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Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest

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ABSTRACT   Intraspecific density-dependent effects in the Barro Colorado Island (Panama) study area are far stronger, and involve far more species, than previously had been suspected. Significant effects on recruitment, many extremely strong, are seen for 67 out of the 84 most common species in the plot, including the 10 most common. Significant effects on the intrinsic rate of increase are seen in 54 of the 84 species. These effects are far more common than interspecific effects, and are predominantly of the type that should maintain tree diversity. As a result, the more diverse an area in the forest is, the higher is the overall rate of increase of the trees in that area, although sheer crowding has by itself a negative effect. These findings are consistent with, but do not prove, an important role for host–pathogen interactions (defined broadly) in the maintenance of diversity. Ways are suggested by which to test host–pathogen models and competing models.

Tropical rainforests vary greatly in tree species richness, but in most of the humid tropics mature communities with diversities of up to 300 species of tree per hectare are common (1, 2). Equilibrium models (3) have been proposed to explain such high species richness and the maintenance of many different species over long periods. These require unique resource-heterogeneity and resource-utilization niches for each species (4, 5). If there is spatial partitioning (reviewed in ref. 6), or temporal partitioning of light gaps created by treefalls, this would increase the number of niches (7–11). Such habitat partitioning predicts positive density- and frequency-dependence within species. The effect of light gaps on niche partitioning has, however, recently been called into question (12).

Another class of models is based on negative density- or frequency-dependence. We define density-dependence as correlations of life history parameters with total biomass at the outset of the census, and frequency-dependence as correlations of life history parameters with the numbers of trees present at the outset of the census. These measures are often, but not always, correlated.

We can divide these models into two categories. The first, which we will call abiotic models, have only rarely been investigated (13). They are based on density-dependent abiotic factors in the immediate environment. Density-dependence might be the result of the removal of nutrients from the soil or of a buildup of toxic waste products. When the density is reduced through mortality, nutrients are replenished and toxins are degraded, allowing the cycle to begin anew. The second category is made up of biotic models, and deals with interactions of tree species with their enemies (pest pressure). As Gillett (14) was the first to point out, pests increase the

diversity of the local environment, effectively increasing the number and diversity of ecological niches for host species in the forest. The best-known of these models is that of Janzen (15) and Connell (16), which predicts that species-specific pests will tend to be more numerous near mature trees. Thus, the probability of survival of recruits should increase with distance from such trees. Models in which single-tree species are attacked by specialized, monophagic pests might be called "simple biotic density-dependence." Another biotic model, recently suggested by one of us (17), is also based on the supposition that many host species have fairly specialized pathogens, but postulates that pests are not absolutely host-specific but rather oligophagic. As with simple density-dependence, if any host becomes locally common, its pathogens can multiply, but the model leads to more complex results. The performance of one species depends on its own density, but also on the density of other species that share its pests. The sheer diversity of the ecosystem will confer a kind of herd-immunity (18) on each host species. In either the simple density-dependence or herd-immunity model, if pathogens are sufficiently time-lagged, local clusters of host trees will build up, so that host species need not necessarily be overdispersed. In either case, the forest would be marked by strong, negative density-dependence on mortality and recruitment, but in the herd-immunity model, overall diversity should correlate positively with the performance of individual species, while this is not so in the simple density-dependence model.

If, in contrast, niches of any type are few, maintenance of high diversity is nevertheless still possible. If competitive exclusion takes place slowly, then high diversity can be reached through a balance of regional speciation, immigration, and local extinction (the "community drift" hypothesis; ref. 19). Alternatively, temporal variation in recruitment rates may give rare species a per capita frequency-dependent advantage, provided that adult trees have overlapping generations (20, 21). Another possibility is that, even in the face of local extinction, a species may be preserved through dispersal (metapopulation source-sink models; ref. 22). It must be emphasized, however, that none of these models predict any within-species frequency- or density-dependence.

We present here a quadrat-based analysis of data from a tropical forest plot in Barro Colorado Island (BCI), Panama, which supports the frequency- and density-dependent class of models. There is little evidence for between-species interactions. We also show strongly positive correlations between diversity measures, particularly evenness, and three population parameters: survival, recruitment, and the intrinsic rate of increase. These correlations are a direct result of the frequency- and density-dependence. Further, the observed effects may be due to biotic rather than abiotic factors. Many species do poorly in quadrats crowded with other trees, in which the density of pathogens would be expected to be high, but there

is no negative correlation of productivity with total biomass as abiotic models would predict. Although this analysis does not rule out nonequilibrium models such as community drift, particularly for the maintenance of rare species, it provides evidence that frequency- and density-dependent equilibria are of great importance in the overall maintenance of diversity.

The study site is a plot of 0.5 km² on BCI, a 15-km² flat hilltop that was isolated in 1913 by the filling of artificial Gatun Lake, part of the Panama Canal. The first complete census of the plot was finished in 1982, followed by two more in 1985 and 1990. The censuses provide the location of each stem, along with information on its rate of growth and whether it was recruited or died during the study period. At each census there were ≈240,000 trees and large shrubs ≥1 cm diameter at breast height, consisting of about 300 species (23). A few of these species have been found only once, while at the other extreme one large shrub species (*Hybanthus prunifolius*) comprises nearly a fifth of all stems. Between 1981 and 1990, 55,231 trees died and 64,051 were recruited.

RESULTS

There Are Strong Density-Dependent Effects on Survival, Recruitment, and Intrinsic Rates of Increase. Table 1 shows

the overall results for the 84 most common species. On the assumption that a species that does not show density-dependent effects on one scale may show them on another, the BCI plot was examined sequentially at four scales: 5000 square quadrats, 10 m on a side; 1250 quadrats, 20 m on a side; 200 quadrats, 50 m on a side; and finally, 50 quadrats, 100 m on a side. For each quadrat at each scale, nonparametric Spearman rank-order correlations were obtained between basal areas (as an approximate indication of biomass) of a given species and three demographic measures: per capita survival, recruitment (always measured per reproductive adult tree), and intrinsic rate of increase [r = (births − deaths)/total trees of that species].

Basal area and number of trees are positively correlated, so that correlations of the form f(a) vs. b/a would be expected to be negative even if there were no density-dependence. Therefore, to determine significance, each correlation was compared with 500 control nonparametric correlations using artificially constructed data sets in which the spatial distribution of trees of a given species was the same as in the original plot but from which any density-dependence had been removed. This was done by repeatedly picking pairs of trees of the same species from the plot at random and switching their properties (initial

Table 1. Numbers of significant intra- and interspecific nonparametric correlations for the 84 most abundant species in the BCI forest

Type of correlation	Significance	Expected no. of significant positive or negative intra- and interspecific correlations	Quadrat size (length and width in meters)								No. of species (or species pairs) showing significant r values at one or more quadrat sizes*	
			10		20		50		100			
			Pos.	Neg.	Pos.	Neg.	Pos.	Neg.	Pos.	Neg.	Pos.	Neg.
			Observed no. significant intra- and interspecific correlations									
a (Basal area of conspecifics in quadrat vs. adult survival)	0.05	1.38 (1.06)	0 (1)	3 (2)	1 (0)	4 (0)	0 (1)	1 (1)	1 (1)	3 (2)	4	16
	0.01	0.27 (0.21)	0 (0)	1 (0)	0 (0)	1 (1)	0 (0)	0 (1)	0 (0)	0 (1)	$P = 0.02$*	
	0.002	0.07 (0.05)	1 (1)	3 (0)	0 (0)	3 (1)	1 (0)	1 (0)	1 (0)	1 (0)	(3)	(5)
		69 (53) ssp.										n.s.
b (Basal area of conspecifics in quadrat vs. juvenile survival)	0.05	1.5 (1.36)	2 (1)	4 (1)	2 (2)	3 (2)	1 (2)	3 (2)	3 (1)	2 (0)	8	18
	0.01	0.3 (0.27)	1 (0)	1 (0)	2 (0)	1 (0)	1 (0)	1 (0)	0 (0)	0 (0)	n.s.	
	0.002	0.08 (0.07)	0 (0)	3 (0)	2 (0)	2 (0)	2 (0)	3 (0)	1 (0)	2 (0)	(3)	(6)
		75 (68) spp.										n.s.
c (Basal area of conspecifics vs. survival for both adults and juveniles)	0.05	1.7 (1.7)	3 (2)	6 (1)	2 (2)	4 (1)	0 (3)	1 (2)	5 (3)	2 (3)	13	20
	0.01	0.34 (0.34)	0 (1)	0 (1)	1 (0)	4 (1)	0 (0)	1 (1)	4 (0)	0 (1)	n.s.	
	0.002	0.09 (0.09)	1 (0)	4 (0)	2 (0)	2 (0)	3 (0)	4 (1)	0 (1)	3 (0)	(4)	(10)
		84 (84) spp.										n.s.
d (Basal area of conspecifics in quadrat vs. no. of recruits per adult)	0.05	1.7 (1.7)	0 (3)	13 (0)	0 (1)	11 (3)	3 (1)	5 (6)	2 (1)	1 (4)	5	67
	0.01	0.34 (0.34)	0 (0)	6 (0)	0 (0)	11 (0)	0 (0)	0 (1)	0 (0)	1 (1)	$P < 0.001$	
	0.002	0.09 (0.09)	0 (0)	35 (0)	0 (0)	23 (0)	0 (0)	5 (0)	1 (1)	5 (0)	(8)	(13)
		84 (84) ssp.										n.s.
e (Basal area of conspecifics in quadrat vs. r)	0.05	1.7 (1.7)	2 (1)	15 (2)	1 (0)	10 (2)	3 (4)	2 (3)	3 (2)	2 (1)	7	54
	0.01	0.34 (0.34)	0 (1)	3 (1)	0 (1)	1 (1)	2 (0)	2 (0)	0 (2)	1 (0)	$P < 0.001$	
	0.002	0.09 (0.09)	0 (0)	28 (0)	0 (0)	23 (0)	1 (0)	5 (0)	0 (0)	4 (0)	(9)	(8)
		84 (84) ssp.										n.s.
f (r of species vs. basal area of all other trees in quadrat)	0.05	1.7	1	1	8	2	4	0	5	5	22	7
	0.01	0.34	3	1	2	0	5	0	0	0	$P < 0.02$	
	0.002	0.09	1	0	3	1	2	0	0	0		
		84 spp.										

Census data from 1982 and 1990 were employed. The data from within-species correlations are presented first, followed by data from between-species correlations in parentheses. The type of correlation is indicated in the first column, and the second shows the three significance levels that were distinguished, along with the number of species used in each correlation. In some cases the number is less than 84. This is because nine species are reproductive by the time they reach 1 cm diameter at breast height (DBH), so that all trees of these species that have been censused must be considered adults. This left 75 species in which juvenile survival could be distinguished, and which could be included in correlation b. In 15 species, fewer than 10 adult trees died, and these species were not included in correlation a. This reduction in numbers also affected the expected numbers of positive or negative correlations based on chance alone, which are shown in column 3. To obtain the recruitment measure, the trees that were recruited (achieved ≥ 1 cm DBH) in each quadrat between 1982 and 1990 were counted and divided by the number of adult trees of that species in the quadrat in 1982. Trees that were recruited in quadrats that contained no adult trees of that species in 1982 were excluded from the calculations.
*Equality of the numbers of species in the last two columns of the table was examined with the sign test, on the assumption that equal numbers of species should be found in the two columns.

size, and whether they had been recruited or died during the census period) while leaving their coordinates the same. This process was repeated $10N_s$ times for each species, where N_s is the total number of trees of that species in the entire BCI plot. As expected, the averages of these control correlations were often significantly negative (data not shown). Therefore, using this shuffling method, we could assess significance of the actual correlations more accurately than if the difference between the actual correlations and zero were used.

If the observed correlation was larger or smaller than 95% of the shuffled correlations, it was taken to be significant at the 0.05 level; if larger or smaller than 99% of the shuffled correlations, it was taken to be significant at the 0.01 level; and if larger or smaller than all the shuffled correlations, it was taken to be significant at the 0.002 level.

The observed numbers of significant correlations may be compared with the numbers expected by chance, given in column 2 of Table 1. Negative density-dependence predicts negative correlations of basal area with per capita survival among adults, juveniles, and all trees (correlations a, b, and c), recruitment (correlation d), and r (correlation e). In each case there are more negative than positive correlations, with the most striking excess being seen in correlations of basal area with recruitment and r, particularly for small quadrat sizes (correlations d and e). The weakest effects are seen in correlations of basal area with survival. These density-dependent effects are often paralleled by similar and equally strong frequency-dependent effects (data not shown).

The last two columns of the Table 1 show that, for at least one quadrat size, 67 species exhibit a negative correlation of recruitment with basal area, and 54 exhibit a negative correlation of r with basal area. These excesses of negative correlations are highly significant by a sign test, but note that it is not possible to determine the numbers of species expected to exhibit such significant correlations by chance. This is because data from different quadrat sizes, which are not independent, have been pooled.

These within-quadrat density-dependent effects are clearly distinguishable from "mass" effects (24), which are due to recruits that originate from parents outside a given quadrat. These effects will be important when a quadrat has few seed-producing adults but is surrounded by quadrats with many such adults. This situation can lead to overestimates of per capita recruitment rates and r, but will not affect measures of survival. We carried out partial parametric regressions of recruitment and r on the number of trees in a given quadrat and on the number of reproductive trees of the same species in the adjacent four or in the adjacent eight quadrats. The first partial measures the magnitude of the within-quadrat effect, and the second measures the mass effect. The mass effect is small compared with the within-quadrat effect, only exceeding it at one or more quadrat sizes in four species. Mass effects are usually most pronounced at small quadrat sizes, as would be expected, because very large quadrats are unlikely to be affected appreciably by the numbers of reproductive trees in the adjacent quadrats. Although mass effects are occasionally strong and highly significant, they are never strong enough to cause the negative within-quadrat relationships to disappear. The eight-quadrat analysis gave similar results.

Intraspecific Effects Are Strong Compared with Interspecific Effects. If there are strong interactions between pairs of tree species that dwarf intraspecific density-dependent effects, these might be sufficient to maintain species diversity. This would be the case if survival or recruitment of the first species is increased when trees of that species are surrounded by trees of the second species. To investigate this possibility, the basal area of one species was correlated with survival, recruitment, or r of a second species. To permit a direct comparison with the 84 sets of within-species correlations, 84 pairwise comparisons were made by choosing pairs of species at random from

among the 84 most common species. The numbers in parentheses in Table 1 show the observed numbers of significant correlations, which are only slightly greater than the numbers expected by chance (a total of 70 observed at the 0.05 level with 63.8 expected by chance, 16 observed at the 0.01 level with 12.8 expected by chance, and 5 observed at the 0.002 level with 3.2 expected by chance). In contrast to the within-species correlations, there were no significant excesses of negative correlations, as measured by the sign test.

There Is Evidence for Stabilization of Numbers of Many Species Because of Time-Lagged Density-Dependent Effects. If density-dependent factors were able to respond instantaneously to changes in the density of trees of a given species, then all tree species should soon reach and reside at their various carrying capacities and there should be no relationship between density and population growth rate. But if these factors take some time to exert their effects, then trees of a given species that are locally rare should exhibit a positive intrinsic rate of increase for that species, and those that are locally common should exhibit a negative rate. This will tend to stabilize the numbers of that species over time. Such an effect should be most noticeable at small quadrat sizes, in which the numbers of trees of a given species vary markedly from quadrat to quadrat. This pattern was seen in 46 of the 54 species that showed a negative relationship between r and basal area, including all of the most common and some of the rarest species in the set of 84. Three of the species showed a rate of increase that was negative at all densities, and five showed a positive rate at all densities, indicating that these species were undergoing an overall decline or increase during the census period.

Although All 84 Species in the Sample Show Significant Patchiness, at Least Over the Short Term Their Patchiness Has Not Changed. The density-dependent effects detected in this study might simply be due to averaging—that is, the forest might be in the process of "smoothing out" from an originally extremely patchy distribution of trees. Indeed, any mass effects would, if allowed to continue unchecked, lead to rapid smoothing. Factors that can generate patchiness, such as time-lagged pest pressure, limited seed dispersal, and chance variation in adult reproductive output, would act in opposition to this process, so that as each patch of trees is destroyed another patch has time to appear elsewhere. Hubbell *et al.* (25) suggested that one cause of such a phenomenon might be the effect of pests in the form of time-lagged waves of infection.

Most of the species in the BCI forest are significantly clustered (25). To determine whether the degree of clustering has changed significantly over time, for each of the 84 species the plot was divided into quadrats having an average of 5 or 10 trees, and the coefficients of variation in 1982 and 1990 were calculated. For 5-tree quadrats, 42 species showed an increase in the coefficient of variation during the census period and 42 showed a decrease. For 10-tree quadrats, 40 showed an increase and 44 showed a decrease. These pairs of numbers were not significantly different from each other using a paired-sample sign test ($P = 0.5$). Further, there was no tendency for species with abundances above or below the median to show an increase or decrease in clustering over time. The substantial mortality and recruitment that have taken place over this period have not altered the overall pattern of clustering in the plot.

The Data Are Not Explained by an Ability of Some Species To Colonize Gaps. The negative density-dependence might be because some species readily invade uncrowded quadrats. These species should show a negative correlation of r with the basal area of all the other species in the quadrat. Correlation f in Table 1 examines this possibility. The analysis turned up seven species with negative correlations, three of which have colonization indices >30% (26, 27). These seven possible good colonizers are far fewer in number than the species that show

density-dependent effects on r, however, so other density-dependent factors must also be involved.

On the other hand, surprisingly, 22 species showed a positive correlation for at least one quadrat size. These species do well in crowded quadrats, which would mimic a positive within-species density-dependence, the reverse of the predominant pattern that is seen in the forest. However, these correlations tend to be weak and tend to be found at only one quadrat size in a given species. Whatever their cause, these effects seem to be short-lived, for otherwise the species involved would presumably soon take over the forest.

All the Common Species Show Density-Dependent Effects. If density-dependent factors really are important for the maintenance of diversity in the rainforest, then all the common species should provide enough data for such effects to be detected. This prediction is examined in Fig. 1, which shows the proportion of species in each abundance class that exhibits significant negative correlations between basal area in a quadrat and r. Species in the highest abundance class all show significant negative correlations. The fraction exhibiting significant correlations decreases with decreasing abundance, presumably at least in part because of inadequate sample size. Note, however, that many of the least abundant species also show significant negative correlations for at least one quadrat size.

There Is Safety in Diversity, But Not in Numbers. The major models that are expected to yield frequency- and density-dependence predict different relationships between crowding or diversity in a quadrat and the productivity of the trees in the quadrat. If the density-dependence is due to abiotic factors, such as the exhaustion of nutrients or buildup of toxins, then the total basal area of the trees in a quadrat should be correlated negatively with the average intrinsic rate of increase for that quadrat. Correlation f of Table 1 shows that this is not the case. If, on the other hand, frequency-dependence is due to biotic factors such as pest pressure, then there should be a negative correlation with the number of trees in the quadrat and a positive correlation with the quadrat's overall diversity, regardless of the quadrat's biomass. This is because the effect of pests would be expected to be more pronounced in quadrats with many trees, because large numbers, independent of size, should encourage the spread of disease. However, if a quadrat happens to contain a diversity of host species, the pests specialized to any one host species or small group of host species will tend not to be numerous and the productivity of such a quadrat should be higher than that of a quadrat with the same number of trees but less diversity.

Table 2 shows the results of a preliminary examination of these questions. All 313 species in the BCI plot were pooled,
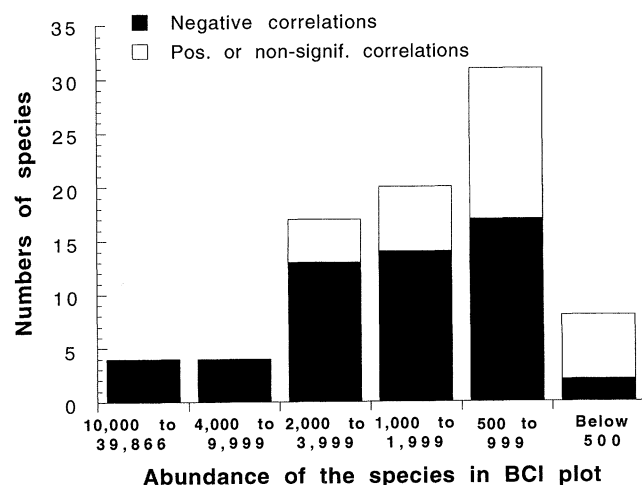

FIG. 1. Number of species that show significant density-dependent effects on r, as a function of the abundance of the species.

and parametric correlations were obtained between the average life-history parameters for each quadrat as a whole and three measures of crowding and diversity. The pattern does not fit the expectation of an abiotic model. The 12 correlations observed between life history parameters and total basal area are small, and only 1 is significant at the 0.05 level. This would not be expected if quadrats with larger biomass are being drained of nutrients from the soil or producing high levels of toxins, except in the unlikely event that there are many such nutrients or toxins and that each is confined in its effects to one or a few species of tree.

The biotic models predict negative correlations between numbers of trees in a quadrat (as distinct from total basal area) and the life history parameters, and it can be seen from Table 2 that in almost all cases these negative correlations are strong and highly significant. The correlations are weakest for survival but are still highly significant for small quadrat sizes.

Finally, both recruitment and the intrinsic rate of increase show strong positive correlations with diversity as measured by the evenness index (28), particularly at small quadrat sizes. Diversity appears to have a protective effect, which is a prediction of the biotic and not of the abiotic models. It must be cautioned, however, that such a relationship will be observed in any forest in which the individual species show density-dependence (see *Discussion*).

DISCUSSION

This analysis of the short-term dynamics of the BCI forest shows that density- and frequency-dependence are much more pervasive than previous studies had indicated. Our prior studies of the BCI plot had found some signs of frequency-dependence in about 20% of the common species (25, 29, 30). Those earlier studies examined the prediction made by Janzen (15) and less explicitly by Connell (16) that absolute recruitment (the total number of recruits) should peak at intermediate distances from the nearest conspecific adult. Only 6 out of 80 common species in the BCI plot showed this effect clearly, and an additional 9 showed slight traces of it (29), which did not seem to us to be strong support for the Janzen–Connell prediction. We also examined relative recruitment, defined as the proportion of recruits of a given species over recruits of all species as a function of distance, which again did not provide strong evidence for the Janzen–Connell effect.

Schupp (31) pointed out that adult population density or total basal area in a quadrat may be a more appropriate independent variable than distance from the nearest conspecific adult. Quadrat-based analyses are likely to be more productive if long-term demographic data are available, and Connell *et al.* (32) have found some frequency-dependent effects in two Queensland (Australia) rainforests.

The most important advance in the current study is the statistical method for removing frequency and density effects on recruitment. In Condit *et al.* (29) and Hubbell and Foster (33), we correlated juvenile density or recruitment with adult density or proximity, but we were unable to separate the effects of limited dispersal and density-dependence. The randomization method used here maintains a population's spatial structure while shuffling individual performances, allowing us to remove only the effects of frequency- and density-dependence.

As pointed out in the introduction, several mechanisms might account for the strong effects seen in the BCI forest.

Abiotic Mechanisms. The analysis summarized in Table 2 shows that there is no tendency for all the trees in a given quadrat to reproduce well or poorly as a function of the total basal area of the quadrat. This shows that the total biomass of a quadrat is not obviously limited by some abiotic factor or factors (e.g., a shortage of soil nutrients or an excess of waste products or toxins).

Thinning. Within-species competition (thinning by a variety of mechanisms) is likely to play an important role in reducing

Table 2. Parametric correlations between the averaged life history parameters of all the trees in a quadrat and numbers of trees, total basal area, and evenness of the quadrat

Life history parameter vs. Measure of diversity or crowding		Correlation coefficients r for quadrats having linear dimensions, (in meters)			
		10	20	50	100
Survival	Total number of trees in quadrat	−0.108***	−0.222***	−0.152*	−0.016, n.s.
	Total basal area of trees in quadrat	−0.017, n.s.	−0.066*	+0.101, n.s.	+0.102, n.s.
	Evenness	−0.024, n.s.	+0.001, n.s.	−0.037, n.s.	+0.015, n.s.
Recruitment	Total number of trees in quadrat	−0.389***	−0.339***	−0.478***	−0.457***
	Total basal area of trees in quadrat	−0.005, n.s.	+0.011, n.s.	+0.094, n.s.	+0.085, n.s.
	Evenness	+0.131***	+0.150***	+0.154*	+0.178, n.s.
Intrinsic rate of increase	Total number of trees in quadrat	−0.384***	−0.463***	−0.521***	−0.494***
	Total basal area of trees in quadrat	+0.002, n.s.	+0.034, n.s.	+0.058, n.s.	+0.056, n.s.
	Evenness	+0.135***	+0.146***	+0.139*	−0.184, n.s.

Evenness is defined in the usual fashion, as the Shannon information index divided by the logarithm of the number of species (28). * and ***, significant at the 0.05 and 0.001 levels, respectively.

the likelihood of recruitment when quadrats are crowded with conspecifics. But it cannot be the entire source of the present results. Note from Fig. 1 that half the species that have between 500 and 999 members in the entire plot show significant density-dependence for at least one quadrat size. It is difficult to see how thinning can be important in such relatively rare species. Each of them make up 1/250th or less of the trees in the plot, and most of them are scattered thinly through the forest. These species are not producing thick ranks of seedlings that are subsequently thinned.

Pest Pressure. Pressure from pests, broadly defined, is likely to prove to be an important contributor to this widespread frequency- and density-dependence. Field experiments in the rainforest have shown that seedlings are particularly vulnerable to pathogens (34). In this connection it is striking that the majority of the density-dependent effects found in the BCI forest are on recruitment rather than survival.

Species Herd-Immunity and the Evolution of Diversity. One of us, with Green (18), has suggested that major histocompatibility complex diversity in vertebrates may be maintained by a kind of genetic herd-immunity. In such a system, hosts carrying genotypes that confer susceptibility to particular diseases are, if they are rare, protected as a result of being surrounded by members of the same species that are resistant. Only if hosts carrying the susceptible genotype become common do they lose this protection. Such a mechanism will actually drive the evolution of host diversity, because a sufficiently diverse host population will always have members that are able to resist any pathogen, no matter how versatile.

In a complex ecosystem such as a rainforest, a similar mechanism of species herd-immunity would also encourage the evolution of biochemical and morphological diversity among host species. Confronted with this diversity, most pests should evolve to specialize on a narrow range of host trees.

Does Diversity Actually Protect? In Table 2, positive correlations are demonstrated between evenness as a diversity measure and the life-history parameters recruitment and the intrinsic rate of increase. However, this apparent protection by diversity can be shown to be a consequence of the negative frequency-dependence exhibited by species that make up the forest. If artificially generated forests are constructed, made up of species that each show negative frequency-dependence, these forests also show strong positive relationships between evenness and life-history parameters when they are analyzed in the same way as in Table 2 (data not shown). This is because many quadrats with high evenness will consist of a number of species, each at low numbers. These species will tend to have high intrinsic rates of increase since they are rare in that quadrat. But a quadrat with low evenness will often have one or more common species, resulting in a low overall intrinsic rate of increase. This raises a chicken-or-the-egg-type ques-

tion. Does a high level of diversity in a region of the forest protect the trees in that region through species herd-immunity, allowing them to reproduce more effectively? Or, is the apparent protection afforded by diversity simply a consequence of a number of frequency-dependent mechanisms that operate independently on different species and that have nothing to do with the activities of pests? Further statistical analyses are being carried out in an attempt to decide between these alternatives, but no firm decision can be reached without extensive observations and experimentation in the field.

The strength and pervasiveness of the density-dependent effects revealed by the current analysis make it likely that experiments designed to investigate their source will be successful. These effects are highly significant in each of the 10 most common species in the BCI plot. Can they be traced to these species' pathogens, to within-species competition, or to some combination of these and other factors?

It will also be possible to design direct experimental tests of the larger role of pathogens in maintaining rainforest diversity. The herd-immunity model predicts that exclusion of one or more kinds of pests from patches of diverse rainforest should lead to reductions in that diversity that will be greater than any reduction seen in equivalent patches from which those pests have not been excluded.

It is possible that the diversity seen in complex ecosystems such as the BCI forest may not only be maintained, but may also have been in part generated, by host-pathogen and host-parasite interactions. If this should turn out to be true, then the preservation of an ecosystem's diversity, including the preservation of its ability to evolve in the future, may require retention of the full range of pathogens and other pests as well as of hosts.

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