
Similar non-random processes maintain diversity in two tropical rainforests

Christopher Wills^{1*} and Richard Condit²

¹*Department of Biology and Center for Molecular Genetics, University of California, San Diego, CA 92093-0116, USA*

²*Smithsonian Tropical Research Institute, Box 2072, Republic of Panama*

Quadrat-based analysis of two rainforest plots of area 50 ha, one in Panama (Barro Colorado Island, BCI) and the other in Malaysia (Pasoh), shows that in both plots recruitment is in general negatively correlated with both numbers and biomass of adult trees of the same species in the same quadrat. At BCI, this effect is not significantly influenced by treefall gaps. In both plots, recruitment of individual species is negatively correlated with the numbers of trees of all species in the quadrats, but not with overall biomass. These observations suggest, but do not prove, widespread frequency-dependent effects produced by pathogens and seed-predators that act most effectively in quadrats crowded with trees. Within-species correlations of mortality with numbers or biomass are not found in either plot, indicating that most frequency-dependent mortality takes place before the trees reach 1 cm in diameter. Stochastic effects caused by BCI's more rapid tree turnover may contribute to a larger variance in diversity from quadrat to quadrat at BCI, although they are not sufficient to explain why BCI has fewer than half as many tree species as Pasoh. Finally, in both plots quadrats with low diversity show a significant increase in diversity over time, and this increase is stronger at BCI. This process, like the frequency-dependence, will tend to maintain diversity over time. In general, these non-random forces that should lead to the maintenance of diversity are slightly stronger at BCI, even though the BCI plot is less diverse than the Pasoh plot.

Keywords: biodiversity; host–pathogen interactions; Janzen–Connell hypothesis

1. INTRODUCTION

High tree species diversity in tropical rainforests has been attributed to many mechanisms, including frequency-dependent activities of pathogens and seed-predators (Augsburger 1983; Clark & Clark 1984; Connell 1971; Janzen 1970; Wills *et al.* 1997), spatial and temporal fluctuations in the environment giving rise to new niches (Chesson & Huntly 1997), new species concentrated in gaps resulting from treefalls (Denslow *et al.* 1998), and an equilibrium situation in which species are lost so slowly in a large forest that new ones can evolve to take their place (Hubbell & Foster 1986). Data sets are now becoming available that can be used to test these and other hypotheses. Here we show that both frequency-dependent processes and chance play important roles in the maintenance of diversity in two different tropical forests. In addition, we show that recruitment is reduced when quadrats are crowded with trees but not in quadrats with high biomass. This latter finding suggests a biological rather than a physical origin of the observed frequency dependence, providing evidence for pathogen and seed-predator effects of the type suggested by Janzen (1970) and Connell (1971).

We examined community-wide patterns rather than a few representative species, because if frequency dependence is in fact an important factor in the maintenance of diversity it must act on many species in the community.

We used quadrat-based analyses of matched data subsets to examine censuses of two 50 ha (1.0 km × 0.5 km) moist rainforest plots, one on Barro Colorado Island in Panama (BCI) and the other in the Pasoh Nature Reserve, Negeri Sembilan, Malaysia (Pasoh). Both plots were until relatively recently part of large continuous forests. Although the BCI plot is now isolated on a small island, and the Pasoh plot is near rapidly encroaching oil-palm plantations, there has been little degradation of diversity in either plot during the census periods. The censuses used were separated by eight years (1983–1990) at BCI and by ten years (1986–1996) at Pasoh. During these census periods there was a severe drought at BCI (Condit *et al.* 1995), but no such extreme events were observed at Pasoh.

To determine significance, correlations were compared with the distributions of 1000 correlations obtained from randomized data sets (Wills *et al.* 1997). The use of matched data subsets meant that some of the commonest trees in both plots were not analysed, but these species showed patterns very similar to those exhibited by the 100 species from each plot that were analysed (Wills *et al.* 1997; C. Wills, unpublished results).

2. STATISTICAL METHODS

(a) *Construction of matched subsets of species*

To ensure that the statistics used to compare the diversities of the forests were applied to equivalent data sets, two matched subsets of the data were constructed from the two plots. The

*Author for correspondence (cwills@ucsd.edu).

BCI subset was adjusted further to compensate for its higher rate of recruitment and mortality. The matched subsets each consisted of 100 species, in which each of the 100 species that were chosen at BCI were matched with a Pasoh species that had a very similar abundance at the beginning of the census period. These two subsets of species did not include the most abundant species in either plot, because these species could not be matched with species that had comparable numbers in the other plot. Indeed, the first pair of species with similar numbers in the two plots consisted of the fifth most abundant species at BCI, *Alseis blackiana*, and the fourth most abundant at Pasoh, *Ardisia crassa*. Very rare species were not used in the analysis, because there were too few quadrats containing both trees that died and trees that were recruited to permit statistical analysis.

At the outset of the census periods there were 116 419 trees in the BCI subset and 115 296 trees in the Pasoh subset with diameter at breast height (DBH) ≥ 1 cm, making up about one-half and one-third of the total number of trees, respectively. In these subsets, recruitment and mortality rates at Pasoh were 49% and 74% of those at BCI during the census periods that were being compared. To make the data sets more comparable, 51% of BCI recruits and 26% of BCI deaths were discarded at random. This could be done safely because there is no significant correlation in either subset between the numbers of a species and the proportion of recruitment or mortality in that species during the census period. Frequency-dependent effects that were statistically indistinguishable from those reported in this paper were also seen when all the data in the BCI matched subset were used (data not shown).

(b) *Correlations between numbers, areas, and life-history parameters*

Both plots were divided into 5000 quadrats, each 10 m on a side. Quadrat sizes of 5 and 20 m were also investigated and gave similar overall patterns of results. However, as in the earlier BCI analysis (Wills *et al.* 1997) different tree species often exhibited their strongest effects at different quadrat sizes (data not shown).

For each species in each quadrat, two life-history parameters were obtained: N_R , the number of recruits, and N_D , the number of deaths during the census period. Recruits were defined as trees that achieved a DBH ≥ 1 cm during the census period. Other numbers that characterized the quadrat at the beginning of the census period were also obtained: N_S , the total number of trees of that species, N_T , the total number of trees of all species, A_S , the total basal area of that species, and A_T , the total basal area of trees of all species. For each species, the only quadrats that were examined were those that had at least one tree of that species present at the beginning of the census period, and in which therefore both recruitment and mortality could be measured.

Parametric and non-parametric (Spearman's rank) correlations were obtained. N_R and N_D were correlated in all possible combinations with N_S , N_T , A_S and A_T . Because the data exhibited autocorrelations, and were often not normally distributed, this would often result in non-zero correlations even if recruitment and mortality were randomly distributed among quadrats. This was compensated for by comparing the magnitudes of these correlations with those obtained from 1000 'scrambled' data sets in which recruitment and mortality were truly random. In these data sets, the coordinates of all the trees of a species were retained, but the sizes of a given tree at the beginning and end of the census period were swapped with the sizes

of another tree of the same species elsewhere in the plot. At the end of the scrambling process, the number of trees and their positions were unchanged, but whether a given tree had died, been recruited, or been present during the entire census period, had been randomized.

Two types of scrambling were carried out, 'total' and 'stratified'. 'Total' scrambling was performed on all the trees of a given species. In 'stratified' scrambling, the trees of a species were divided into three categories based on their sizes at the beginning of the census period: DBH less than 2 cm, DBH between 2 and 10 cm, and DBH greater than 10 cm. Scrambling was then carried out within each category. 'Stratified' scrambling corrected for the possibility that spurious correlations could be introduced as a result of a non-random distribution of size classes across quadrats. In all the analyses, total and stratified scrambling produced statistically indistinguishable results.

We tested the distributions of the correlations that were obtained by the scrambling process, to determine whether they approximated normality. If they did so, then we would be justified in using a *t*-test to determine whether an observed correlation deviates significantly from the mean of a set of scrambled correlations.

All the sets of total and stratified parametric and non-parametric correlations were collected from 20 species picked at random from each of the matched data subsets. This made up a total of 1280 sets of 1000 correlations each. Each set of scrambled correlations was tested for deviations from normality by the Kolmogorov-Smirnov procedure (Zar 1984). Forty-two of these 1280 distributions were significantly different from normality at the 0.05 level, seven at the 0.01 level and five at the 0.001 level, compared with expected values, given the null hypothesis that all distributions were normal, of 51.2, 11.5 and 1.28, respectively. The distributions of the scrambled correlations were therefore indistinguishable statistically from normal distributions.

3. RESULTS

(a) *Similarities between the two plots*

A few of the BCI species are commoner than the commonest species at Pasoh, but otherwise the shapes of the species abundance curves are similar in both (Condit *et al.* 1996). Distributions of the more abundant tree species were examined by Ripley's *K* (Ripley 1977; Haase 1995). Although the species in each forest plot show a wide variety of distributions, ranging from extremely clustered to slightly overdispersed, the distribution of *K*-values is the same in both (data not shown). Any differences between the plots are therefore not the result of different patterns of tree abundance distribution.

(b) *Overall differences between the two plots*

In addition to being less diverse than Pasoh, BCI also has fewer trees with DBH ≥ 1 cm (235 424 compared with 335 323 at the start of the census periods). Both recruitment and mortality rates per unit time are higher in the BCI forest. Expressed as a fraction of the total trees present at the beginning of the census period, the BCI recruitment rate is 0.038 per year, compared with only 0.013 at Pasoh; the BCI mortality rate is 0.028 compared with 0.017 at Pasoh. During the census period ten species were lost and ten were gained at BCI, whereas only five were lost and nine gained at Pasoh even though it has more than twice as many species.

(c) Overall characteristics of the matched subsets

Trees in the BCI subset tend to be larger, with an average DBH of 5.03 ± 9.61 cm, whereas for the Pasoh subset the average is only 3.69 ± 6.31 cm. This difference primarily reflects the greater abundance of small stems at Pasoh, although very large trees are also commoner at BCI. The variation among species in recruitment and mortality, after adjustment for the larger recruitment and mortality rates at BCI, is very similar in the two matched subsets. For the 100 species in each subset, the variances of the fraction that died or was recruited were determined. For recruitment, $F_{\text{Pasoh/BCI}} = 1.24$ (n.s.); for mortality, $F_{\text{BCI/Pasoh}} = 1.25$ (n.s.).

We also examined variation across species in probability of survival in the matched subsets. It might be, for example, that trees of many species in one plot tend to die when they are large, and trees of many species in the other tend to die when they are small. For each species we calculated t -values for the differences between the mean size of the trees that died during the census period and the mean size of those that survived. The means of the t -value distributions are not significantly different from zero in either subset, and the variances are similar in the two subsets ($F_{\text{BCI/Pasoh}} = 1.06$, n.s.). However, the variances in both subsets are greater than expected by chance. For BCI, $t = -0.142 \pm 2.80$, and for Pasoh $t = +0.161 \pm 2.72$. These standard deviations would be expected to be ± 1.0 if mortality were taking place entirely at random, without any relationship to tree size. This larger than expected variation is because, in each subset, trees of some species tended to die when they were larger than average, and trees of other species tended to die when they were smaller than average. Whatever the non-random factors that determine these differences may be, they appear to have produced very similar overall results in the two matched subsets.

(d) Distributions of t -values for correlations

For each of the 100 species in each of the matched subsets, eight parametric and eight non-parametric correlations were calculated. Each of these correlations was compared with distributions of 1000 correlations obtained from scrambled data that were produced by the total and by the stratified scrambling methods. It was therefore essential to summarize this large amount of data. This was done, as noted in §2, by calculating t -values for the difference between the observed correlations and the mean of the distribution of scrambled correlations, a statistically valid procedure because the distributions of the sets of scrambled correlations are normal. Significant negative t -values indicate a negative relationship between the life-history parameter and numbers or biomass across quadrats; significant positive t -values indicate the reverse relation.

Once the t -values for a given type of correlation for all 100 species were obtained, the distribution of this set of t -values could itself be examined to determine whether it deviated from random expectation. If only random processes affect the distributions of recruitment and mortality in all the species in the subset, the expected mean of such a distribution of t -values is zero, and the expected standard deviation (and variance) is unity. Differences from these expectations indicate the presence of non-random processes.

The within-species distributions of t -values shown in figure 1a–d are from non-parametric correlation analyses, using the stratified scrambling procedure. The other analytical methods yielded very similar results.

For each type of correlation, the means of each BCI and Pasoh distribution were compared to zero and to each other with t -tests. The variances of the t -value distributions from the BCI and Pasoh subsets were compared by means of F -tests, and skew values were calculated for each distribution. Statistical details are shown in table 1.

Figure 1a, mortality plotted against numbers, shows that once trees have reached 1 cm DBH, mortality appears to be random with respect to conspecific crowding. The distributions of t -values in both subsets are very close to those expected if there are no non-random effects operating in either subset.

Figure 1b, mortality against areas of conspecifics, shows that, although both t -distributions have means indistinguishable from zero or from each other, the BCI subset has a variance significantly higher than that of the Pasoh subset. This difference is likely to reflect the greater variance in tree sizes at BCI.

Figure 1c,d, recruits plotted against numbers and against areas, demonstrate the results of tests on the effects of crowding or within-species biomass on recruitment. Negative relations would be expected, for example, if Janzen–Connell effects were widespread. Both BCI and Pasoh show very similar distributions, and in each case the average t -value is significantly negative. Further, for recruits plotted against numbers, there is a significant negative skew to both sets of t -values. In each case the skews can be traced to a small number of species with very strong negative correlations, but in each case the majority of species also show negative values.

Figure 1e–h shows results for correlations between mortality or recruitment and the numbers or areas of all other trees (of whatever species) in the quadrat. Statistical details are shown in table 1. Numbers and areas are measures of overall crowding and overall biomass, respectively. Similar results were obtained when only the trees that are in the subsets were counted (data not shown). The most striking feature of this data set is the strong negative relation, in both the BCI and Pasoh data sets, between recruits and numbers of others (figure 1g) and the complete lack of any such relation in either data set between recruits and areas of others (figure 1h). The effect of crowding on recruitment is significantly stronger at BCI. This striking difference between the effects of overall crowding and the effects of overall biomass is strong evidence that biotic rather than abiotic interactions are primarily responsible for the frequency-dependent effects on recruitment (see §4).

There is a significant, and puzzling, difference between the BCI and Pasoh subsets in mortality against numbers of others (figure 1e). The distribution of correlations is significantly positive at BCI, indicating a tendency for mortality to be higher in more crowded quadrats. At Pasoh, in contrast, it is significantly negative, showing that in this subset mortality tends to be higher in less crowded quadrats.

These results all come from non-parametric correlations and stratified scrambling. Table 2 compares some of the results from the different analytical methods used, for

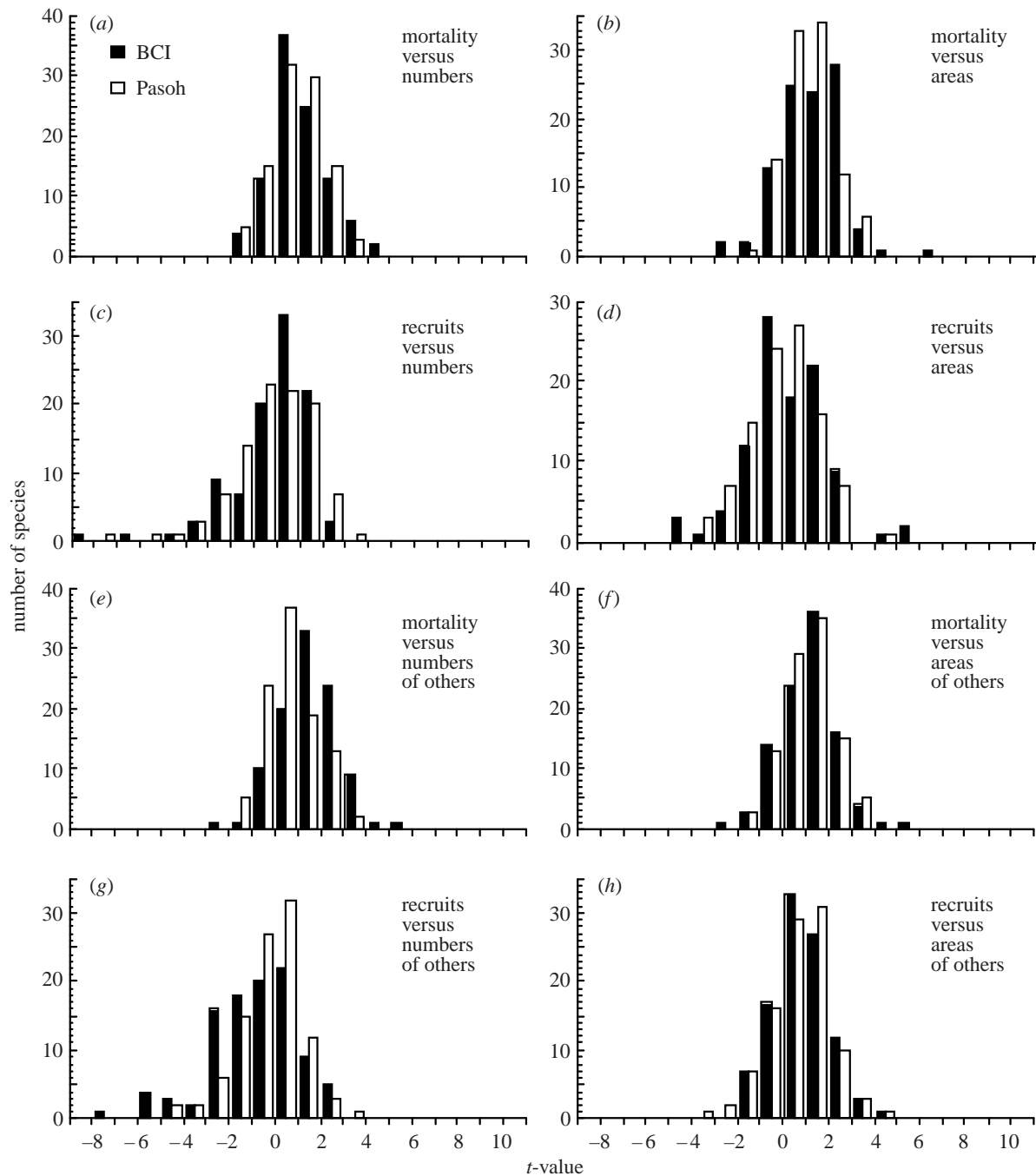


Figure 1. (a–d) Within-species comparisons: distributions of t -values for the 100 matched species of the BCI and Pasoh subsets, for correlations between life-history parameters and crowding (numbers) or biomass (area at breast height). (e–h) Between-species comparisons: distributions of t -values for life-history parameters with overall crowding or biomass in the quadrat. See text for further details; see table 1 for details of statistics.

recruits against numbers of others. There are no significant differences in the t -value distributions obtained, regardless of whether total or stratified sampling was used, or whether the correlations were parametric or non-parametric. A similar lack of difference among the various analytical procedures was seen in the remainder of the analyses (data not shown).

(e) Influence of treefall gaps

Are gaps that have been introduced by treefalls an explanation for the very strong tendency for trees to be recruited in quadrats in which few trees are already present? Information on such gaps, gathered at 12 points

before and during the census period, is available for BCI, although equivalent data are not available for Pasoh. Gaps tend to be small in area, and although a few persist most are quickly healed. We divided the quadrats into two halves, those with the smallest and those with the largest area of gaps during the census period. At any one time gaps covered only a mean of 0.72% of quadrat area in the less disturbed half and 6.9% of quadrat area in the more disturbed half. We then determined the distributions of the correlations of recruitment with numbers, numbers of others, and areas, in the less and the more disturbed halves of the quadrats, and found that they were still highly significantly negative (t -values for means were

Table 1. *Statistical details of results presented in figure 1*(Levels of significance: n.s., not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.)

figure 1 part	t (between subsets)	BCI			Pasoh			$F_{BCI/Pasoh}$
		mean \pm s.d.	skew	t (mean = 0)	mean \pm s.d.	skew	t (mean = 0)	
(a)	0.94 (n.s.)	0.051 \pm 1.25	0.35 (n.s.)	0.40 (n.s.)	-0.108 \pm 1.12	0.023 (n.s.)	-0.97 (n.s.)	1.25 (n.s.)
(b)	0.88 (n.s.)	0.233 \pm 1.36	0.22 (n.s.)	1.71 (n.s.)	0.083 \pm 1.02	0.345 (n.s.)	0.80 (n.s.)	1.71**
(c)	-0.12 (n.s.)	-1.18 \pm 1.83	-1.64***	-6.45***	-1.15 \pm 1.77	-1.13***	-6.57***	1.09 (n.s.)
(d)	0.76 (n.s.)	-0.79 \pm 1.76	-0.08 (n.s.)	-4.48***	-0.96 \pm 1.50	-0.18 (n.s.)	-6.52***	1.42 (n.s.)
(e)	4.83***	0.492 \pm 1.30	0.041 (n.s.)	3.80***	-0.336 \pm 1.13	0.167 (n.s.)	-2.99**	1.32 (n.s.)
(f)	0.30 (n.s.)	0.169 \pm 1.27	0.016 (n.s.)	1.33 (n.s.)	0.119 \pm 1.05	0.105 (n.s.)	1.11 (n.s.)	1.40 (n.s.)
(g)	-2.56**	-1.88 \pm 1.95	0.83***	-9.64***	-1.25 \pm 1.49	0.641***	-8.41***	1.71**
(h)	0.28 (n.s.)	-0.166 \pm 1.20	0.082 (n.s.)	-1.38 (n.s.)	-0.216 \pm 1.33	-0.32 (n.s.)	-1.62 (n.s.)	0.81 (n.s.)

Table 2. *Comparison of the four different analytical methods used in determining the distribution of t -values*(Non-p, non-parametric; p, parametric; 't for mean' tests the difference between the mean of the t -distribution and zero.)

type of correlation:		BCI				Pasoh				$F_{BCI/Pasoh}$
recruit with numbers of others	scrambling	mean	var	skew	t for mean	mean	var	skew	t for mean	
non-p	total	-1.66	3.84	-1.08***	-8.45***	-1.27	2.22	-0.58*	-8.53***	1.72**
non-p	stratified	-1.88	3.80	-0.83***	-9.64***	-1.25	2.22	-0.64**	-8.41***	1.71**
p	total	-1.89	3.72	-1.27***	-9.81***	-1.44	2.56	-0.80***	-8.99***	1.45*
p	stratified	-2.06	3.65	-1.34***	-10.8***	-1.41	2.46	-0.62*	-8.95***	1.48*

-4.42, -7.19 and -7.06, respectively, for the less disturbed quadrats and -4.10, -4.90 and -6.82 for the more disturbed quadrats). Gaps therefore have little effect on these correlations at BCI.

(f) Effects of species turnover

Table 3 shows the magnitude of the average change per quadrat in numbers and in numbers of species over the census periods in the two matched subsets. The variances of these changes are the same after the BCI subset is adjusted for recruitment and mortality. However, when the BCI subset is compared with the Pasoh subset without the recruitment and mortality correction, the variances in these parameters at BCI are significantly greater. The result of this more rapid turnover of species at BCI is that the likelihood per unit time that a species will go locally extinct at BCI is greater than it is at Pasoh.

(g) Changes in diversity measures over time

We then examined diversity in the two matched subsets, to determine how diversity changes over time. If recruitment is negatively correlated with numbers and biomass for each species, indicating frequency dependence, then this should tend to maintain diversity over time.

The diversity measures evenness (Pielou 1975), Simpson's index (Simpson 1949) and McIntosh's index (McIntosh 1967) were calculated for each 10 m quadrat at the start and the end of the census period. The matched BCI and Pasoh subsets were used, after adjustment for recruitment and mortality differences. Table 4a shows that

Table 3. *Average changes in total numbers and species numbers in 10 m quadrats during the census periods*

(B_A , the BCI subset with recruitment and mortality adjusted to match the Pasoh subset; B_U , the unadjusted subset. Levels of significance as in table 1. Note that the means change from positive to negative in the unadjusted and adjusted BCI subsets, because more instances of mortality than recruitment were discarded during the adjustment process.)

	Pasoh	B_A	$F_{B_A/P}$	B_U	$F_{B_U/P}$
Δ nos.	-0.9 \pm 4.0	-0.9 \pm 3.9	0.96	0.8 \pm 6.0	1.49***
Δ spp.	-0.4 \pm 2.2	-0.5 \pm 2.3	1.00	0.3 \pm 3.2	1.40***

in both matched subsets the distributions of these measures are strongly negatively skewed, with many quadrats showing high diversity but a minority forming a 'tail' of low-diversity quadrats. The skew is more pronounced at BCI than at Pasoh. The table also shows that the variance of these measures at the start of the census period is significantly higher in the BCI than the Pasoh subset.

Table 4b shows the variance in the change in diversity over time, and again this variance is far greater at BCI than at Pasoh even after adjustment for different rates of recruitment and mortality. Strikingly, there is a strong positive skew in the distribution of these values at BCI, and a weaker negative skew at Pasoh, showing that at BCI there is a strong tendency for some quadrats to gain substantially in diversity over time.

Table 4. (a) Comparison of variances in diversity measures at the outset of the census period across 10 m quadrats in the two matched subsets

(Levels of significance indicated as in table 1.)

diversity measure	BCI			Pasoh			$F_{\text{BCI/Pas}}$
	mean	variance	skew	mean	variance	skew	
evenness	0.905	0.0021	-4.00***	0.915	0.000 89	-2.21***	2.35***
Simpson's	0.954	0.0012	-5.04***	0.960	0.000 24	-2.98***	5.02***
McIntosh's	0.859	0.0033	-2.73***	0.869	0.001 3	-1.53***	2.46***

(b) Comparison of variances in the change in diversity measures over time

evenness	0.001 2	0.000 32	2.94***	0.001 9	0.000 17	-0.75***	1.88***
Simpson's	0.000 28	0.000 17	2.93***	0.000 36	0.000 05	-0.56***	3.32***
McIntosh's	0.000 64	0.000 51	1.61***	0.002	0.000 25	-0.48***	2.04***

Table 5. Diversity measures at the outset of the census period in the matched BCI and Pasoh subsets, correlated non-parametrically with the subsequent change in these measures over time

(Levels of significance indicated as in table 1.)

diversity measure	BCI			Pasoh		
	real corr	mean of scamb corrs	<i>t</i> -value	real corr	mean of scamb corrs	<i>t</i> -value
evenness	-0.28	-0.13	-6.4***	-0.24	-0.20	-1.3 n.s.
Simpson's	-0.20	-0.08	-5.0***	-0.25	-0.17	-2.9**
McIntosh's	-0.24	-0.10	-5.7***	-0.22	-0.17	-2.0*

Table 5 shows non-parametric correlations between the diversity in a quadrat at the outset of the census period and the subsequent change in that diversity. Only trees in the matched subsets were used to calculate these values. The correlations are negative, as would be expected simply from regression towards the mean. To compensate for this effect, the actual correlations were compared with the distribution of 1000 correlations obtained after total scrambling (the scrambling process was carried out species by species, as in the earlier analyses). At BCI, there is a strong tendency for quadrats with low diversity to increase in diversity over time. At Pasoh, this effect is still generally significant but much weaker.

4. DISCUSSION

These analyses show that frequency-dependent effects are important at both BCI and Pasoh, and that diversity is maintained by these effects. The most likely explanation is that pathogens and seed-predators are primarily responsible for these effects, and that their influence is widely felt through both forests.

Use of numbers rather than rates of recruits in the correlations presented here circumvents a problem inherent in the analyses presented in our earlier paper dealing with BCI (Wills *et al.* 1997) and that was also raised by Peter Chesson (personal communication). In that paper, correlations with recruitment rate rather than with absolute numbers of recruits were examined. In quadrat-based

analyses, dispersal from outside a quadrat will tend to raise the recruitment rate artificially. However, the predominance of negative *t*-values seen in figure 1c when numbers rather than rates are used shows that there is a tendency for recruitment to take place more often in less crowded quadrats, regardless of the source of the recruits.

The pattern seen in figure 1 indicates that, once trees have reached 1 cm DBH, mortality is approximately random, but that very non-random processes must be taking place during the period when trees are very small. It appears from the data presented here that differential mortality takes place primarily during the most vulnerable period of the trees' lives. This is consistent with the likelihood that much of this early mortality is the result of frequency-dependent activities of pathogens at early stages in the life cycle, as originally suggested by Janzen and Connell. There is growing evidence emerging from studies at BCI that this effect may be even greater earlier in the life cycle. Seed-germination is strongly frequency dependent for the species *Trichilia tuberculata* and *Miconia argentea* at BCI (H. Muller-Landau, personal communication), although the pattern of this frequency dependence is very different in the two species.

There is, however, a suggestion in these data that mortality among trees larger than 1 cm DBH may not be completely random at BCI. The variance of *t*-values for mortality against areas is significantly larger at BCI than at Pasoh (figure 1b), although the means of the *t*-distributions in the two matched subsets are not significantly

different from each other or from zero. This analysis shows that at BCI there is a detectable tendency for some species to show higher mortality later in life and for others to show higher mortality earlier in life. This finding agrees with the observation made at the beginning of the results section that, in both subsets and taking the data as a whole, there are some tree species that have higher mortality when they are small and others that have higher mortality when they are large. Condit *et al.* (1995) found very complex relations between the mortality due to drought and the sizes of trees, microclimate, and degree of specialization on slope. It is probable that tree life span, susceptibility to pathogens, degree of specialization, and other factors all play a role in increasing the variance of mortality versus size among these tree species.

Figure 1*e–h* summarizes the effects of trees of other species that are present in the quadrat, which can be taken as a measure of overall crowding, on mortality and recruitment. The most substantial effect, seen in figure 1*g*, is a negative one of overall crowding on recruitment. In general, there is a tendency for species to recruit poorly in quadrats crowded with other trees, regardless of species. Both at BCI and at Pasoh, but particularly at BCI, the species most affected by conspecific crowding (figure 1*c*) are those most affected by overall crowding (figure 1*g*). The correlation between the figure 1*c* and 1*g* sets of *t*-values is +0.708 at BCI and +0.342 at Pasoh. Both correlations are highly significant, but at BCI the sensitivity of some species to both conspecific and overall crowding is much more pronounced.

It is striking that a similar negative effect on recruitment is not seen when the effect of the total biomass of other trees, measured as the total area at breast height, is examined. The means of the *t*-distributions for both BCI and Pasoh are not significantly different from zero or from each other, the variances are close to unity, and there is no significant negative skew to either *t*-value distribution.

The effect of overall crowding on recruitment might be the result of some limiting physical resource: light, nutrients in the soil, even water. If such a shortage is driving this relation, it might be supposed that these factors would also be in shorter supply in quadrats with high biomass. Insolation that might influence recruitment, for example, should be low in quadrats with large trees. On the other hand, it has been shown that nutrients returned to the soil by leaf fall increase soil fertility in Australian rainforests (Herbohn & Congdon 1998), and such litter-fall would be expected to be higher in quadrats with high biomass. In general, the connection between inorganic factors and productivity is not an obvious one. For example, added nitrogen had little effect on productivity in a mature Hawaiian rainforest (Vitousek *et al.* 1993).

The complete lack of a relation between recruitment and overall biomass seen in these data suggests that abiotic or biotic factors associated with biomass either are not present or tend to cancel each other out. However, the strong negative relation between recruitment and overall crowding suggests that effects of overcrowding itself, such as a tendency for diseases to spread readily among small and susceptible plants, may be an important factor in both plots.

The effects of overall crowding on mortality (figure 1*e*) show the clearest differences between the two matched subsets. There is a weak positive relation at BCI, and a weak negative one at Pasoh, and the differences between the two matched subsets are highly significant. It is not obvious why, among trees that have already achieved 1 cm DBH, there should be a benefit to survival of overall crowding at BCI and a deleterious effect of overall crowding at Pasoh. However, this observation suggests that there are likely to be a number of important differences between the forests that have yet to be discovered, much less understood.

Treefall gaps affect a small fraction of the BCI forest at any one time, and it has been possible to show that they have little influence on the frequency- and density-dependent factors examined here. Further, it has now been shown at BCI that recolonization of treefall gaps has little effect on biodiversity (Hubbell *et al.* 1999). This stands in marked contrast to the situation in hurricane-damaged Nicaraguan forests, in which species diversity increases in a rapid and non-random fashion (Vandermeer *et al.* 1995; J. Vandermeer, personal communication). In such damaged forests, recolonization of disturbed areas appears to play a large role in the maintenance of diversity, as would be predicted by the intermediate-disturbance hypothesis (Connell 1978; Huston 1979).

The analysis presented in table 3 shows that, before adjustment for differences in recruitment and mortality, the variances of gain and loss in numbers and in species per quadrat are substantially higher in the BCI subset. This effect disappears when the BCI subset is adjusted so that its recruitment and mortality rates match those of the Pasoh subset. This shows that stochastic effects resulting from more rapid turnover are major contributors to a higher rate of local species gain and loss at BCI. If the rapid turnover at BCI has been continuing for some time, it may have led to the pattern that is seen in table 4, a greater variance in diversity across quadrats at BCI.

Is the increased turnover at BCI by itself sufficient to explain the smaller number of species in the BCI plot? This seems unlikely because, as is seen in table 5, there is a stronger tendency at BCI than at Pasoh for low-diversity quadrats to increase in diversity over time. This should counteract the effects of high turnover.

Although it has been noted by Phillips *et al.* (1993) for a variety of New and Old World mature wet forests, that species turnover is in general positively rather than negatively correlated with species richness, the correlation is not a strong one. There were some forests in their data set with low diversity and high turnover and *vice versa*. The situation in any given forest is likely to be complex. It is therefore prudent to conclude that the non-random factors acting on the BCI and Pasoh forests that have resulted in such different species numbers must include influences other than an increased rate of local extinction at BCI.

In almost all the cases shown in figure 1, including the non-significant ones, the variance of *t*-values at BCI is greater than the corresponding variance at Pasoh. Similar patterns are seen at other quadrat sizes and using other methods of analysis (data not shown). This suggests that non-random processes acting on forest diversity are in general stronger at BCI.

In both matched subsets of the forests, but particularly at BCI, recruitment is negatively density dependent, and this will tend to preserve species diversity. Further, as shown in table 5, there is a stronger tendency at BCI than at Pasoh for quadrats with low diversity to increase in diversity during the census period, even after adjustment for differences in recruitment and mortality. This may be traceable to the slightly more pronounced frequency-dependent effects seen at BCI. However, in spite of the stronger non-random forces acting on the BCI subset, there are no significant changes in the means of the diversity measures during the census period in either subset. Neither subset has gained or lost appreciable amounts of diversity. Thus, the non-random forces acting at Pasoh appear to be sufficient to maintain its diversity.

As more data sets of this type become available (Ashton 1997), further comparative studies will clarify the evolutionary histories of these complex and delicate ecosystems, and will suggest other experimental approaches that can be taken to investigate the balance of forces maintaining that diversity. In the meantime, in view of the evidence presented here that pathogens and seed-predators may be involved in maintaining overall diversity in two different tropical ecosystems, conservationists should be aware that the overall health of complex ecosystems may depend on preserving their pathogens as well as the more visible and obvious host species (Wills 1996).

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