived from analysis of single, 0.1-hectare stands in the cove and spruce-fir forests, respectively. Also, they represent all vascular plants, not just woody plants; and the importance values are based on annual net primary production. The respective dry-forest and rain-forest curves, however, are based on larger quadrats (13.44 and 1.0 hectares), but only woody plants; and the respective importance values are based on basal area and above-ground biomass. The quantitative effects of these differing methods are difficult to assess, but fortunately the effects are partially canceling (larger plots mean more species, but eliminating nonwoody species means fewer species). If there is a greater percentage of nonwoody plants in temperate forests, the difference between the species richness of temperate and tropical forests may be somewhat underestimated in Fig. 8.

59. M. P. Johnson and P. H. Raven, *Evol. Biol.* **4**, 127 (1970); S. J. McNaughton and L. L. Wolf, *Science* **167**, 131 (1970).

60. R. M. May, in *Theoretical Ecology: Principles and Applications*, R. M. May, Ed. (Saunders, Philadelphia, 1976).

61. H. Caswell, *Ecol. Monogr.* **46**, 327 (1977).

62. R. MacArthur, *Am. Nat.* **94**, 25 (1960); G. Sugihara (unpublished result) has also developed a "sequential breakage" model that generates lognormal patterns.

63. Losses are governed by the hypergeometric distribution. Thus, for the ith species the probability of losing j individuals, $j \leq D \leq N_{it}$, where N_{it} is the population of species i at the current time t, is given by

$$\binom{N_{it}}{j}\binom{K - N_{it}}{D - j} \bigg/ \binom{K}{D}.$$

64. A disturbance can be as small as the death of a single tree.

65. Recruitment to fill the D disturbance vacancies is governed by the binomial distribution. Let N'_{it} be the number of the ith species at time t after disturbance. For the ith species, the probability of contributing m replacement individuals, $m \leq D$, is:

$$\binom{D}{m}\left(\frac{N'_{it}}{K - D}\right)^m \left(\frac{K - N'_{it} - D}{K - D}\right)^{D - m}$$

66. It is easy to prove that rare species are more likely to go extinct per unit time than are common species: If $N_{it} > D$, there is no chance that species i will go extinct in the next disturbance; but if $N_{it} \leq D$, there is a nonzero chance of extinction in the next disturbance. Therefore, the mean time to extinction of a species j with $N_{jt} > D$ must exceed that of a species i with $N_{it} \leq D$ by at least the mean time it takes for N_j to decrease to D. If a "rare" species is one for which $N \leq D$, then increasing D will increase the number of rare species going extinct per disturbance over successive disturbances.

67. In this example, I chose a large D simply to speed up the process of random-walk extinction. These transient distributions obey the "canonical hypothesis" of F. W. Preston [*Ecology* **43**, 185 and 410 (1962)]. It has been shown (*21*) that the canonical lognormal is the result of imposing a fixed ceiling, K, on the total number of individuals of all species in the community. This result has also been discovered independently by G. Sugihara (personal communication). The Monte Carlo simulations were performed at the University of Iowa Computer Center on an IBM 360/70.

68. Because the species can random walk up or down in abundance, either outcome (extinction or complete dominance) is possible. I chose to illustrate a species with $K/2$ individuals because it represents the abundance at which a species is equally likely to go to either outcome. It is also the abundance with the longest mean transient time, both outcomes considered.

69. The model is a Markovian random walk of the abundance of the ith species between 0 and K. Mean transient times from a starting abundance of $K/2$ individuals were found from the fundamental matrix determined for particular values of D and K.

70. There is an added risk of extinction for rare species if they are more clumped than common species, such that a single disturbance might kill all individuals in a given local area.

71. The extinction of many temperate tree species is well documented in Europe (*73*).

72. For example, see M. L. Heinselman, *Quat. Res.* **3**, 329 (1973); J. D. Henry and J. M. A. Swan, *Ecology* **55**, 772 (1974).

73. M. B. Davis, *Geosci. Man.* **13**, 13 (1976).

74. R. Foster, personal communication; S. P. Hubbell, personal observations.

75. B. S. Vuilleumier, *Science* **173**, 771 (1971); J. E. Damuth and R. W. Fairbridge, *Bull. Geol. Soc. Am.* **81**, 189 (1970); J. Haffer, *Science* **165**, 131 (1969); B. S. Simpson and J. Haffer, *Annu. Rev. Ecol. Syst.* **9**, 497 (1978).

76. The model in its simplest form as presented here corresponds to the "equal chance hypothesis" discussed by Connell (*10*), provided that per capita chances of reproduction or death are made the same for all species. For greater realism, species differences in dispersal, fecundity, competitive ability, and resistance to environmental stresses need to be treated.

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