Habitat associations of trees and shrubs in a 50-ha neotropical forest plot

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Summary

1 Tests of habitat association among species of tropical trees and shrubs often assume that individual stems can be treated as independent sample units, even though limited dispersal conflicts with this assumption by causing new recruits to occur near maternal parents and siblings.

2 We developed methods for assessing patterns of association between mapped plants and mapped habitat types that explicitly incorporate spatial structure, thereby eliminating the need to assume independence among stems.

3 We used these methods to determine habitat-association patterns for 171 species of trees and shrubs within the permanent 50-ha Forest Dynamics Project plot on Barro Colorado Island, Panama.

4 Many fewer significant habitat associations result from the new methods than from traditional, but inappropriate, chi-square tests. The low-lying plateau, the most extensive habitat on the 50-ha plot, had nine species positively associated with it and 19 species negatively associated, leaving 143 species whose distributions were not biased with respect to this habitat. A small swamp in the plot was the most distinct habitat, with 32 species positively and 20 species negatively associated, leaving more than two-thirds of the species neither positively nor negatively associated.

5 To the extent that habitat association reflects habitat specialization, our results suggest that local habitat specialization plays a limited role in the maintenance of species diversity in this forest.

Key-words: environmental heterogeneity, maintenance of species diversity, niche differentiation, spatial autocorrelation, specialization

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Introduction

Niche differentiation with respect to resources remains a prominent hypothesis to account for the maintenance of tree species diversity in tropical forests (Ashton 1969; Connell 1978; Leigh 1999). One manifestation of resource-based niche differentiation consists of habitat specialization, such that different species of trees are best suited to different habitats, where they are competitively dominant and relatively more abundant (Hubbell & Foster 1983; Tilman & Pacala 1993). To determine the relative contribution of habitat specialization to the maintenance of diversity in tropical forests requires rigorous quantification of the relationships between species' distributions and habitat variables, as well as the identification of the causes underlying those patterns (Hubbell & Foster 1986a; Burslem *et al.* 1995; D.B. Clark *et al.* 1999; Webb & Peart 2000).

The distribution of individuals within a population of plants is rarely random across a landscape, especially as the scale of focus increases from the local neighbourhood outwards (Greig-Smith 1979; Levin 1992). For example, the dispersion patterns of tropical trees and shrubs are generally more clumped, or aggregated, than random (Hubbell 1979; Condit *et al.* 2000; Plotkin *et al.* 2000). Furthermore, tropical trees and shrubs often display distributional biases with respect to environmental

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variables, across spatial scales of several ha to many km² (Hall & Swaine 1981; Gentry 1992). Nevertheless, a common assumption required by many of the statistical tests used in studies of habitat association is that trees are independently distributed with respect to conspecifics (Greig-Smith 1952; Condit 1996; Clark *et al*. 1998).

The independence assumption is often violated by the patterns produced by dispersal and recruitment. Most tree seeds fail to disperse far from the maternal parent (Janzen 1970; Connell 1971; Clark J.S. *et al.* 1999; Hubbell *et al*. 1999), giving rise to seedlings found near conspecifics (Hubbell *et al*. 1999; Connell & Green 2000; Harms *et al*. 2000). The aggregating influence of limited dispersal may create or contribute to spatially autocorrelated patterns of distribution (Condit 1996; Clark *et al*. 1998; Plotkin *et al*. 2000).

Hubbell & Foster (1983, 1986c) described the striking degree to which the distributions of several species matched particular topographic features of the 50-ha Forest Dynamics Project (FDP) plot of Barro Colorado Island (BCI), Panama. Although they acknowledged that trees are not distributed independently, they used chi-square goodness-of-fit tests, which rely on the assumption that each stem is an independent sample unit (Snedecor & Cochran 1980; Clark *et al*. 1998). Chi-square tests of independence (Clark *et al*. 1995, Clark *et al.* 1998), as well as the ordination methods employed by Lieberman *et al*. (1985), the canonical correspondence analysis of Oliveira-Filho *et al*. (1994) and the Komolgorov-Smirnov tests of Pacheco & Henderson (1996), similarly require independence among stems or among the contiguous quadrats within which trees were counted. However, if spatial structure exists within the tree populations, at the scale of the study, then neither individual trees nor contiguous quadrats can be treated as independent sample units and standard statistical tests are not appropriate (Legendre & Legendre 1998).

Multiple, non-contiguous plots were used by D. B. Clark *et al.* (1999), Pitman *et al*. (1999) and Svenning (1999) to examine habitat-association patterns among neotropical trees and palms, and by Webb & Peart (2000) to compare and contrast the habitat association patterns of seedlings and trees in a Bornean forest. When plots are widely spaced across a range of habitat types, spatial autocorrelation may be weak or absent among plots. However, before using tests that assume independence among sample units, the degree of spatial autocorrelation within the data should be shown to be consistent with the requirements of the tests (Cressie 1991).

Our objective in this study is to re-assess patterns of habitat association for species inhabiting the 50-ha FDP plot on BCI, knowing that spatial autocorrelation exists for both the plants and the habitats in question. We asked whether the distributions of species with respect to habitat variables were likely to have arisen by chance, given the spatially autocorrelated habitat map and the short-distance seed-dispersal and recruitment patterns of the trees and shrubs. In order to improve upon previous investigations of these patterns, a

procedure was required for generating appropriate null models of the distributions of stems with respect to habitats (Gotelli & Graves 1996). Spatial autocorrelation could not be ignored (Legendre 1993) and we developed procedures for testing patterns of association that incorporate critical properties of the spatial structure observed in both the plant and habitat data sets.

Methods

We examined the habitat-association patterns of trees and shrubs within the 50-ha Forest Dynamics Project (FDP) plot of Barro Colorado Island (BCI), Panama (Hubbell & Foster 1983, 1986a,b,c). Detailed descriptions of the climate, geology, flora and fauna of BCI can be found in Croat (1978), Leigh *et al*. (1982) and Gentry (1990).

The FDP plot was established in 1980, when a topographic survey was completed to provide elevations for each intersection of a 20-m grid throughout the plot. All stems of free-standing trees and shrubs ≥ 1-cm diameter at breast height (d.b.h.) have since been mapped, identified, tagged and measured on five separate occasions (Hubbell & Foster 1983, 1992; Condit 1998). The median time that a 1-cm d.b.h. sapling has spent growing to that size and becoming established in the plot is 16.6 years (Hubbell 1998). To determine overall patterns of habitat association of established individuals, we used all stems ≥ 1-cm d.b.h. in our analyses.

The site for the FDP plot was originally chosen for its relative uniformity of relief and other physical conditions; the elevational range of the plot is only 38 m (Condit *et al*. 2000). Nevertheless, variation in topography, edaphic conditions, species composition and forest age exists across the plot (Hubbell & Foster 1983, 1986c; Condit 1998) and we focused on small-scale topographic heterogeneity. All but 66 of the 1250 20 × 20-m quadrats of the FDP plot could be unambiguously assigned to one of six habitat categories (young forest, high plateau, low plateau, slope, streamside, and swamp; see below, Table 1 and Fig. 1). The 66 remaining quadrats were designated as mixed habitat and were excluded from tests of association.

The north-eastern edge of the FDP plot is bordered by secondary forest (*c*. 100 years old) which extends into just under 2 ha of the plot (Hubbell & Foster 1983, 1986c; Condit 1998). The remaining 48 ha have never been clearcut for agriculture (Piperno 1992). We chose to examine only patterns evident within the old growth forest, thereby eliminating forest age as a habitat variable.

BCI consists almost entirely of well-drained upland soils (Dietrich *et al*. 1982; Hubbell & Foster 1986c; Condit 1998), although a seasonally inundated swamp is present on the FDP plot. The 1.5-ha swamp, defined by the extent of standing water at the end of the wet season in 1992, was considered as a separate habitat type because swamps are often floristically distinct from the

Table 1 Areas of each habitat, total numbers of stems ≥ 1-cm d.b.h. in the 1990 census, and total stem densities by habitat for the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panama

Habitat	Slope (degrees)	Elevation (m)	Total area (ha)	Total number of stems [density (no. ha⁻¹)]
Old forest – Low plateau	< 7	< 152	24.80	126,417 (5097.46)
Old forest – High plateau	< 7	≥ 152	6.80	31,156 (4581.76)
Old forest – Slope	≥ 7	All	11.36	55,419 (4878.43)
Old forest – Swamp	All	All	1.20	3355 (2795.83)
Old forest – Streamside	All	All	1.28	5679 (4436.72)
Young forest	All	All	1.92	9629 (5015.10)
Mixed habitats	All	All	2.64	12,359 (4681.44)
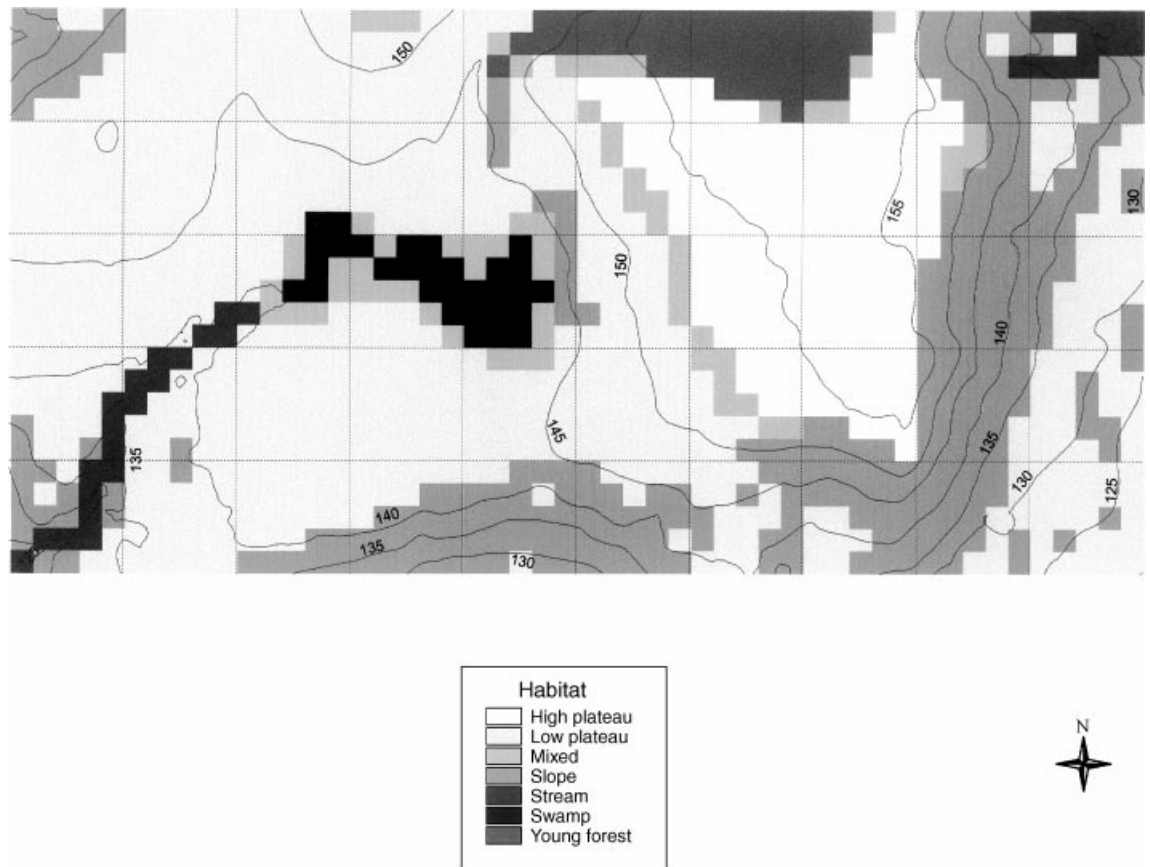
Fig. 1 The 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panama, divided into habitats assigned to 20 × 20-m quadrats.

surrounding vegetation, primarily due to physiological requirements to tolerate water-logged soils (Kwan & Whitmore 1970; Lieberman *et al*. 1985).

Streams, usually flanked by relatively steep ravines, are found in the north-east and the south-west corners of the plot, the latter draining the swamp. Although seasonal, the streams usually contain water well into each dry season (Hubbell & Foster 1986c; Condit 1998). Without direct moisture estimates in the 20 × 20-m quadrats that include streams, we make the *a priori* assumption that they are among the areas with the highest soil-water availability in the 50-ha plot (excluding the swamp). We identify these streamside quadrats as a distinct habitat type based on the common observation, at other sites, that some tree species are restricted to riparian habitats (Oliveira-Filho *et al*. 1994).

Due to the geology and hydrology of BCI, the sloping areas of the FDP plot provide more moisture later into the dry season than plateau sites (Hubbell & Foster 1986c; Condit 1998), as shown, for instance, in direct soil moisture estimates along two transects covering slope and plateau sites (Becker *et al*. 1988). A cap of andesite underlies the central plateau (Johnsson & Stallard 1989; Leigh 1996) and water drains via the slopes at its edges, which form the slopes of the 50-ha plot.

For each 20 × 20-m quadrat, elevation was calculated as the mean of values at its four corners and slope as the mean angular deviation from horizontal of each of the four triangular planes formed by connecting three of its corners. We chose a slope of 7° as the criterion for distinguishing slope from plateau quadrats, since this criterion included most of the southern and eastern

slopes that fall away from the main plateau of the FDP plot. Using a steeper angle as the criterion eliminated sections of those slopes, while shallower angles included many more quadrats away from those main slopes. We chose 152 m above mean sea level to separate high plateau from low plateau, since even small changes in elevation can result in changes in vegetation (e.g. Lieberman *et al.* 1985) and 152 m is the approximate mid-elevation of the principal sloping regions of the plot.

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We calculated chi-square goodness-of-fit statistics for patterns of habitat association to provide a comparison with our alternative methods. Each habitat provided a chi-square deviation of observed relative to expected numbers of stems for each species. To assess the goodness-of-fit for each species in each habitat, we used the conservative test that the single-habitat chi-square deviation be equal to or greater than the critical chi-square value for the full five-habitat test, i.e. $\chi^2_{df=4} = 9.488$.

To account for differences in total stem density among habitats, we calculated expected values on a density, rather than area, basis. The expected value for a given species-habitat combination was calculated as the total number of stems of the focal species summed over all five habitats, then multiplied by the proportion of stems of all species in the five habitats accounted for by the focal habitat.

A chi-square test using five habitats requires that each of the five expected values be > 1 (Snedecor & Cochran 1980 p. 77). An expected value < 1 was obtained for the least extensive habitat (the swamp) when a species had ≤ 65 stems. We therefore restricted our analyses to the 171 most abundant species in the five focal habitats on the FDP plot in 1990, all with > 65 stems ≥ 1-cm d.b.h.

Chi-square goodness-of-fit tests are two-tailed, since deviations of equal magnitude of observed values away from their corresponding expected values result in the same test statistics irrespective of the direction of the deviation. We used α = 0.05 to determine statistical significance throughout this study.

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Our alternative methods for testing patterns of habitat association involve developing a null hypothesis that allows us to determine how strongly associated with each habitat a species would be if associations were caused by coincidental similarity between the spatial structure of the species' population and the arrangement of habitats. We compared the observed relative densities of stems when they were superimposed on the true habitat map with expected, or null, distributions of expected relative densities generated using many simu-

lated habitat maps. Relative densities were calculated as the proportions of stems of all species belonging to each species in each habitat. Simulated habitat maps were generated by both an agglomerative randomization algorithm (hereafter referred to as randomized habitats) and by moving the true habitat map about a two-dimensional, or flat, torus (hereafter referred to as torus translations). Critical properties of the spatial structure of both the habitats and plant populations were thus maintained, while altering the positions of habitats with respect to the trees (see Clifford *et al.* 1989 for a criticism of fully randomizing a single variable when assessing the association between two spatially autocorrelated variables). Our methods are complementary to those used by Plotkin *et al.* (2000), who developed Poisson-cluster modelling to redistribute trees with respect to habitats in their tests of habitat association.

The randomized-habitats procedure created a series of simulated habitat maps in which non-overlapping areas corresponded in extent to the five principal habitats of the true map. Each simulated map therefore included exactly 620 low plateau, 170 high plateau, 284 slope, 32 streamside and 30 swamp quadrats, as well as 114 unused quadrats (corresponding to the young forest and mixed habitats).

Each simulated habitat map was initiated by assigning the swamp quadrats. A single quadrat, chosen at random from the 1250 comprising the 50-ha plot, was designated as the 'seed' quadrat for the swamp habitat, a second quadrat was chosen from the seed's neighbours, and subsequent quadrats from the neighbours of any already allocated until the simulated swamp was complete (i.e. 30 quadrats in size). The streamside habitat was then initiated by chosing a quadrat at random from the remaining 1220 unassigned quadrats and completed by progressively adding a further 31 random quadrats from those bordering the growing habitat. We always started simulations with the least extensive habitat and proceeded to the most extensive; high plateau, slope and low plateau habitats were constructed in the same way as the swamp and stream habitats. The entire procedure was repeated 1000 times.

In most simulations, the habitats were in five separate but internally contiguous blocks of quadrats, i.e. all quadrats within each habitat could be traced to all other quadrats of the habitat through shared edges or corners of quadrats of only that habitat. However, one unused corner of the plot occasionally became isolated during creation of earlier habitats. If a subsequent habitat's seed quadrat was chosen in this corner and the habitat filled the available space before completion, a second seed quadrat was chosen at random from the remaining unassigned quadrats and the growing habitat was finished around that second seed, resulting in a divided habitat. Divided habitats were rare and we chose to allow them because slope, stream and low plateau habitats are divided in the true map (Fig. 1).

The torus-translation procedure consists of moving the true habitat map about a two-dimensional, or flat, torus by 20-m increments in the four cardinal directions (Harms 1997). Imagine a map of the habitats of the FDP plot lying beneath a map of the trees and being moved, i.e. translated, by 20-m increments. As strips of quadrats are moved beyond a border of the plot, they are placed inside the opposite border. Related toroidal randomizations and restricted permutations have been used to incorporate horizontal spatial structure into tests of spatial association, as between two spatial point processes, e.g. interspecific spatial associations (Bailey & Gatrell 1995; Palmer & van der Maarel 1995; Roxburgh & Chesson 1998), and the spatial co-occurrence of ecological boundaries (Fortin *et al.* 1996).

The FDP plot consists of a 50 (N-S) × 25 (E-W) grid of 20 × 20-m quadrats and 1250 unique torus translations of the habitat map are therefore possible (including the 0,0 translation). A further three maps can be generated from each translation: 180° rotation, mirror image and 180° rotation of the mirror image. Together, these procedures provide 4999 unique habitat maps, each differing from the true, untranslated habitat map (the original 0,0 translation).

For the tests of association, each simulated map was overlain by the true distribution of trees and the relative density of each species (see above) was calculated for each habitat. Evaluation of all randomly seeded maps ($n = 1000$) and all torus-translated maps ($n = 4999$) gave frequency distributions of relative-density estimates for each species in each of the five principal habitats, one set of distributions for the randomized-habitats tests and one set for the torus-translation tests, respectively.

If the relative density of a species determined from the true habitat map was more extreme than at least 97.5% of the simulated relative densities (i.e. $\alpha = 0.05$ level of significance for a two-tailed test), then it was considered to be statistically associated (either positively or negatively) with the habitat. In other words, a species was determined to be positively associated with a particular habitat if and only if: Proportion {simulated map relative density < observed map relative density} ≥ 0.975; a species was negatively associated if and only if: Proportion {simulated map relative density > observed map relative density} ≥ 0.975.

We illustrate our tests for significance with torus-translation results for tree species that have contrasting distribution patterns with respect to the slope of the 50-ha plot (Fig. 2; *Chamguava shippii* [Myrtaceae], negatively associated; *Chrysoclamys eclipes* [Guttiferae], positively associated; *Pouteria reticulata* [Sapotaceae], neutrally associated). Figure 3 shows the frequency distributions of expected values for relative stem densities and the corresponding observed values.

Results

We found many fewer significant habitat associations using our alternative methods than we did using chi-square tests. Chi-square tests resulted in 317 significant positive and negative associations out of a potential 855 species-habitat combinations, compared with 124 from randomized-habitat tests and 171 from torus-translation tests (Table 2). In addition, there were more species (128 out of 171; 75%) significantly positively or negatively associated with at least one habitat type using the chi-square tests than there were using the randomized-habitats tests (87 out of 171; 51%) or the torus-translation tests (110 out of 171; 64%) (Appendix 1). Nevertheless, most significant associations according to the randomized-habitats tests (95% of positive associations and 77% of negative) and torus-translation tests (95% of positive and 77% of negative) were also significant using chi-square tests (Appendix 1).

Table 2 Chi-square, randomized-habitats and torus-translation tests for habitat associations on the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panama. The first column for each test contains results for 171 species for which there were > 65 stems in the five focal habitats in the 1990 census. The second column for each test contains results for the 50 most common species, all of which had ≥ 855 stems in the five focal habitats in the 1990 census. For each habitat, '+' indicates significant positive association and '−' indicates significant negative association ($\alpha = 0.05$ for all three tests)

| Habitat association	Chi-square		Randomized habitats		Torus translation	
	171 species	50 species	171 species	50 species	171 species	50 species
High plateau +	22	13	6	4	4	3
Low plateau +	26	15	3	1	9	7
Slope +	43	18	26	7	33	11
Swamp +	39	9	32	0	32	5
Streamside +	31	11	9	5	19	4
Total +	161	66	76	17	97	30
High plateau −	55	25	15	7	14	5
Low plateau −	36	15	10	0	19	5
Slope −	31	18	8	3	18	7
Swamp −	22	19	15	0	20	15
Streamside −	12	11	0	11	3	2
Total −	156	88	48	21	74	34
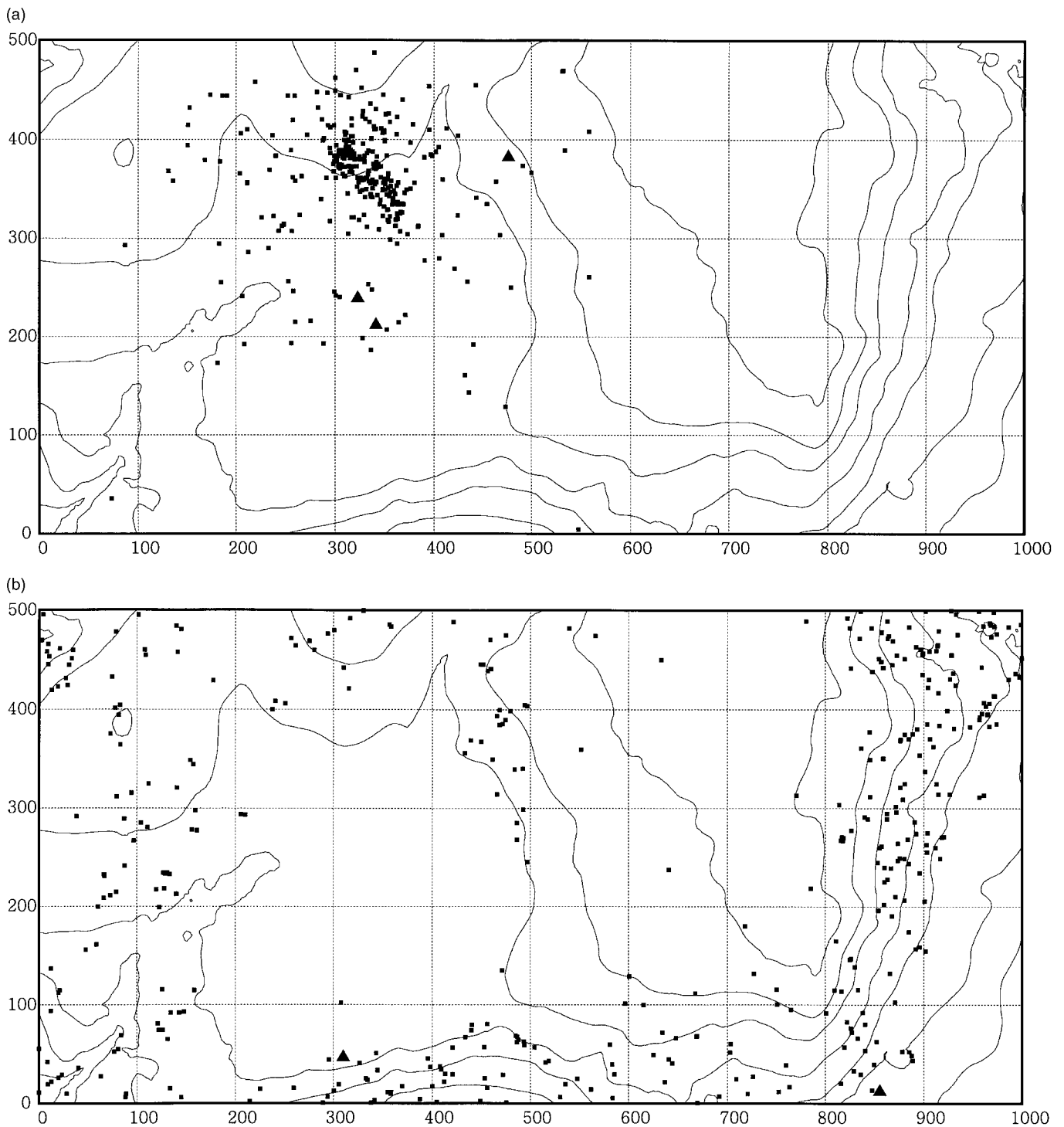
Fig. 2 Stem distributions on the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panama, for: (a) *Chamguava shippii* [Myrtaceae], (b) *Chrysoclamys eclipes* [Guttiferae], and (c) *Pouteria reticulata* [Sapotaceae].

Discrepancies between the chi-square tallies and those for the other two methods were increased by excluding species that were significantly positively or negatively associated only with the swamp. We found fewer such species using chi-square tests (16 compared with 27 from randomized-habitats tests and 25 from torus-translation tests), so the proportion of species significantly associated with at least one other habitat was more reduced for randomized-habitats tests (to 42% of species) and torus-translation tests (to 58%) than for chi-square tests (to 72%).

The discrepancies between chi-square results and the other tests were more pronounced for some of the habitats (Table 2). In particular, the majority of plateau associations indicated by the chi-square tests vanished under the alternative tests, so that the fraction observed was not much different from the 5% expected by chance alone. In contrast, for slope and swamp, and to a lesser
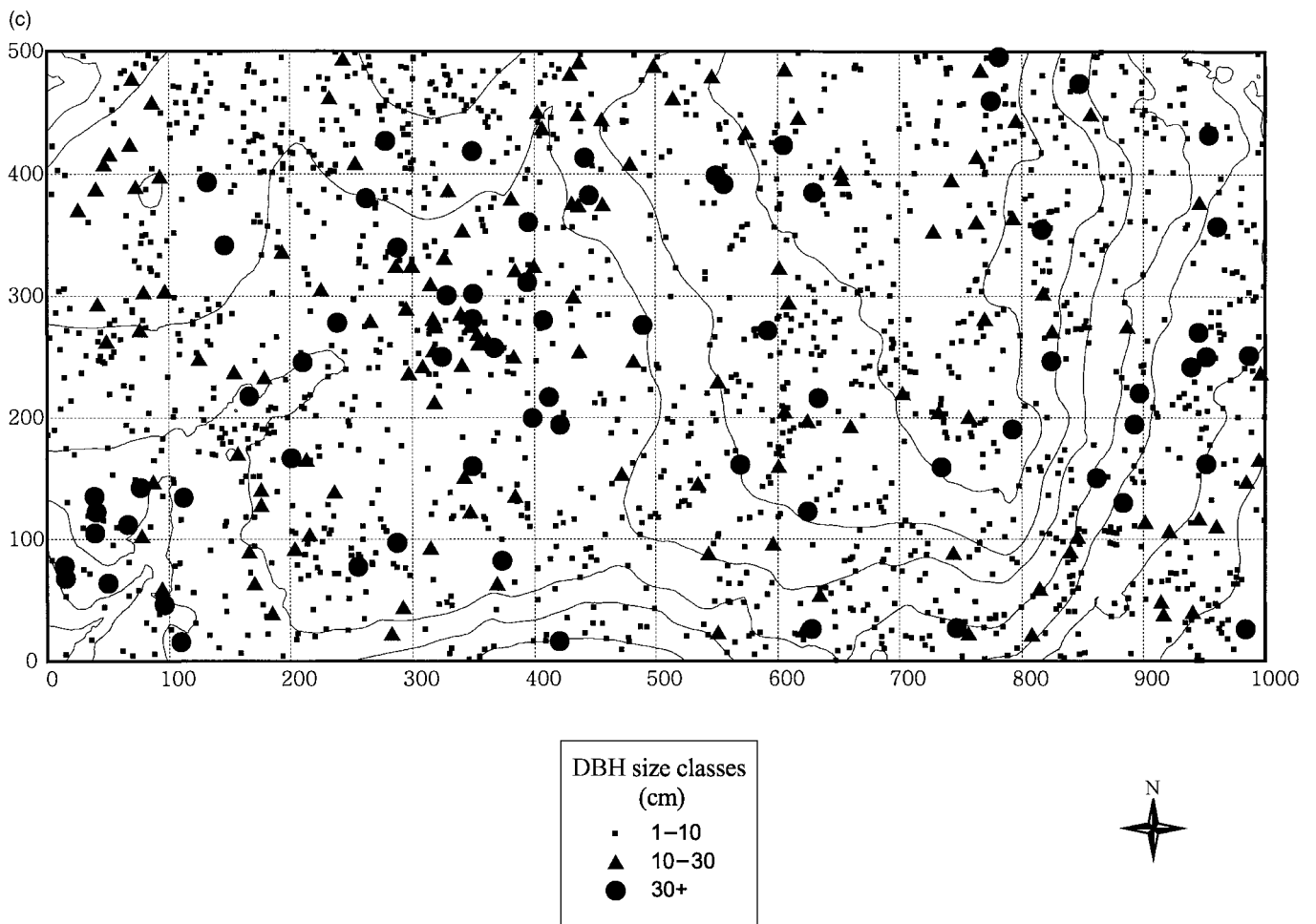
(c)

DBH size classes
(cm)

- 1–10
▲ 10–30
● 30+

Fig. 2 *Continued*

extent for the streamsides, although many associations were lost, a majority of associations indicated by chi-square persisted under the more conservative tests.

The 50 most abundant species within the old growth forest on the BCI 50-ha plot accounted for 83.8% of all stems in the 1990 census. Although many of these species show at least one positive or negative habitat association, a substantial proportion of the abundant species are neutrally associated with each habitat (Table 2).

Our tests of habitat association are designed to identify habitats in which species are disproportionately over- or under-represented relative to all other species. In theory, a very abundant species could be statistically associated with a habitat with only a slight difference in density among habitats. To determine the strength of associations, we therefore examined density differences among habitats by calculating the ratio of each species' density in a habitat relative to its density in the low plateau, the most extensive habitat on the FDP plot. Condit *et al*. (1996) chose ratios of > 1.5 to define slope- and swamp-'specialists' (meaning a 50% higher density on the slope or swamp, respectively, than on the low plateau), and these criteria appear to conform well

with our results for patterns of habitat association. In both the slope and swamp habitats, almost all species with density ratios > 1.5 were significantly positively associated with the slope or swamp, respectively. Species with ratios < 1.5 were never positively associated with either the slope or swamp (Fig. 4).

Significant negative association with the slope occurred when the density ratio for the slope was < 0.77, but never when the ratio was > 0.77 (Fig. 4). Significant negative association with the swamp only occurred when the ratio of density in the swamp was < 0.25 of the density on the low plateau (Fig. 4). Thus, only fairly strong associations resulted in statistical significance using the torus-translation method.

Upon comparing habitats in a pair-wise manner, there were surprisingly few species with significant associations, either positive or negative, in more than one habitat (Table 3; only torus-translation tests are shown, but randomized-habitats results were similar). Although we might anticipate species to be distributed similarly with respect to the wetter, albeit well-drained habitats, only seven species were significantly positively associated
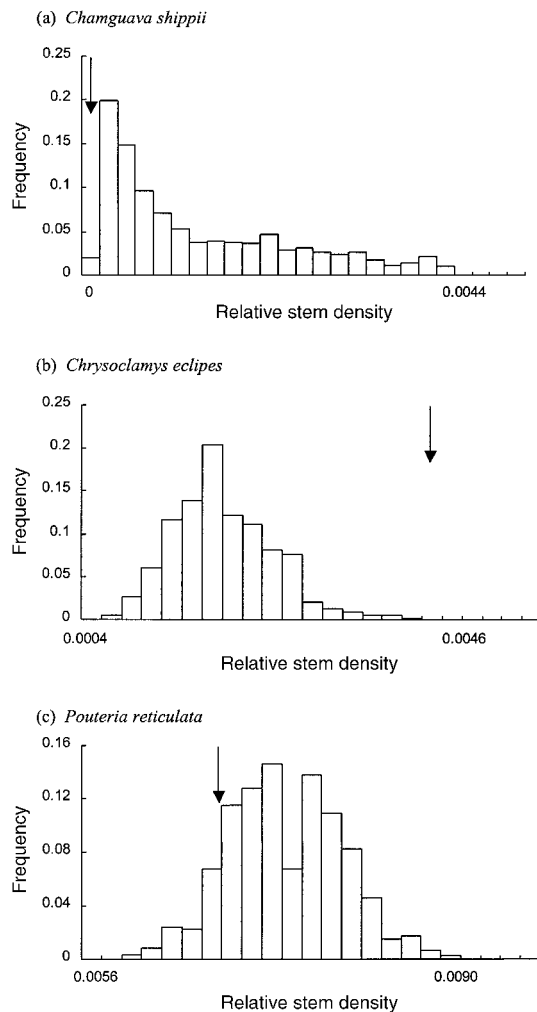
Fig. 3 Results of the torus-translation test for slope association applied to: (a) *Chamguava shippii* [Myrtaceae], (b) *Chrysoclamys eclipes* [Guttiferae], and (c) *Pouteria reticulata* [Sapotaceae]. The frequency histogram represents the distribution of expected relative stem densities obtained from the torus-translated habitat maps, while the arrow indicates the observed relative stem density on the true habitat map.

with both the slope and streamsides. No other pair of habitats shared more than two species that were significantly and congruently associated (Table 3).

With five principal habitat types and three possible association patterns with respect to each habitat (positive, negative or neutral) there are $3^5 = 243$ different possible ways for species to be distributed with respect to the five focal habitats. Therefore, if differences in overall patterns of association were maximized, each of the 171 species could show a different set of habitat associations. Chi-square tests, however, produced only 64 of the possible sets, and the randomized-habitats method and torus-translation methods produced even fewer (25 and 36 sets, respectively; Appendix 1). Using torus-translation tests, 64 species exhibited the most common set of associations (neutral associations with all five habitats). Twenty-five species were associated only with the swamp (15 positively and 10 negatively), while 13 species were associated (positively) only with

the slope; the remaining 32 overall patterns of association each characterized six or fewer species.

Discussion

A primary assumption of many traditional tests of habitat association is that the sample units can be treated as independent (Snedecor & Cochran 1980; Legendre 1993; Clark *et al.* 1998). However, this assumption is often in direct conflict with the recruitment processes of plants (Condit 1996; Hubbell *et al.* 1999; Connell & Green 2000; Harms *et al.* 2000). *Anaxagorea panamensis*, a shrub with balistically dispersed seeds, provides an extreme example. All 588 of its stems on the FDP plot were found in the most north-western hectare (see map in Condit 1998 p. 187) and limited seed dispersal has probably played a dominant role in creating this pattern. Since most of the stems of *A. panamensis* are found within slope habitat, a chi-square test results in a strongly significant association with the slope, even though this species is absent from the extensive slopes along the eastern and southern portions of the FDP plot. In contrast, *A. panamensis* is not significantly associated with the slope according to our alternative statistical methods. Our alternative methods are more conservative than chi-square tests, since species are unlikely to show significant associations unless habitat biases are consistent over large portions of the study area.

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In agreement with Hubbell & Foster (1983, 1986c), many species show no apparent distributional biases with respect to habitat boundaries. Nevertheless, several species are strongly positively or negatively associated with specific habitats.

A group of species is strongly associated with the slopes, including *Beilschmiedia pendula* (see map in Hubbell & Foster 1986a p. 328), *Chrysochlamys eclipes* (Fig. 2), *Poulsenia armata* (see map in Hubbell & Foster 1983 p. 30), *Unonopsis pittieri* (see map in Hubbell & Foster 1986c p. 213) and *Virola surinamensis*. Unlike most species in this forest, the autecology of *V. surinamensis* has been studied extensively. Howe and colleagues (Howe 1986, 1990; Fisher *et al.* 1991) have shown that *V. surinamensis* is associated with slopes and streamsides on BCI, and that seedling survivorship is enhanced in these habitats. Increased water potentials during the dry season on the slope, relative to plateau sites, may impose an ecological filter that prevents *V. surinamensis* and other drought-sensitive species from occurring off the slope. The hypothesis that some species are associated with the slopes due to greater water availability in otherwise well-drained soils is supported by seven species being positively associated with both slope and streamside habitats, while only two species are positively associated with both slope and swamp (Table 3).
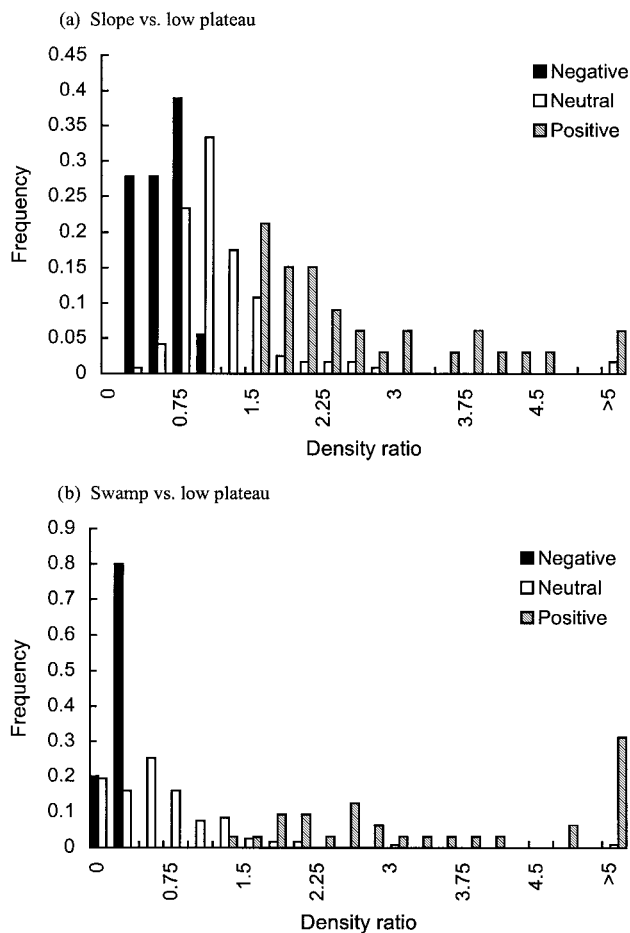
Fig. 4 Strength of associations for 171 species using density ratios: (a) slope vs. low plateau, and (b) swamp vs. low plateau. Each density ratio was calculated as the density in the first habitat over the density in the second. Species are divided into three categories according to the results of the torus-translation tests, i.e. species significantly positively, neutrally or negatively associated with the first habitat.

Table 3 Cross-tabulations of habitat associations according to the torus-translation method. Each subtable is a single pair-wise comparison for two habitats of the distribution of 171 species among three association categories ('+' = significant positive association; '–' = significant negative association; N = neutral association): HiP = High plateau; LoP = Low plateau; Slp = Slope; Str = Stream; Swp = Swamp

	HiP +	HiP N	HiP –		Swp +	Swp N	Swp –
LoP +	0	8	1	HiP +	1	3	0
LoP N	3	128	12	HiP N	27	108	18
LoP –	1	17	1	HiP –	4	8	2

	Slp +	Slp N	Slp –		Str +	Str N	Str –
LoP +	0	4	5	HiP +	0	3	1
LoP N	26	104	13	HiP N	18	133	2
LoP –	7	12	0	HiP –	1	13	0

	Swp +	Swp N	Swp –		Swp +	Swp N	Swp –
LoP +	0	6	3	Slp +	2	26	5
LoP N	26	101	16	Slp N	25	81	14
LoP –	6	12	1	Slp –	5	12	1

	Str +	Str N	Str –		Str +	Str N	Str –
LoP +	0	9	0	Slp +	7	25	1
LoP N	15	125	3	Slp N	11	108	1
LoP –	4	15	0	Slp –	1	16	1

	Slp +	Slp N	Slp –		Str +	Str N	Str –
HiP +	0	3	1	Swp +	2	30	0
HiP N	27	110	16	Swp N	15	101	3
HiP –	6	7	1	Swp –	2	18	0

Several species appear to avoid the swamp, while species positively associated with the swamp include several species of figs (*Ficus* spp.) and palms, which are often important floristic components of Neotropical swamps (Henderson 1995). Species positively associated with the swamp may be extremely drought intolerant, light demanding (light levels may be higher in the swamp due to reduced stem densities compared with other habitats, Table 1), or capable of surviving prolonged periods in water-logged soils and standing water.

Some of the species that were excluded from our analyses may be locally rare due to specialized requirements for relatively uncommon habitat types, such as the swamp and streamsides. For example, *Eleais oleifera* [Arecaceae], the American oil palm, had too few stems on the FDP plot to test for associations, even though all 16 of its stems were found in the swamp (see map in Condit 1998 p. 195). However, when we examined the habitat associations of rarer species within the plot, we found no compelling differences between rarer and commoner species in the degree to which they were associated with habitats. Among the 56 species with ≥ 15 and ≤ 65 individuals, 32 (57%) showed at least one significant association according to the torus-translation method, similar to the 64% obtained for the 171 species with > 65 stems.

Habitat associations in this paper are based on all stems $\geq$ 1-cm d.b.h. Nevertheless, habitat associations may be size-class dependent (Webb & Peart 2000), either due to ontogenetic niche shifts (*sensu* Clark & Clark 1992) or due to processes unrelated to habitat variables, e.g. invasion history (Hubbell & Foster 1986a).

Our habitat map was created from a relatively coarse set of habitat variables (see Methods) and associations between trees and finer-scale environmental variables may become apparent once finer-scale data become available.

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There are several potential mechanisms that could cause, or contribute to, an observed match between the distribution of a sessile organism and a particular environmental variable (Pickett & Bazzaz 1978; Goldberg 1985; Wesser & Armbruster 1991; Thomson *et al.* 1996), including: (i) historical patterns of dispersal, colonization or previous physical conditions (Hubbell & Foster 1986a); (ii) anthropogenic causes (Clark *et al.* 1995); (iii) the influence of competitors or other biological enemies (Connell 1961; Paine 1966); and (iv) habitat specialization or habitat-related competitive superiority (Hubbell & Foster 1986a).

Limited, or habitat-biased, distribution patterns may be the ephemeral or transient result of a population's history of seed dispersal and immigration (Primack & Miao 1992; Losos 1995). Species, such as *A. panamensis*, that show significant patterns of association according to chi-square tests, but not according to more conservative tests, may be typical examples. A contrasting example may be provided by *Drypetes standleyi*, a species that is significantly positively associated with the slope habitat according to both the chi-square and torus-translation tests (Appendix 1). Nevertheless, this association may reflect a transient, coincidental match between the current distribution and the slope habitat. *D. standleyi* appears to be invading the plot from the east, the slopes are primarily found in the eastern third of the plot and the significant association with the slope may disappear if *D. standleyi* continues to spread across the FDP plot.

For a given species, different carrying capacities across a landscape, e.g. in different habitats, may result from inherent physiological differences, or norms of reaction, or may be imposed by competitors or pests. At least since Hutchinson (1957) it has been recognized that the fundamental niche of an organism cannot be inferred from measuring the realized niche as interactions with other species, e.g. competitors, predators or pathogens, can result in a limited range of conditions, habitats or locations in which a species is found (Connell 1961; Paine 1966). Realized patterns of habitat association could therefore be partially, or wholly, caused by interactions with other species.

The relative contributions of source-sink population dynamics (*sensu* Pulliam 1988) and mass effects (*sensu* Shmida & Wilson 1985) to habitat associations cannot be determined by analysing static patterns alone. For example, distributions that are widespread among habitats may result from either habitat generalization or from source-sink population dynamics in which recruitment subsidies from favourable habitats maintain sink subpopulations in less favourable habitats (Pulliam 1988). Nevertheless, in practice, sink locations may often be characterized by lower stem densities as a consequence of decreased demographic performance relative to source locations.

Since a given pattern of habitat associations could have been produced by a variety of alternative causes, experimental studies are generally required to determine the relative efficacy of potential mechanisms to produce the patterns evident in any static study of habitat association (Burslem *et al.* 1995; Clark *et al.* 1995; Clark *et al.* 1998; D. B. Clark *et al.* 1999).

If realized habitat associations can be used as estimates of the degree to which species are specialized to particular habitats, the torus-translation procedure clearly shows more 'slope-specialists' than 'plateau-specialists', despite the fact that slope sites represent a substantially smaller percentage of the FDP plot than do plateau sites.

If negative associations can be used to identify sink subpopulations within the FDP plot, then the list of species neutrally or positively associated with a particular habitat type would be the number capable of sustaining populations if the plot were composed of only that habitat type. Out of 171 species with > 65 stems on the

FDP plot in 1990, there were 161 species neutrally or positively associated with the low plateau according to the randomized-habitats tests and 152 species according to the torus-translation tests. The habitat with the largest number of negative associations, the swamp, was avoided by 15 species according to the randomized-habitats tests and 20 according to the torus-translation tests, leaving 156 and 151 species, respectively, neutrally or positively associated. This exercise demonstrates that, if we were to assume that static patterns of association reflect source and sink subpopulations, the vast majority of species might still be found in the FDP plot if it were composed of a single habitat type. This suggests that very little of the plot's diversity (> 300 species total) can be attributed to local habitat variation.

Our results contribute to the growing body of evidence suggesting that many species of tropical trees are differentially distributed with respect to habitat variables at both local and regional scales (Clark *et al.* 1995; Clark *et al.* 1998; D. B. Clark *et al.* 1999; Pitman *et al.* 1999; Svenning 1999; Webb & Peart 2000). Nevertheless, and in accord with recent studies in other tropical forests (Pitman *et al.* 1999; Webb & Peart 2000), our results do not support the hypothesis that habitat specialization is among the principal mechanisms of coexistence maintaining a large fraction of the alpha diversity within communities of tropical trees.

Acknowledgements

Supplementary material

The following material is available from http://www.blackwell-science.com/production/journals/suppmat/jec/jec641/jec641.sm.htm

Appendix 1 Tree and shrub habitat associations within the BCI 50-ha forest plot.

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