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Nearest-neighbor tree species combinations in tropical forest: the role of chance, and some consequences of high diversity

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In three permanent inventory plots comprising 12.4 ha of undisturbed forest at La Selva, Costa Rica, all stems $\geq$10 cm dbh were mapped and identified to species. There were 1628, 1478 and 1954 trees in the plots, representing 168, 166 and 171 species respectively. We determined the species of each nearest-neighbor pair of trees, and asked whether the occurrence of species pairs conforms to a simple random mixing model. If trees are randomly mixed in terms of species, the expected frequency of any nearest neighbor species combination is a function of the relative abundance of the two species. Departures from random mixing could arise from species interactions, differential responses to habitat, or both. The number of possible ij species combinations increases approximately as the square of the number of species. For the 168 species in plot 1, for example, there are 14 196 possible combinations. We compared the expected frequency of each species combination in the three plots (42 736 combinations in all) with observed frequencies. Over 98% of the combinations had observed frequencies of zero and expected frequencies close to zero. A consequence of high diversity is low density of most individual species, and exceedingly low frequencies of the vast majority of species combinations. For each of the 805 combinations with observed frequencies >0, we used simulation to generate a distribution of expected frequencies. We used a t-test to compare the observed frequency with the mean of the simulated distribution for each combination. Only 40 combinations (0.09% of the possible species combinations in the plots) departed from expected frequencies; 39 combinations were more common, and one less common than expected. The overwhelming majority of nearest neighbor species combinations occur at frequencies predictable from their individual abundances.

The most remarkable single feature of tropical rain forests is their great wealth of tree species (Richards 1996), and much has been written on the origin and maintenance of tropical diversity (Tilman and Pacala 1993, Givnish 1999, Hubbell 2001, Wright 2002). This paper focuses instead on some of the consequences of high diversity in tropical tree assemblages, as revealed by detailed analyses of tree distribution patterns in permanent inventory plots at La Selva Biological Station in Costa Rica.

In high diversity forests, the pool of available tree species suited to a given set of conditions is large with respect to the number of individual trees that can physically co-occur in a given stand. Thus, in areas without marked environmental differences, chance may influence which species germinate and establish in a given area, leading to a kaleidoscopic shifting of species composition over space in time, a concept put forward by Aubréville (1938) and referred to by Watt (1947) and Richards (1952) as the mosaic or cyclical theory (Burslem and Swaine 2002, Chazdon and Denslow 2002).

If chance alone determines which tree species grows as the nearest neighbor of any other tree, then the frequencies of nearest-neighbor species pairs should follow a simple model of random mixing. In such a model, the frequency of each ij nearest-neighbor species combination is determined simply as the product of the individual frequencies of the two species under consideration.

If interactions (positive or negative) between tree species affect their successful establishment and hence their location with respect to one another, one should find substantial, systematic and repeated departures from a random model of species pairs. Such departures should be most evident at the level of nearest neighbors: trees, as sessile organisms, only interact directly with individuals quite close to themselves.

If habitat variability is sufficient within the stand, tree species distribution patterns could be influenced by environmental factors, causing the observed frequencies of nearest neighbors to depart from a random mixing model. Species that share a preference for some subset of the available conditions should occur as nearest neighbors more often than predicted, and those that occur preferentially in a different subset of conditions should be found as nearest neighbors less often than expected by chance.

Departures from random mixing among nearest-neighbor species pairs could be produced by species interactions (positive or negative), by environmental factors (some sites being more suitable for the species than others), or by both (Simberloff and Connor 1981). If, however, observed frequencies do not depart from those expected with random mixing, the most parsimonious interpretation is that neither species interactions nor environmental factors are important in shaping tropical forest species composition at the scale under consideration.

Based on tree distribution patterns in permanent inventory plots at La Selva Biological Station, we compare the observed frequencies of all nearest-neighbor species pairs with frequencies predicted by random mixing, assessing the relative importance of species interactions, environmental factors, and chance in determining the species identities of nearest neighbors.

Study area

The research was conducted in primary, undisturbed forest at La Selva Biological Station (10°26′N, 83°59′W) in northern Costa Rica, at the transition between the Caribbean lowlands and the low, steep foothills of the Cordillera Volcanica Central. The mean annual rainfall of 4000 mm and mean monthly temperature of 25.8°C support tropical wet forest. Deforestation for cattle pastures and banana plantations in the region has been widespread, but the magnificent forest within La Selva's boundaries and in the adjacent Braulio Carrillo National Park remains intact. Detailed information on characteristics of the La Selva site and its ecology can be found in Gentry (1990a) and McDade et al. (1994).

Three permanent inventory plots with a total area of 12.4 ha were established in 1969, and were recensused in 1982, 1985, 1989 and 1997. Information from the 1989 inventory is used in this study. The plots represent a range of elevations, topography, drainage and soil parent material (Table 1). Within the plots, all stems ≥10 cm diameter at breast height (dbh) are tagged, mapped to the nearest meter, measured in diameter to the nearest mm at a height of 1.3 m above ground level, measured in height, and identified to species.

Small-scale floristic variation was studied within the three La Selva permanent inventory plots, at the lowland extreme of the La Selva-Volcan Barva gradient (M. Lieberman et al. 1985); the plots range in elevation from 32 m–71 m over a distance of less than 1.5 km. Species composition in 20 × 20 m subplots was found to vary continuously, but weakly, with elevation, likely reflecting differences in edaphic factors including drainage. The most marked floristic variation was found in plot 2, where some tree species were more abundant in the poorly-drained swamp forest and others restricted to the upland portions of the plot. At this scale, despite the demonstrable floristic trend, most of the 269 tree species represented in the study occur over most or all of the elevation range under consideration.

Tropical forest demography at La Selva

Tree density

The number of individual trees that can be packed into a given area of forest is finite. Tree density in primary tropical rain forest varies within wide limits and depends on many factors. In mature forest with adequate drainage, the density of trees ≥10 cm dbh is usually 300–700 individuals per hectare (Hall and Swaine 1981, Whitmore 1984, Swaine et al. 1987,

Table 1. Characteristics of three permanent inventory plots in La Selva, Costa Rica.

	Plot 1	Plot 2	Plot 3
Plot area (ha)	4.4	4.0	4.0
Topography	plateau 90% swamp 10%	swamp 50% rolling hills 50%	steep hills 75% plateau 25%
Elevation (m)	34–48	32–45	33–71
Soil parent material	old alluvium	old alluvium-colluvium	basalt
Density (stems ha^{-1})	369.1	369.5	488.5

Gentry 1990b, Richards 1996). Tree density at any given tropical forest site tends to be fairly consistent over time (Manokaran and Kochummen 1987, Swaine et al. 1987, D. Lieberman et al. 1990). In forest along the La Selva-Volcan Barva gradient, from 32 m–2600 m elevation, tree density in 1-ha plots varies from 350–650 (D. Lieberman et al. 1996). In the La Selva plots, the mean density of trees ranges from 369–489 per ha (Table 1). Local densities in La Selva and in forest in the region are thus in keeping with tree densities reported for tropical forests elsewhere.

Species richness

Species richness of trees in primary tropical rain forests is substantially higher than in temperate forests. Values for tropical rain forests worldwide are between 60–150 species per ha for trees ≥10 cm dbh, with exceptional values of 200–300 per ha in very species-rich areas in western South America and parts of southeast Asia (Gentry 1988, Richards 1996, Whitmore 1998). As the size of the area sampled increases, the number of tree species increases in a non-linear fashion, and such species-area curves for tropical forest assemblages show little tendency to level off even in areas of 4 or 5 ha (Whitmore 1998). In the La Selva plots, the number of tree species in 12 individual 1-ha subplots ranges from 79–107, with a median value of 95 species per ha. The number of species per plot, in an area of 4 ha, ranges from 166–171.

Individual species abundances

As the diversity of any mixture increases (whether the component classes are biological species or entities of any other kind), the density of individual component species declines. For this reason, the population density of individual tree species in high diversity tropical forest mixtures is low. Twenty-eight percent of the species in the La Selva plots are represented by a single individual.

Methods and analysis

Observed data

The data used in these analyses are from the 1989 inventory of the La Selva permanent plots. There were a total of 1628, 1478 and 1954 trees, respectively, in the three plots (Table 2). For each tree in these plots we determined species identity, location to the nearest meter and species identity of the nearest neighbor. The number of nearest neighbors in a plot is equal to number of trees in the plot, as each tree has exactly one nearest neighbor. The mean distance between each tree and its nearest neighbor in the La Selva plots is approximately 2.5 m.

The theoretical number of possible nearest neighbor species combinations is a function of the number of species s in the plot, $s(s+1)/2$, which may be represented by a half-matrix of ij species combinations, with the diagonal containing conspecific pairs. Note that the number of possible nearest neighbor species pairs in the assemblage increases roughly in proportion to the square of the number of species present.

For each of the three plots, the actual observed species list in the given plot was used to prepare a half-matrix of potential species pairs for that plot. The number of tree species occurring in the plots were 168 (plot 1), 166 (plot 2) and 171 (plot 3). The numbers of potential ij species combinations so defined were 14 196, 13 861 and 14 706, respectively, or a total of 42 763 species combinations (Table 2).

For all of these 42 763 potential combinations in the study, we determined (1) the observed frequency; (2) the expected frequency based on explicit binomial probabilities; and (3) the expected frequency based on a simulation approach.

Null model I: explicit binomial probabilities

If tree species distributions at the scale of nearest neighbors are governed exclusively by chance, then the

Table 2. Numbers of individuals and species in the three permanent inventory plots, showing numbers of possible ij species combinations for the assemblage and those actually represented in the stand.

	Plot 1	Plot 2	Plot 3
Number of stems ≥10 cm dbh	1628	1478	1954
Number of species s	168	166	171
Ratio of stems:species	9.7	8.9	11.4
Percent of species with only 1 individual in plot	29.2%	28.3%	26.3%
Possible species-pair combinations [$s(s+1)/2$]	14 196	13 861	14 706
Species combinations actually present in plot	259	222	282
Percent of possible combinations actually present	1.80%	1.60%	1.90%
Possible conspecific species-pair combinations	168	166	171
Conspecific species combinations actually present	13	9	16
Percent of possible conspecific combinations actually present	7.74%	5.42%	9.36%

frequency of nearest neighbor species combinations is simply a function of the relative abundances of the individual species.

Using the observed abundance of each individual species, the expected relative frequency of each kind of nearest neighbor combination may be calculated using the theory of independent experiments based on the product rule (Feller 1957). The frequency with which conspecific trees would be expected to occur together, if mixing of trees is random, is $(pA)^2$, where pA is the proportion of individuals belonging to species A within the plot as a whole. When the trees of a nearest neighbor pair are not of the same species, the relative frequency is predicted by the expression 2(pA)(pB).

The expected number of each kind of species combination is calculated by multiplying the expected relative frequency by the total number of trees in the plot.

Null model II: simulated frequencies

Based on the null expectation that nearest neighbor combinations in a plot reflect a process of random sampling from the assemblage in the plot, we used a simulation approach to generate a distribution of expected frequencies for each potential ij species combination in each plot.

The null distribution for each ij species combination was generated using the following 4-step simulation procedure: (1) two trees were sampled independently and at random, with replacement, from the complete list of individual trees in the plot. (2) The species identities of the pair were noted, and a counter, initially set at zero, was incremented if the randomly chosen pair matched the ij species combination under consideration. (3) This was repeated until the number of pairs drawn was equal to the number of trees in the plot. (4) This procedure was repeated 150 times, producing a null distribution of 150 expected counts for the given ij species combination. The mean and variance of each null distribution was calculated.

Inspection of the means of the simulated expected values showed them to be equal to, or very nearly equal to, the explicit binomial probabilities, supporting the validity of the simulation procedure.

Results

Observed frequencies

The total number of nearest neighbor species pairs observed in a plot equals the actual number of trees in the plot, or 1628, 1478 and 1954, respectively (Table 2). Given the number of species in the three plots, the possible kinds of ij species combinations are 14 196, 13 861 and 14 706. In plot 1, 2 and 3, the kinds of ij species combinations actually observed were 259, 222 and 282, respectively, or only 1.8%, 1.6% and 1.9% of the potential number of species pairs for the given plot. Over 98% of the possible ij combinations, defined by the observed list of species, are not in fact realized as nearest neighbors in the plots. The percentage of realized ij combinations is exceedingly small, because the species richness is so high with respect to the number of individual trees in the stand.

When the numbers of individuals in some species increase, the numbers of individuals in others must decrease, given the constraint on total tree numbers imposed by the size of a given plot. The fact that some species are more abundant than others (that is, that natural assemblages of trees do not show perfect evenness) further decreases the probability that trees in any given ij species combination will in fact co-occur.

The number of kinds of conspecific species pairs possible – those belonging to the same species – is equal to the number of species in a plot, or 168, 166 and 171 respectively in the three plots. We asked how many of these conspecifics actually occur in the stand as nearest neighbors. As shown in Table 2, the numbers of conspecific pairs observed in the plots is low: only 13, 9 and 16 species were found to occur as conspecific nearest neighbor pairs in plot 1, 2 and 3, respectively. These values represent 7.7%, 5.4% and 9.4% of the total possible kinds of conspecific pairs.

Tests of the null hypothesis

A review of the complete list of 42 763 possible ij species combinations indicated that for all cases in which the observed frequency of a species pair was zero, the expected frequencies were essentially the same, close to zero. We therefore excluded from statistical analysis all species combinations in which the observed frequency was zero. A total of 41 958 combinations were excluded from statistical analysis on this basis, and for these we concluded that no difference was demonstrable between the observed and expected frequencies.

For all remaining potential ij species combinations in each plot, we used a Student's t-test to compare the observed frequency, for which there is one value per ij combination, with the mean expected frequency generated by the simulation procedure for that ij combination in that plot ($n = 150$). The null hypothesis in each case was that the observed frequency of a given species combination did not differ from the simulated expected mean frequency based on a random drawing of pairs of trees from the plot list. Taking into account the very large number of statistical tests involved, we used a critical value of $\alpha = 0.01$ for rejection of the null; this was intended to make the tests more conservative by reducing type I error and minimizing the number of spurious rejections of the null hypothesis.

A total of 805 species combinations were tested statistically; there were 247 in plot 1, 231 in plot 2, and 327 in plot 3. The null hypothesis was rejected ($\alpha = 0.01$) in 40 cases out of 805 species combinations tested (Table 3). The remaining 765 combinations tested statistically (95% of the cases tested) were found to conform to a model of random mixing. Thus the overwhelming majority of tree species combinations occur as nearest neighbors at frequencies that are predictable from their individual abundances, as expected by a random mixing model.

The number of nearest-neighbor species combinations occurring significantly more frequently or less frequently than expected by chance ($\alpha = 0.01$) varied among plots, as did the species identities of the pairs and the direction of the deviation from expected values. In plot 1, there were 11 species combinations (representing 4.5% of those that were analyzed statistically, and 0.08% of the total number of combinations considered) that occurred more frequently than expected by chance; none occurred less often than expected. In plot 2, a total of 17 combinations (7.4% of those analyzed statistically, and 0.12% of the total considered) departed from expectations: 16 occurred more frequently than expected, and 1 occurred less frequently. In plot 3, 12 combinations (3.7% of those analyzed statistically, and 0.08% of those considered overall) occurred more frequently than expected from a random model, and none occurred less frequently.

Thus, in the three plots overall, 40 species combinations out of the 42 763 considered did not conform to a random mixing model, or 0.09% of the total. In sum, 39 combinations were observed more often than expected with a random mixing model, and one combination was observed less often than expected. The one instance in which the combination occurred less often than expected involved *Macrolobium costarricense* and *Pentaclethra macroloba* in plot 2.

Altogether 37 species are represented in the list of species combinations for which the null hypothesis was rejected (Table 3). The very abundant canopy tree *Pentaclethra macroloba* occurred in the list more often than any other species; it is represented in 18 of the 40 combinations for which the observed frequency was found to differ from the expected. *Pentaclethra* is the most common tree species in La Selva, accounting for 14% of the stems in the stand. Two other very abundant species, the palm *Welfia georgii*, and the subcanopy tree *Warscewiczia coccinea*, are each represented four times in the list.

Conspecific combinations in the three plots did not depart from random expectations at the 0.01 level. Thus for all species analyzed, individuals belonging to the same species occur as nearest neighbors as frequently as would be expected by chance, consistent with a random mixing model.

For every ij species combination for which the null hypothesis was rejected, the rejection was an isolated instance, found in a single plot and not repeated in other plots where the two species were also found.

Discussion

The early perception of tropical rain forest as a vast formation of essentially homogeneous floristic composition has long since been abandoned in the wake of improved information on the taxonomy and ecology of tropical tree species (Chazdon and Denslow 2002). Studies at continental and regional scales show that tree species composition varies in response to climate and biogeography, confirming that individual tree species are distributed over tropical landscapes in accordance with their particular tolerances and adaptations (Holdridge 1967, Webb 1968, Whitmore 1973, 1984, 1998, Hall and Swaine 1976, 1981, Jacobs 1988). At scales of a few square kilometers to a few hectares, responses of tree species composition to environmental differences are clearly demonstrable (M. Lieberman et al. 1985, D. Lieberman et al. 1996, Hubbell 1998), although chance is also of importance where the pool of available species is large and the species are broadly adapted to the range of conditions present (M. Lieberman et al. 1985, 1995, Hubbell and Foster 1986, Chazdon and Denslow 2002).

Variation in tree species composition with respect to major ecological gradients arises because individual species vary in terms of their environmental tolerances and adaptations. Those species that occur at any given site within the landscape are adapted to, and share a tolerance for, the conditions at that site. This study demonstrates that at small scales – on the order of 4 hectares, in stands comprising 1500–2000 individual trees – distribution patterns of at least 765 species combinations of nearest-neighbor pairs (95% of those tested statistically, and 99.91% of all combinations considered) can be explained by a model of random mixing. Other factors, whether abiotic or biotic, do not appear to cause substantial, systematic, or repeated departures from a null model of random mixing of tree species as nearest neighbors.

The fact that the overwhelming majority of species pairs conformed to binomial expectations is prima facie evidence that, for the assemblage of trees present, the plots can be effectively considered to be environmentally homogeneous. By repeating these analyses over larger and larger plot areas it should be possible to determine the scale at which environmental heterogeneity becomes important for the assemblage.

Table 3. Results of Student's t-test comparing observed and expected frequencies of tree species combinations occuring as nearest neighbors. Species combinations for which the null hypothesis was rejected ($p < 0.01$) are shown for each plot. The observed frequency ($n = 1$) was compared with the null distribution of frequencies generated by the simulation procedure ($n = 150$). The names of species i and j for each combination are shown, followed by the number of individuals of each of the species in the plot, n(i) and n(j); f(obs) = observed number of times species i and j occurred as a nearest-neighbor pair; f(exp) = expected number based on the simulation procedure (mean of 150 runs); f(binom) = expected number based on explicit binomial probabilities; obs-exp indicates whether the observed number was larger (>) or smaller (<) than the expected frequency. **p < 0.01; ***p < 0.001.

Species i	Species j	n(i)	n(j)	f (obs)	f (exp)	f (binom)	obs-exp	t	p
Plot 1									
Guatteria aeruginosa Standl.	*Pentaclethra macroloba* (Willd.) Ktze.	6	199	5	1.36	1.47	>	2.995	**
Dendropanax arboreus (L.) Dec. & Planch.	*Casearia arborea (Rich.)* Urban	32	39	6	1.52	1.53	>	3.803	***
Cordia dwyeri Nowicke	*Welfia georgii* Wendl.	7	294	8	2.67	2.53	>	3.392	***
Protium costaricense (Rose) Engl.	*Pentaclethra macroloba* (Willd.) Ktze.	15	199	9	3.83	3.67	>	2.917	**
Protium pittieri (Rose) Engl.	*Laetia procera* (Poeppig) Eich.	34	28	5	1.14	1.17	>	3.886	***
Protium pittieri (Rose) Engl.	*Naucleopsis naga* Pittier	34	24	4	1.07	1.00	>	2.779	**
Protium pittieri (Rose) Engl.	*Warscewiczia coccinea* (Vahl) Klotzsh	34	69	7	2.94	2.88	>	2.654	**
Casearia arborea (Rich.) Urban	*Laetia procera* (Poeppig) Eich.	39	28	5	1.27	1.34	>	3.459	***
Rheedia edulis	*Warscewiczia coccinea* (Vahl) Klotzsh	14	69	5	1.19	1.19	>	3.280	**
Naucleopsis naga Pittier	*Virola sebifera* Aubl.	24	39	4	1.13	1.15	>	2.631	**
Welfia georgii Wendl.	*Psychotria grandistipula*	294	4	8	1.45	1.44	>	5.507	***
Plot 2									
Macrolobium costaricense Burger	*Pentaclethra macroloba* (Willd.) Ktze.	31	257	2	10.72	10.78	<	2.920	**
Lonchocarpus oliganthus Hermann	*Astrocaryum alatum* Loomis	14	59	4	1.13	1.12	>	2.934	**
Lonchocarpus velutinus	*Pentaclethra macroloba* (Willd.) Ktze.	10	257	11	3.61	3.48	>	4.045	***
Pterocarpus officinalis Jacq.	*Otoba novogranatensis* Moldenke	33	28	7	1.36	1.25	>	4.443	***
Pterocarpus officinalis Jacq.	*Iriartea gigantea* Wendl. ex Burret	33	108	11	4.68	4.82	>	2.724	**
Pterocarpus officinalis Jacq.	*Welfia georgii* Wendl.	33	73	10	3.09	3.26	>	4.076	***
Carapa nicaraguensis C. DC.	*Pentaclethra macroloba* (Willd.) Ktze.	64	257	39	22.68	22.26	>	3.506	***
Carapa nicaraguensis C. DC.	*Otoba novogranatensis* Moldenke	64	28	9	2.33	2.42	>	4.100	***
Carapa nicaraguensis C. DC.	*Apeiba membranacea* Spruce ex Benth.	64	21	7	1.64	1.82	>	4.120	***
Guarea guidonia (L.) Sleumer	*Iriartea gigantea* Wendl. ex Burret	11	108	6	1.73	1.61	>	3.369	**
Pentaclethra macroloba (Willd.) Ktze.	*Astrocaryum alatum* Loomis	257	59	42	19.97	20.52	>	4.674	***
Pentaclethra macroloba (Willd.) Ktze.	*Chimarrhis parviflora* Standl.	257	5	5	1.78	1.74	>	2.631	**
Pentaclethra macroloba (Willd.) Ktze.	*Faramea terreyae*	257	4	6	1.62	1.39	>	3.348	**
Pentaclethra macroloba (Willd.) Ktze.	*Pouteria silvestris* T. D. Penn.	257	7	8	2.45	2.43	>	3.403	***
Otoba novogranatensis Moldenke	*Astrocaryum alatum* Loomis	28	59	13	2.19	2.24	>	6.360	***
Otoba novogranatensis Moldenke	*Colubrina spinosa* Donn. Smith	28	34	7	1.19	1.29	>	4.577	***
Astrocaryum alatum Loomis	*Apeiba membranacea* Spruce ex Benth.	59	21	8	1.53	1.68	>	4.729	***
Plot 3									
Annona montana Macfad.	*Pentaclethra macroloba* (Willd.) Ktze.	4	248	5	1.03	1.02	>	3.897	***
Veconcibea pleiostemona (D.-Sm.) Pax & Hoffm.	*Pentaclethra macroloba* (Willd.) Ktze.	4	248	5	0.83	1.02	>	4.943	***
Pterocarpus hayesii Hemsl.	*Pentaclethra macroloba* (Willd.) Ktze.	11	248	11	2.50	2.79	>	5.294	***
Pterocarpus hayesii Hemsl.	*Welfia georgii* Wendl.	11	188	8	2.20	2.12	>	3.884	***
Pterocarpus hayesii Hemsl.	*Warscewiczia coccinea* (Vahl) Klotzsh	11	90	4	1.04	1.01	>	2.904	**
Ocotea bijuga (Rottb.) Bernardi	*Pentaclethra macroloba* (Willd.) Ktze.	4	248	4	1.09	1.02	>	2.900	**
Pentaclethra macroloba (Willd.) Ktze.	*Stryphnodendron excelsum* Harms	248	4	4	0.80	1.02	>	3.338	**

Table 3 (*Continued*)

Species i	Species j	n(i)	n(j)	f (obs)	f (exp)	f (binom)	obs-exp	t	p
Pentaclethra macroloba (Willd.) Ktze.	*Neea amplifolia* Donn. Sm.	248	5	5	1.29	1.27	>	3.343	**
Pentaclethra macroloba (Willd.) Ktze.	*Coussarea taurina*	248	5	5	1.13	1.27	>	3.615	***
Pentaclethra macroloba (Willd.) Ktze.	*Paullinia* sp.	248	4	4	0.95	1.02	>	3.194	**
Pentaclethra macroloba (Willd.) Ktze.	*Apeiba membranacea* Spruce ex Benth.	248	9	7	2.17	2.28	>	3.547	***
Warscewiczia coccinea (Vahl) Klotzsh	*Goethalsia meiantha* (D.-Sm.) Burret	90	11	5	0.97	1.01	>	4.028	**

In species-rich tropical forest at La Selva, around 98% of the possible ij combinations defined by the observed list of species were not found to occur in the three plots. This is a simple but profoundly important consequence of high diversity: as richness increases, the population density of individual species decreases, and the probability that trees of a given species combination will be found as nearest neighbors becomes exceedingly small. Because the number of potential ij species combinations is so large with respect to the number of trees in the stand, the array of possible combinations is vastly undersampled by the forest at any given time and place.

This undersampling problem cannot necessarily be mitigated by simply expanding the area surveyed in order to achieve a more complete representation of the possible species combinations: with increasing plot size the number of species continues to climb, first as the α–diversity of the assemblage is more thoroughly sampled, and secondly with increasing β-diversity as new habitats, environments, and landscapes are encountered (D. Lieberman et al. 1996). With increasing area, the number of stems increases linearly, the number of species increases as a logarithmic function of the number of stems, and the potential number of ij species combinations increases approximately as the square of the number of species. Thus in diverse tropical forests, even with very large sampling areas, the forest itself will still tend to vastly undersample the potential species combinations. This has fundamental implications for both the ecology and evolution of tropical forest trees.

Plot 2 showed the greatest number of rejections of the null hypothesis (17 species combinations) and the greatest percentage of rejections (7.4% of the combinations tested in this plot, or 0.12% of all potential combinations in the plot). The plot is heterogeneous in terms of topography and drainage, with half the plot area in swamp forest and half in well-drained upland forest, and tree species composition has been shown to reflect this habitat difference (M. Lieberman et al. 1985). Because the analyses in this plot were carried out over an environmentally heterogeneous area, a certain amount of non-random assortment among the tree species in the plot is likely to have occurred. For example, where two species prefer different habitats, they occur as nearest neighbors less often than expected by a model of random mixing; in this case, *Macrolobium costaricense*, a species restricted to the upland portion of plot 2, occurs less often than expected with *Pentaclethra macroloba*, a species that grows well in all parts of the plot.

Where two species share a preference for one subset of the available habitat, they tend to occur as nearest neighbors more often than expected by chance. This is seen for example in the combination of *Lonchocarpus oliganthus* and *Astrocaryum alatum*, or the combination of *Pterocarpus officinalis* and *Otoba novogranatensis*, all of which are species found in swamp forest in plot 2. Thus environmental variation within the area studied – in this case, differences in soil drainage conditions – may either increase or decrease the frequency that a particular pair of species is found together as nearest neighbors, leading to departures from the random mixing model.

Previous work has shown that although fast-growing, short-lived tree species in this forest occur and thrive in canopy gaps (D. Lieberman et al. 1985, 1990), they are not restricted to them (M. Lieberman et al. 1995). Brokaw and Busing (2000) reviewed the literature on establishment of trees in different microsites within treefall gaps and concluded that niche differences contribute less, and chance events more, to the establishment of tree species within canopy openings. None of the species combinations that departed from random mixing in the present study involved pairs of fast-growing, short-lived species, and we conclude that nearest neighbor species combinations in these plots do not arise from shared canopy closure preferences.

The paradigm of Janzen (1970) and Connell (1971) proposes that interactions with specialized natural enemies (herbivores and pathogens) should bring about negative density-dependent recruitment or mortality patterns within a tree population, causing individual trees in a single species to occur farther from one another than would be predicted by chance. An explicit prediction of Janzen-Connell spacing is that conspecific trees should occur less frequently as nearest neighbors than would be expected by chance. This paradigm is not supported by the distribution of trees in this study. In our analyses of conspecific combinations in the three plots, in no case did a conspecific combination depart from the expected frequency based on random mixing. This is entirely consistent with findings from our analyses of spatial dispersion patterns of tree populations in the La Selva plots (M. Lieberman and D. Lieberman 1994).

How important is interspecific competition in the ecology of tropical forest trees? The mathematical models put forward by Lotka (1925) and Volterra (1926) to explore the behavior of interacting species pairs and species swarms led to the proliferation of an array of allied concepts (May 1981a, b), foremost among which are the ideas of competitive exclusion, the exclusive niche, and the limiting similarity of species (Hutchinson 1959, 1978, MacArthur and Levins 1967, Pianka 1981). While many approaches have been brought to bear in the study of these themes, from mathematical modeling to laboratory experiments to field observations and manipulations, the studies comprising the voluminous literature that has emerged characteristically deal with very small numbers of species (2 or 3 in general), and are concerned almost entirely with animals, not plants.

Notwithstanding the enormous diversity of plant species in the tropics, all species of green plants make use of the same set of raw materials to support their metabolic functions and are remarkably similar to one another in terms of resource demands, energy sources, method of nutrient uptake, and even biochemistry; in terms of the general similarity of one species to another, plants are utterly unlike animal species (Harper 1984). Tree species within a given area of undisturbed tropical forest do not exploit markedly different resources, nor do they exploit resources in fundamentally different ways, a fact that challenges the applicability of the dogma of exclusive niche theory to tree species in high diversity assemblages.

The notion of the exclusive niche, which postulates that all co-occurring species must differ from one another in at least one of their niche characteristics, predicts that there should be a great many species pairs that occur less often than expected by chance. Only one species combination in one plot occurred less often than expected by chance, and this could logically result from interspecific competition, different habitat preferences, or both (Simberloff and Connor 1981). Thus, interspecific competition appears not to be a major determinant of tropical tree species distribution patterns.

We do not infer from these results that trees do not compete with one another for a particular position, but rather that the outcome of such competition is not predictable on the basis of species membership. Interspecific competition per se is unlikely to influence species distribution patterns in these forests. Competition between trees based on height, on the other hand, appears ubiquitous and may be of enormous importance in the ecology of tropical forests (M. Lieberman and D. Lieberman 1994). We suggest that tree height differences (perhaps in combination with other characteristics) supersede species membership as the framework for competitive interactions. This would account for the finding that the grand majority of species combinations occur at frequencies consistent with a random mixing model.

How important is interspecific competition in the evolution and adaptation of tropical forest trees? We have seen that a consequence of the high species richness in tropical forest assemblages is the low individual abundance of tree species, which in turn produces exceedingly low frequencies of any particular combination of species. The overwhelming majority of potential species combinations, and hence interactions, are never in fact realized in a given stand at a given point in time, and those combinations that do occur tend to be remarkably rare. As was framed hypothetically by Hubbell and Foster (1986), the evolutionary consequences of rare encounters between members of a given ij species pair, set against the backdrop of a multiplicity of encounters with other species, would probably be imperceptible.

The frequencies of nearest-neighbor species pairs in these plots are predictable in that they follow the simple laws of statistical probability. Underlying the predictability of the distribution of outcomes is the unpredictability of individual outcomes: given the species identity of a particular tree, the identity of its nearest neighbor is not predictable. Theories purporting to explain case-by-case tree species distribution patterns on the smallest scale, that of nearest neighbors within homogeneous sites, are thus unlikely to contribute to our understanding of these forests.

It has been stressed in this study that a consequence of high species diversity such as that of tropical forest vegetation is that interspecific interactions appear not to affect the local distribution of tree species, and that species-level competitive strategies are unlikely to emerge over evolutionary time. It would be instructive to carry out a parallel study in lower-diversity forests in the temperate zone.

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