dictions about dispersal distances, the role of larval traits, and biogeographic and genetic patterns, which are consistent with emerging empirical data (6, 28, 35). Further experimental tests of model predictions, as well as incorporation of higher resolution biophysical models, will serve to improve the predictability of dispersal kernels, our understanding of the processes driving the dispersal outcome for explicit locations, and, ultimately, application of appropriate scaling to spatial management of marine populations.

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Nonrandom Processes Maintain Diversity in Tropical Forests

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An ecological community's species diversity tends to erode through time as a result of stochastic extinction, competitive exclusion, and unstable host-enemy dynamics. This erosion of diversity can be prevented over the short term if recruits are highly diverse as a result of preferential recruitment of rare species or, alternatively, if rare species survive preferentially, which increases diversity as the ages of the individuals increase. Here, we present census data from seven New and Old World tropical forest dynamics plots that all show the latter pattern. Within local areas, the trees that survived were as a group more diverse than those that were recruited or those that died. The larger (and therefore on average older) survivors were more diverse within local areas than the smaller survivors. When species were rare in a local area, they had a higher survival rate than when they were common, resulting in enrichment for rare species and increasing diversity with age and size class in these complex ecosystems.

Most of the mechanisms that have been proposed for the maintenance of species diversity in ecosystems do not assume that locally rare species will survive preferentially. These mechanisms include the intermediate disturbance hypothesis and classic niche differentiation (1); lottery competition for space, coupled with storage effects, which can take place in a variable environment or when recruitment is limited (2); the source-sink hypothesis (3); and the neutral theory of biodiversity (4). The last of these assumes that within a trophic level of an ecosystem—such as the trees of a tropical forest—ecological drift governs local community dynamics.

Three important models invoke frequency-dependent mechanisms that lead to higher survival of locally rare species. The first of these is the Janzen-Connell hypothesis (5, 6), in which diversity is maintained by frequency- or density-dependent interactions between hosts and specialized pathogens, herbivores, or predators. The Janzen-Connell model predicts that diversity should increase as a group of individuals ages, because more common species are selectively removed by pathogens and predators. The mix of surviving species will also depend on the past history of local host-pathogen or plant-resource interactions, so that it is likely to vary over both time and space. There is experimental evidence for the Janzen-Connell model (7–11).

The second of these models, the niche complementarity hypothesis (12, 13), posits that species differ in the sub-environments or resources they exploit, and as a result, individuals compete more intensively with conspecifics than with individuals of other species. Because locally rare species are subject to relatively less conspecific competition than more common species, they are at a relative advantage (14). In this model, an increase in diversity can be traced to variations in the physical characteristics of the environment rather than the effects of pathogens and predators. In the third model, facilitation (15), diversity may increase if an individual facilitates (benefits) nearby nonconspecifics. Similar to the niche complementarity hypothesis, facilitation has the effect of making interspecific interactions more positive than intraspecific interactions and thus provides an advantage to locally rare species.

Possible frequency-dependent effects have recently been proposed for six forest sites (16), but these postulated effects are based on extrapolations from theory rather than actual birth and death rates. Frequency-dependent recruitment and mortality have been observed

in common species of forests in Barro Colorado Island (BCI), Panama and in Pasoh, peninsular Malaysia (17–19), but such observations are unable to distinguish the Janzen-Connell model from the two other models that depend on local frequency-dependent effects. The relative importance of each of these three frequency-dependent models in the maintenance of diversity can only be determined by detailed studies of ecosystems exhibiting a range of diversities (20). In all three of these mechanisms, species diversity can increase in a way analogous to the frequency-dependent advantage of rare alleles that can increase the number of alleles and the average heterozygosity at a genetic locus (21). If these processes act throughout the lifetimes of the organisms, they will lead to an increase in diversity with age class.

All three of these mechanisms should act locally rather than globally. If infections by pathogens are responsible for the differential survival of locally rare and common species, such infections are likely to be local in extent. Similarly, niche complementarity and facilitation would be expected to have their strongest effects among near-neighbor trees. A complex

ecosystem can be thought of as a mosaic in which local diversity is increasing everywhere, regardless of the local mix of species that is present.

We investigated whether local diversity patterns in tropical forests were consistent with the presence of local frequency dependence by carrying out a quadrat-based analysis of seven tropical forest dynamics plots (FDPs). The FDPs, located in the New and Old World tropics, range in size from 16 to 52 ha. They have a wide range of species richnesses and tree densities and have all been censused more than once (Fig. 1). Each is managed by a host-country institution belonging to a research network that is coordinated by the Center for Tropical Forest Science based at the Smithsonian Tropical Research Institute.

For each FDP census, the locations of all trees with diameters ≥ 1 cm at 1.3 m above the ground (DBH) were determined, and the trees were identified to the species level. Trees that were recorded as recruits in the second census but not the first were therefore not new seedlings but trees that had reached 1 cm DBH during the census interval. We divided the FDPs into quadrats with dimensions 10, 20, 30, 40, or 50 m. Censuses used in the present analysis were separated by 10 years in two FDPs (BCI and Pasoh) and by 5 years in the other FDPs. The intermediate BCI census was examined, and the two successive 5-year intervals yielded the same pattern as the 10-year interval but with lower significance levels.

To quantify diversity, we used the rarefaction index, which estimates the average number of species to be expected in samples of a fixed number of individuals taken from a quadrat. Other commonly used diversity measures are correlated with tree density, which varies widely among quadrats in all the FDPs and confounds the analysis. In the present study, rarefaction is not correlated with densities of trees in the quadrats (22).

We examined the diversities of four demographic categories of tree within each quadrat.

The first two of these categories consisted of the trees that died and the trees that were recruited during the census period. The third and fourth categories consisted of the younger and older surviving trees (those observed at both censuses), respectively. Although it was not possible to partition the survivors directly into age classes, we noted that within each species small survivors were likely to be younger than large survivors. We therefore grouped into the small-survivor category the members of the survivors of each species in a quadrat that fell within the smallest quartile of DBH values for the survivors of that species at the first census. The large-survivor category was made up of the remaining three quarters of the survivors of each species in the quadrat. Only trees that increased in size or stayed the same size during the census period, usually more than 90% of the surviving stems (table S1), were included in the analysis. By partitioning the tree size data within species, we avoided the problem that some species are shorter-lived than others. Differences in life span alone would result in diversity differences between small and large individuals if a cutoff were applied equally across all species. Division of the survivors into size classes within species avoided this possible source of bias and provided a comparison uninfluenced by species life history differences.

The within-quadrat differences in diversity of trees in each of the four demographic categories are shown in Fig. 2. In almost all cases, the diversities of the trees that died, the recruits, and the small survivors were significantly lower than the diversities of the large survivors. In most of the cases in which the differences were not significant, the number of degrees of freedom was low. These patterns were seen at all five quadrat sizes, but in general the most pronounced and most highly significant differences were seen at small quadrat sizes. This observation is in agreement with the prediction of the Janzen-Connell,

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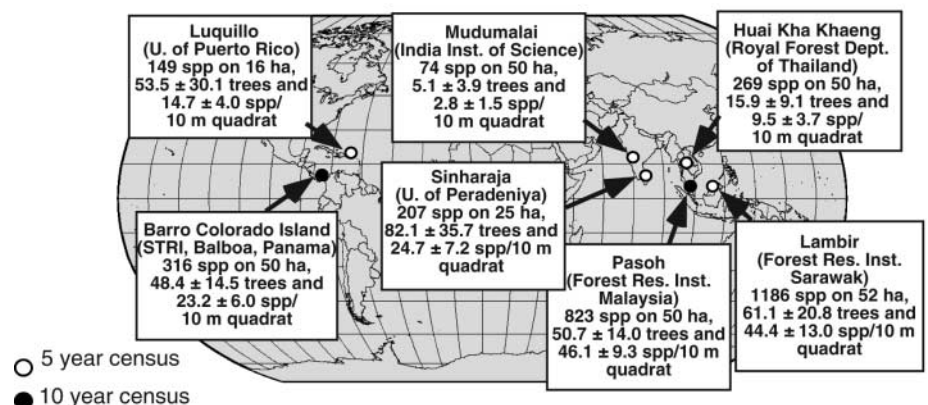
Fig. 1. Locations and species diversities of the seven FDPs included in this analysis. Shown in parentheses are the host-country institutions that manage the plots for the Smithsonian Tropical Research Institute. Means ± SD are shown for number of trees and number of species (spp) per 10-m quadrat.

niche-complementarity, and facilitation models that locally rare species should be at an advantage. The size of the effects diminishes at larger quadrat sizes because species that are common in some small quadrats are rare in others; when larger quadrats were examined, the diverse small quadrats were pooled together.

Fig. 2. Comparisons of diversities between different categories of tree, measured as rarefaction samples of size 10. The FDPs were divided into quadrats of dimensions 10, 20, 30, 40, or 50 m, and comparisons were made for all quadrats in which there were at least 10 trees in each category. The differences between the mean diversities are shown as colored bars. The top of each bar indicates the mean diversity of the large survivors, and the bottom of that bar indicates the mean diversity of the category of trees that is being compared to the large survivors. Nonsignificant differences are shown as white bars. Error bars are the 95% confidence intervals for pairwise *t* tests, and the degrees of freedom are given below each bar. Similar results were obtained for rarefaction values of 2 and 5. The diversities vary among FDPs because of differences in species richness. (**A**) Comparisons between the diversities of trees that died during the census period and those of large survivors. (**B**) Comparisons between the diversities of trees that were recruited during the census period and those of large survivors. (**C**) Comparisons between the diversities of small survivors (the smallest quartile of each species) and large survivors (the largest three quarters of each species).

The smallest differences were seen between small survivors and large survivors. Thus, diversity tended to increase from the recruits through the smaller survivors to the larger survivors. The trees that died also had low diversity, as expected if commoner species were disproportionately subject to mortality.

As a further check that these diversity estimates were not biased by the densities of trees in the quadrats, we examined size-equivalent subsamples of the quadrat data (Fig. 3). These subsamples consisted of pairs of quadrats chosen such that the numbers of survivors in one quadrat were matched with a different quadrat from the same FDP that had the same number of trees that died or were recruited during the census period. The differences in diversity between the equal-sized demographic categories in these pairs of quadrats were, with a few exceptions, statistically significant when compared by unpaired *t* tests. The magnitudes of the differences were similar to those found with the use of the entire data set. Only 10- and 20-m quadrats could be used in this analysis, because larger quadrats had large numbers of survivors, making it impossible to find pairs of quadrats with the same number of trees in different categories.

We then examined whether species that are locally common have higher mortality than those that are locally rare and whether this effect diminishes at larger quadrat sizes. We also examined whether species that are locally common recruit at a higher rate than those that are locally rare, so that in the absence of other factors recruitment should diminish diversity over time. We carried out these analyses for all FDPs and all quadrat sizes.

We obtained the frequencies of each of the species in all of the quadrats, and then correlated this set of frequencies against a matched set of differences in mortality or recruitment rates. Each of these differences consisted of the difference between the observed mortality or recruitment rate of the species in the quadrat and the mortality or recruitment rate of that species in the FDP as a whole. If a species had lower-than-average mortality or recruitment when it was locally rare, then the difference between the two rates would be negative. If it had higher-than-average mortality or recruitment when it was locally common, then this difference would be positive. The result would be a positive correlation between these differences and the local frequencies of each species in each quadrat.

Figure 4 shows a typical analysis presented in graphical form. Table 1 lists the correlation coefficients and degrees of freedom of all these analyses. In each case, the correlation was positive and highly significant, but the strength of the correlation diminished as quadrat size increased. Species that were locally common had higher mortality than would be predicted from their overall mortality rates and higher recruitment than would be predicted from their
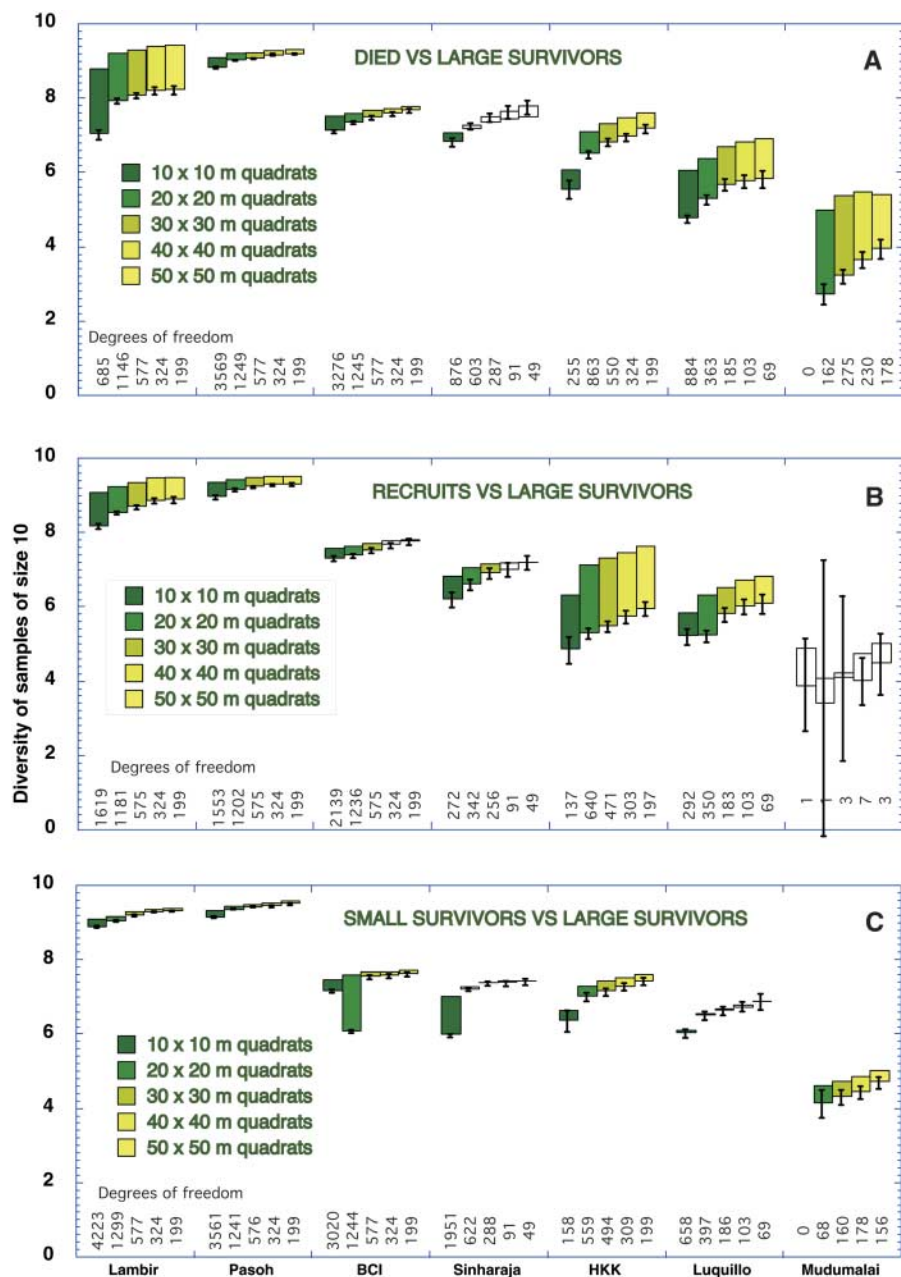
Table 1. Within-quadrat frequency for each species, correlated with the excess or deficiency of within-quadrat mortality or recruitment for that species when compared with recruitment or mortality for the species in the entire FDP (see Fig. 4 for an example of this analysis in graphical form). df, degrees of freedom.

| FDP	10-m quadrats		20-m quadrats		30-m quadrats		40-m quadrats		50-m quadrats	
	r	df	r	df	r	df	r	df	r	df
Mortality										
Lambir	+0.545	231,127	+0.319	162,337	+0.257	123,548	+0.201	95,043	+0.157	74,863
Pasoh	+0.750	230,993	+0.485	155,412	+0.415	112,558	+0.331	83,765	+0.261	63,849
BCI	+0.488	115,815	+0.204	67,012	+0.182	45,088	+0.132	32,310	+0.098	23,741
Sinharaja	+0.446	61,786	+0.221	31,642	+0.199	20,408	+0.110	8,053	+0.070	5,277
HKK	+0.562	47,611	+0.295	30,098	+0.264	21,201	+0.212	15,724	+0.162	12,093
Luquillo	+0.302	23,616	+0.127	11,924	+0.112	7,582	+0.088	5,152	+0.068	3,874
Mudumalai	+0.509	14,389	+0.296	8,454	+0.221	5,674	+0.161	4,098	+0.124	3,092
Recruitment										
Lambir	+0.638	238,007	+0.406	165,849	+0.216	125,552	+0.135	96,172	+0.090	75,558
Pasoh	+0.764	216,478	+0.549	148,567	+0.478	108,588	+0.389	81,589	+0.304	62,441
BCI	+0.577	111,902	+0.290	64,535	+0.250	43,429	+0.194	31,029	+0.151	22,877
Sinharaja	+0.541	59,223	+0.332	30,632	+0.280	19,875	+0.136	7,837	+0.181	5,141
HKK	+0.491	43,407	+0.294	27,846	+0.247	19,800	+0.203	14,820	+0.173	11,379
Luquillo	+0.517	22,147	+0.251	11,325	+0.232	7,157	+0.168	4,886	+0.140	3,682
Mudumalai	+0.767	11,693	+0.676	7,253	+0.702	4,983	+0.652	3,683	+0.569	2,806
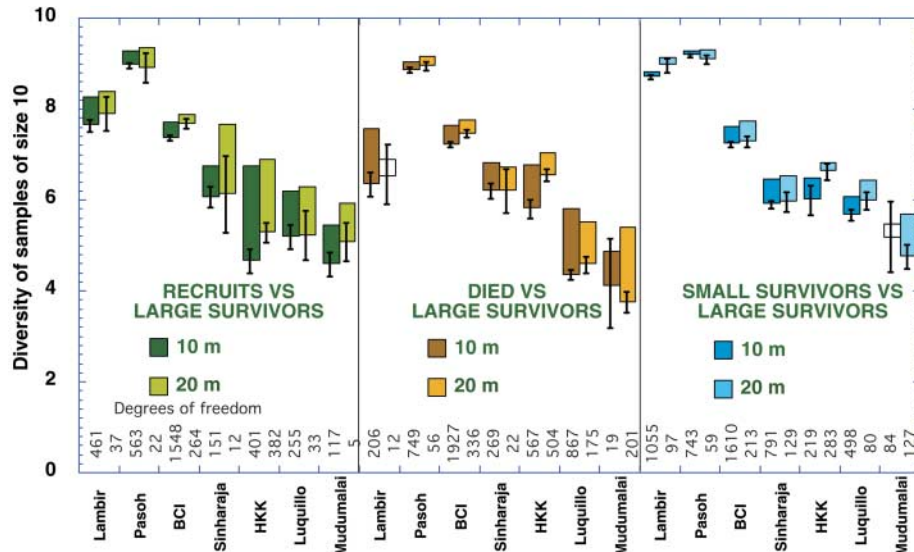
Fig. 3. A test for whether numbers of trees in each quadrat influenced the diversity estimates. Here, the comparisons have been made between matched pairs of quadrats that had the same number of trees in each of the two categories being compared. In these comparisons the *t* tests used to obtain the 95% confidence intervals were unpaired because the comparisons were made between different quadrats.

Fig. 4. Plot of Luquillo 10-m quadrat mortality data, in which the frequency of each species in a quadrat (abscissa) is plotted against the difference between the mortality rate of the species in that quadrat and the mortality rate of the species in the FDP as a whole (ordinate). Solid line, linear regression fit to the data. Summaries of analyses of this type for all FDPs at five quadrat sizes are shown in Table 1.

overall recruitment rates. When species were locally rare, this pattern was reversed. The correlations diminished with increasing quadrat size, showing that these nonrandom effects were primarily acting at the local level.

We next asked whether changes in diversity in the FDPs were evenly distributed or concentrated in certain areas. An overall increase in diversity with age throughout the FDPs would be predicted if increases in diversity were being driven by local factors that operated everywhere in the FDPs. Figures S1 and S2 show filled contour plots of the differences in diversity between demographic categories in the

Luquillo and BCI FDPs, with the use of the data from the 10-by-10-m quadrats. The overall trend was for diversity to increase relatively uniformly throughout the FDPs.

In a previous detailed survey of the BCI FDP, the diversity of seedlings was found to be greater than the diversity of the seeds from which they came (*23*). Our findings extend the BCI seed-to-seedling results to include cohorts of trees at later stages of maturity and show that the same increase in diversity has taken place in six other FDPs from around the world. The increase in diversity from trees that died and recruits to survivors may be due in part to
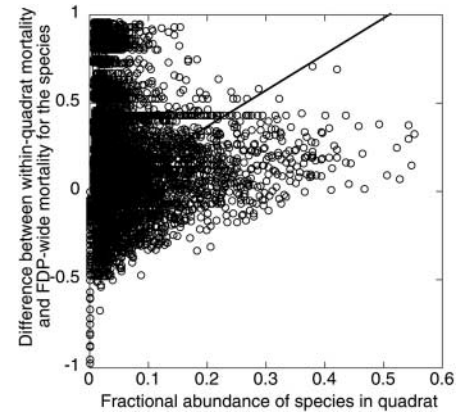
differences in life history between rare and common species, but the diversity differences between relatively larger and relatively smaller survivors can be due only to local frequency-dependent processes.

Further censuses planned for these and other FDPs should let us follow in detail increases in diversity over a span of decades, to determine whether these gains are sufficient to maintain diversity in the FDPs. We will also be able to measure more precisely why the changes in diversity vary in their magnitude from plot to plot (Fig. 2).

Is the low diversity of recruits in the FDPs the result of recent worldwide environmental

changes, possibly generated by human activity? Recent changes in weather patterns and a wide variety of anthropogenic effects (24, 25), along with losses of pollinators and herbivores from all tropical ecosystems (26), may have contributed to a reduced diversity of recruits in all these FDPs. Such effects cannot be ruled out, but the increase in diversity observed from seeds to seedlings at BCI (23) and the low diversity of trees that died during the census interval at all the FDPs in the current study indicate that the changes in diversity reported here have largely been the result of ongoing natural processes. It remains to be discovered, however, what fraction of these increases in local diversity can be attributed to Janzen-Connell effects, to the ability of rare tree species to take advantage of a complex local environment, and to positive interactions among rare tree species themselves. Thorough testing of these possibilities may require experimental manipulation of small areas within mature tropical forests through the deliberate introduction of large numbers of seeds or seedlings of a variety of common or rare species followed by a detailed examination of the fate of these introductions over time.

The nonrandom maintenance of diversity has two consequences, one short term and one longer term. In the short term, ecosystems that have lost diversity after temporary damage may be able to recover their former diversity levels rapidly, provided that any extinctions that have taken place in the affected ecosystems are local and diversity can be restored through immigration. Such a rapid recovery in diversity would not be possible if individuals of different species replaced each other at random (4). In the longer term, natural selection will tend to increase morphological and biochemical differences among host species (27, 28). In the case of Janzen-Connell effects, these differences will be selected because they result in pathogen range restriction. This restriction will in turn increase the effectiveness of frequency-dependent selection for host species that are rare, because their pathogens will also be rare (29). In the case of niche complementarity and facilitation, differences between tree species will increase over time because these differences will aid the efficient utilization of different physical environments or will increase the benefit of interspecific interactions. Thus, the evolutionary result of frequency-dependent mechanisms for the maintenance of ecosystem diversity will be the generation of further diversity among the species of each trophic level.

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An Architectural Framework That May Lie at the Core of the Postsynaptic Density

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The postsynaptic density (PSD) is a complex assembly of proteins associated with the postsynaptic membrane that organizes neurotransmitter receptors, signaling pathways, and regulatory elements within a cytoskeletal matrix. Here we show that the sterile alpha motif domain of rat Shank3/ProSAP2, a master scaffolding protein located deep within the PSD, can form large sheets composed of helical fibers stacked side by side. Zn^{2+}, which is found in high concentrations in the PSD, binds tightly to Shank3 and may regulate assembly. Sheets of the Shank protein could form a platform for the construction of the PSD complex.

Signaling pathways in eukaryotic cells are often physically linked in large protein complexes (1). A particularly dramatic example is the PSD, a disk-shaped protein assembly on the postsynaptic side of neuronal synapses, which is roughly 40 to 50 nm thick, up to 500 nm wide, and contains more than 100 different proteins (2–5). The PSD likely aids the appropriate communication of incoming signals to cytoplasmic targets and contributes to neuronal plasticity by readily changing its composition and structure in response to neural activity (6–9).

A number of scaffolding proteins link components of the PSD (10). The Shank family of proteins (also known as ProSAP, SSTRIP, CortBP, Synamon, or Spank) are considered master scaffolding proteins in the PSD, because they bind to a number of other scaffolding proteins including guanylate kinase–associated protein/SAP90/PSD-95–associated proteins (GKAP/SAPAPs),

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ERRATUM

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Reports: "Nonrandom processes maintain diversity in tropical forests" by C. Wills *et al.* (27 Jan. 2006, p. 527). The analysis presented in the paper was flawed because of a programming error. The error affects the analysis presented in Table 1 and alters the ordinate of Fig. 4, which was derived from the same analysis. Sentence 2 of paragraph 4 of column 3 of page 529 should read "Each of these differences consisted of the difference between the observed mortality or recruitment rate of the species in the quadrat and the mortality or recruitment rate of that species in a random sample of the same size taken from that quadrat." Sentences 2 and 3 of the next paragraph should read: "Table 1 lists the average *t* values and degrees of freedom of all these analyses. In most cases, the *t* value was positive and highly significant, but the size of the *t* value diminished as quadrat size increased." Corrected versions of Table 1 and Fig. 4 are shown here with their corrected captions.

	10 m quadrats			20 m quadrats			30 m quadrats			40 m quadrats			50 m quadrats		
	Mean number of trees per species		Paired t-value, *df*	Mean number of trees per species		Paired t-value, *df*	Mean number of trees per species		Paired t-value, *df*	Mean number of trees per species		Paired t-value, *df*	Mean number of trees per species		Paired t-value, *df*
	Real	Random		Real	Random		Real	Random		Real	Random		Real	Random	
Mortality															
Lambir	1.279	1.096	26.0, *4505*	1.482	1.195	23.9, *1299*	1.629	1.294	21.7, *578*	1.747	1.407	19.6, *325*	1.897	1.539	17.5, *200*
Pasoh	1.149	1.108	15.3, *4981*	1.373	1.309	14.1, *1249*	1.615	1.543	11.7, *577*	1.917	1.830	10.6, *324*	2.280	2.188	8.8, *199*
BCI	1.550	1.435	18.4, *4971*	2.221	2.082	12.3, *1249*	2.869	2.740	8.2, *577*	3.635	3.527	4.8, *324*	4.544	4.469	2.8, *199*
Sinharaja	1.490	1.463	2.2, *2377*	2.101	2.136	−1.3, *624*	2.792	2.843	−1.2, *288*	4.072	4.269	−1.5, *91*	5.522	5.872	−2.1, *50*
HKK	1.540	1.362	14.0, *3750*	1.891	1.644	9.4, *1243*	2.345	2.068	10.0, *577*	2.880	2.556	11.6, *324*	3.571	3.209	8.9, *199*
Luquillo	3.046	2.265	23.0, *1443*	5.020	3.729	16.0, *399*	7.091	5.432	12.5, *186*	9.734	7.598	10.2, *103*	11.891	9.584	8.1, *69*
Mudum	2.660	1.908	22.8, *1696*	3.643	2.076	14.3, *974*	4.681	2.556	8.1, *543*	5.532	3.200	9.5, *318*	6.872	4.142	7.3, *199*
Recruitment															
Lambir	1.239	1.114	19.6, *4558*	1.451	1.244	21.0, *1281*	1.632	1.375	21.7, *578*	1.849	1.533	19.4, *325*	2.092	1.719	18.4, *200*
Pasoh	1.123	1.075	13.3, *4350*	1.266	1.197	13.9, *1247*	1.439	1.352	12.6, *577*	1.635	1.546	10.5, *324*	1.895	1.789	9.2, *199*
BCI	1.454	1.353	15.0, *4816*	2.066	1.903	13.3, *1249*	2.701	2.490	11.8, *577*	3.436	3.166	10.5, *324*	4.299	4.006	8.7, *199*
Sinharaja	1.440	1.340	5.8, *1499*	1.811	1.692	4.6, *559*	2.233	2.089	3.8, *282*	3.062	2.885	2.4, *92*	3.970	3.748	2.1, *51*
HKK	1.975	1.456	19.4, *2730*	2.442	1.596	14.9, *1138*	2.947	1.884	14.7, *567*	3.404	2.268	12.2, *323*	4.078	2.776	12.8, *199*
Luquillo	1.771	1.487	11.3, *1367*	2.530	2.109	8.9, *397*	3.334	2.874	6.4, *186*	4.255	3.794	5.0, *103*	5.162	4.681	4.1, *69*
Mudum	1.591	1.363	2.7, *67*	1.694	1.370	3.6, *84*	1.673	1.370	3.5, *93*	1.935	1.460	3.3, *80*	1.815	1.472	2.9, *79*

Table 1. The mean number of trees per species of trees that died and were recruited in each quadrat was compared with the mean number of trees per species of samples of trees of the same size that were drawn at random from survivors + died or survivors + recruited in the same quadrat. Sampling of all quadrats with two or more trees that died or were recruited was carried out 100 times. The mean *t* values of the paired comparisons between the real and randomized values, along with their degrees of freedom (df), are shown. The expectation was that if trees that died or recruits were a random sample of the trees in the quadrat, there should be no difference in mean numbers of trees per species between the real died or survived categories and the randomized samples from the same quadrats. In almost all cases, the observed mean numbers of trees per species were significantly larger than the mean numbers of trees per species of random samples of the same size. This is the result that would be expected if commoner species were overrepresented and rarer species underrepresented among the trees that died and the trees that were recruited. The significance of the difference between real and random data sets diminished with increasing quadrat size, as expected if the nonrandom effects were strongest in the local regions represented by small quadrat sizes.

Fig. 4. Plot of Luquillo 10-m quadrat mortality data, in which the frequency of each species in a quadrat (abscissa) is plotted against the difference between the number of trees of the species that died in that quadrat and the number that "died" in a random sample of the same size taken from survivors + died in that quadrat (ordinate). Solid line, linear regression fit to the data.

y = −0.088025 + 5.3047x
R = 0.24558 for 1441 d.f., p <<0.0001