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Species–habitat associations in a Sri Lankan dipterocarp forest

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Abstract: Forest structure and species distribution patterns were examined among eight topographically defined habitats for the 205 species with stems $\geq$ 1 cm dbh inhabiting a 25-ha plot in the Sinharaja rain forest, Sri Lanka. The habitats were steep spurs, less-steep spurs, steep gullies and less-steep gullies, all at either lower or upper elevations. Mean stem density was significantly greater on the upper spurs than in the lower, less-steep gullies. Stem density was also higher on spurs than in gullies within each elevation category and in each upper-elevation habitat than in its corresponding lower-elevation habitat. Basal area varied less among habitats, but followed similar trends to stem density. Species richness and Fisher's alpha were lower in the upper-elevation habitats than in the lower-elevation habitats. These differences appeared to be related to the abundances of the dominant species. Of the 125 species subjected to torus-translation tests, 99 species (abundant and less abundant and those in different strata) showed at least one positive or negative association to one or more of the habitats. Species associations were relatively more frequent with the lower-elevation gullies. These and the previous findings on seedling ecophysiology, morphology and anatomy of some of the habitat specialists suggest that edaphic and hydrological variation related to topography, accompanied by canopy disturbances of varying intensity, type and extent along the catenal landscape, plays a major role in habitat partitioning in this forest.

Key Words: Environmental heterogeneity, habitat specialization, rain forest, Sinharaja Forest Dynamics Plot, species-habitat associations, Sri Lanka, torus translations

INTRODUCTION

Both niche partitioning and dispersal-assembly processes have been invoked to explain species co-existence and controls on plant distribution in species-rich tropical tree communities (Hubbell 2001, Potts *et al.* 2004, Whitfield 2002, Wright 2002). A role for niche partitioning is suggested by associations between plant distributions and environmental conditions at a variety of spatial scales in both the New and Old World Tropics (Baillie *et al.* 1987, Debski *et al.* 2002, Fine *et al.* 2005, Gartlan *et al.* 1986, Gimaret-Carpentier *et al.* 1998, 2003; Harms *et al.* 2001, Itoh *et al.* 2003, Phillips *et al.* 2003, Potts *et al.* 2002). The dispersal-assembly perspective proposes that communities are non-equilibrium assemblages of species brought together by accidents of dispersal, and that localized niche partitioning plays a limited role in species coexistence. The importance of seed-dispersal limitation for determining the distribution of species at small scales has been demonstrated in recent research in tropical forests (Dalling *et al.* 2002, Hubbell *et al.* 1999, Webb & Peart 2001). However, the relative importance of the two sets of mechanisms in controlling structure of tropical rain-forest communities that are rich in closely related species is poorly understood. This results in part because, in most cases, the potentially subtle differences in life-history characteristics among species with contrasting habitat associations have not been examined.

Central to understanding the distribution patterns of plant species is the identification of habitats at scales that are relevant to plant populations. The limitations of small plots in differentiating local habitats have led to

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the establishment of large plots (16–52 ha) in tropical forests where all individuals ≥ 1 cm diameter at breast height (dbh) have been mapped, measured and identified to species (Condit 1995, Condit *et al.* 1996, Harms *et al.* 2001, Losos & Leigh 2004, Manokaran *et al.* 1992, Sukumar *et al.* 1992, Valencia *et al.* 2004). Such data sets now provide opportunities to test species-habitat relationships as one step towards understanding the factors that determine species-distribution patterns.

The 25-ha Forest Dynamics Plot (FDP) at Sinharaja, south-west Sri Lanka, is among the most topographically heterogeneous FDPs co-ordinated within the network of the Center for Tropical Forest Science (CTFS), and has the highest elevational range (151 m) of the CTFS plots (comparative data for the various CTFS plots are available on the CTFS website: http://www.ctfs.si.edu). While supporting a very large number of stems per unit area relative to the other large plots, the Sinharaja FDP also has several series of closely related congeneric, sympatric species (Ashton *et al.* 2004, Gunatilleke *et al.* 2004). The majority of these are endemic to Sri Lanka. Understanding the presence or absence of habitat preferences, especially among these congeneric species could shed some light on the means by which they coexist.

Species-habitat associations have now been described for FDPs in a semi-deciduous forest on Barro Colorado Island in Panama (Harms *et al.* 2001), lowland evergreen forests at Yasuni in Ecuador (Valencia *et al.* 2004) and Lambir in Sarawak (Davies *et al.* 2005). At Sinharaja, unlike the other three sites, our interpretation of differences in species distribution was facilitated by a substantial body of experimental research that has investigated the mechanistic basis of species-habitat associations among closely-related and sympatric species within the important tree genera *Shorea*, *Mesua* and *Syzygium* (Ashton 1995, Ashton & Berlyn 1992, Ashton *et al.* 1995, 2001, 2006, Burslem *et al.* 2001, Gamage *et al.* 2003, Gunatilleke *et al.* 1997, Singhakumara *et al.* 2003). The combination of habitat associations plus species traits and performance characteristics provides a powerful opportunity to address the challenge of determining the extent to which differences in species responses to resource availability contribute to their co-existence in species-rich tropical forests (Hubbell 2001).

The Sinharaja FDP was divided into eight habitats based on elevation, convexity and slope to address the following questions: (1) Do stem density, basal area, species richness and representation by different growth forms vary among habitats? (2) What proportion of species is significantly associated with one or more of these habitats? (3) Are more species associated with some habitats than with others? (4) Are more-abundant species differentially associated with habitats compared with less-abundant species? (5) Do species of different growth forms, i.e. structural guilds, differentially associate with these habitats? (6) Are significant associations, especially differences among congeneric species, consistent with the available experimental evidence for their ecophysiological differences?

METHODS

Study area

The area studied is the Sinharaja Forest Dynamics Plot (FDP), a 500 × 500-m (25-ha) permanent study plot (Figure 1). The Sinharaja FDP is located in the lowland rain forest of the Sinharaja UNESCO World Heritage Site at the centre of the ever-wet south-western region of Sri Lanka (6° 21–26′N, 80° 21–34′E). The forest has been classified as a *Mesua–Doona* community (de Rosayro 1942), and on a regional scale it represents a mixed dipterocarp forest (Ashton 1964, Whitmore 1984).

Topographically, the Sinharaja FDP spans the elevational range of 424 m to 575 m asl. The Sinharaja FDP includes a valley lying between two slopes, a steeper higher slope facing south-west and a less-steep slope facing north-east (Figure 1). Seepage ways, spurs, small hillocks, at least two perennial streams and several seasonal streamlets cut across these slopes. The floristics and forest structure within the plot as a whole have been documented in Gunatilleke *et al.* (2004). The Sinharaja FDP is representative of the ‘ridge-steep slope-valley’ landscape of the lowland through mid-elevational rain forests of south-western Sri Lanka. This landform is a result of differential weathering and erosion of lithologically less-resistant Precambrian metamorphic bedrock along structurally controlled parallel strike ridges and valleys (Cooray 1984, Erb 1984).

Vegetation sampling

To establish the Sinharaja FDP, we followed the methodology established by Hubbell & Foster (1983) and Manokaran *et al.* (1992), to maintain census uniformity with similar plots within the CTFS network. The Sinharaja FDP was established in 1993, when it was demarcated on the horizontal plane into 625 quadrats of 20 × 20 m (400 m^2) each. The trees in the plot were censused over the period 1994–1996, when the diameters of all free-standing stems ≥ 1 cm dbh were measured. Each stem was mapped and identified to species, using the National Herbarium of Sri Lanka, and Dassanayake & Fosberg (1980–2000).

Topographic parameters and habitat categorization

Habitats of the Sinharaja FDP were identified by three physical parameters, viz. elevation, slope and convexity, in each of the 20 × 20-m quadrats. The mean of the

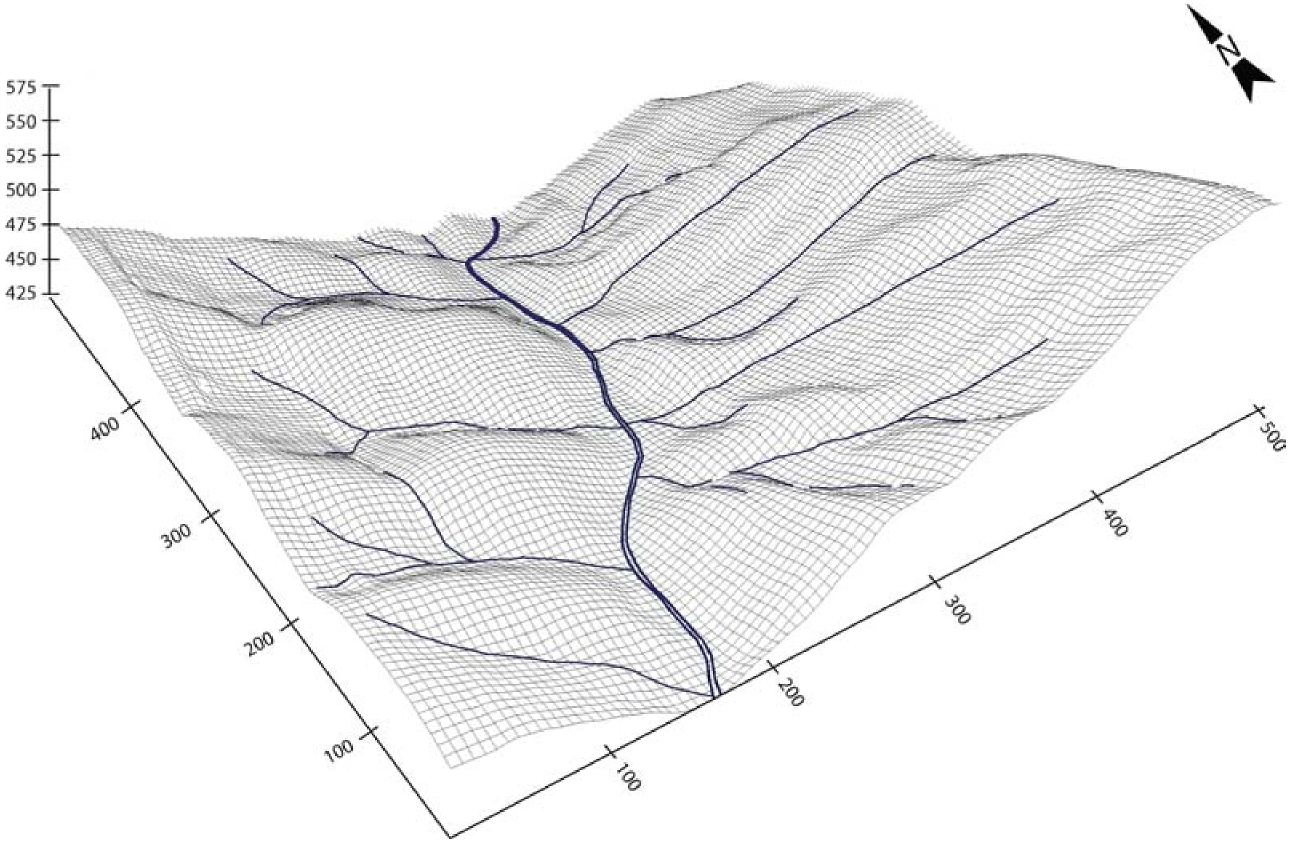

Figure 1. Topography of the 25-ha forest dynamics plot (all scales in metres) in Sinharaja, Sri Lanka.

elevations at the four corners of each quadrat gave the quadrat's elevation. Each quadrat was divided into four triangular planes, each formed by joining three corners of the quadrat. The average angular deviation of these planes from horizontal provided the slope (Harms *et al.* 2001). Convexity was calculated as in Yamakura *et al.* (1995), i.e. as a quadrat's mean elevation relative to the mean elevations of its eight immediate neighbouring quadrats (the focal quadrat mean elevation minus the mean elevation of the neighbouring quadrats). For each of the perimeter quadrats of the plot, for which the number of neighbouring quadrats was < 8, convexity was calculated as the elevation of the centre point of the focal quadrat minus the mean elevation of its four corners. Positive values indicate convex surfaces, whereas negative values indicate concave surfaces.

Bivariate scatterplots for each pair of topographic variables confirmed that they were independent of each other, with r^2 values ranging between 0.0356 and 0.141. These three variables represent mutually orthogonal topographic properties, so we used all three to define eight topographic habitats. Each 20 × 20-m quadrat was assigned to one of two categories of elevation (upper vs. lower, divided by the median elevation value for the FDP), slope (steep vs. less-steep divided by the median slope value), and convexity (Table 1, Figure 2a).The abbreviations of the habitat categories used in the entire paper are explained in Table 1.

Table 1. The physical parameters used to define habitat categories of each 20 × 20-m quadrat of the Sinharaja Forest Dynamics Plot.

Habitat category	Elevation (m)	Slope (°)	Convexity	Number (and %) of quadrats	Total area on plot (ha)
Upper-elevation steep spurs (USS)	> 460	> 25	> 0	104 (17)	4.2
Upper-elevation steep gullies (USG)	> 460	> 25	≤ 0	68 (11)	2.7
Upper-elevation less-steep spurs (ULS)	> 460	≤ 25	> 0	108 (17)	4.3
Upper-elevation less-steep gullies (ULG)	> 460	≤ 25	≤ 0	32 (05)	1.3
Low-elevation steep spurs (LSS)	< 460	> 25	> 0	52 (08)	2.1
Low-elevation steep gullies (LSG)	< 460	> 25	≤ 0	59 (09)	2.4
Low-elevation less-steep spurs (LLS)	< 460	≤ 25	> 0	48 (08)	1.9
Low-elevation less-steep gullies (LLG)	< 460	≤ 25	≤ 0	155 (25)	6.2

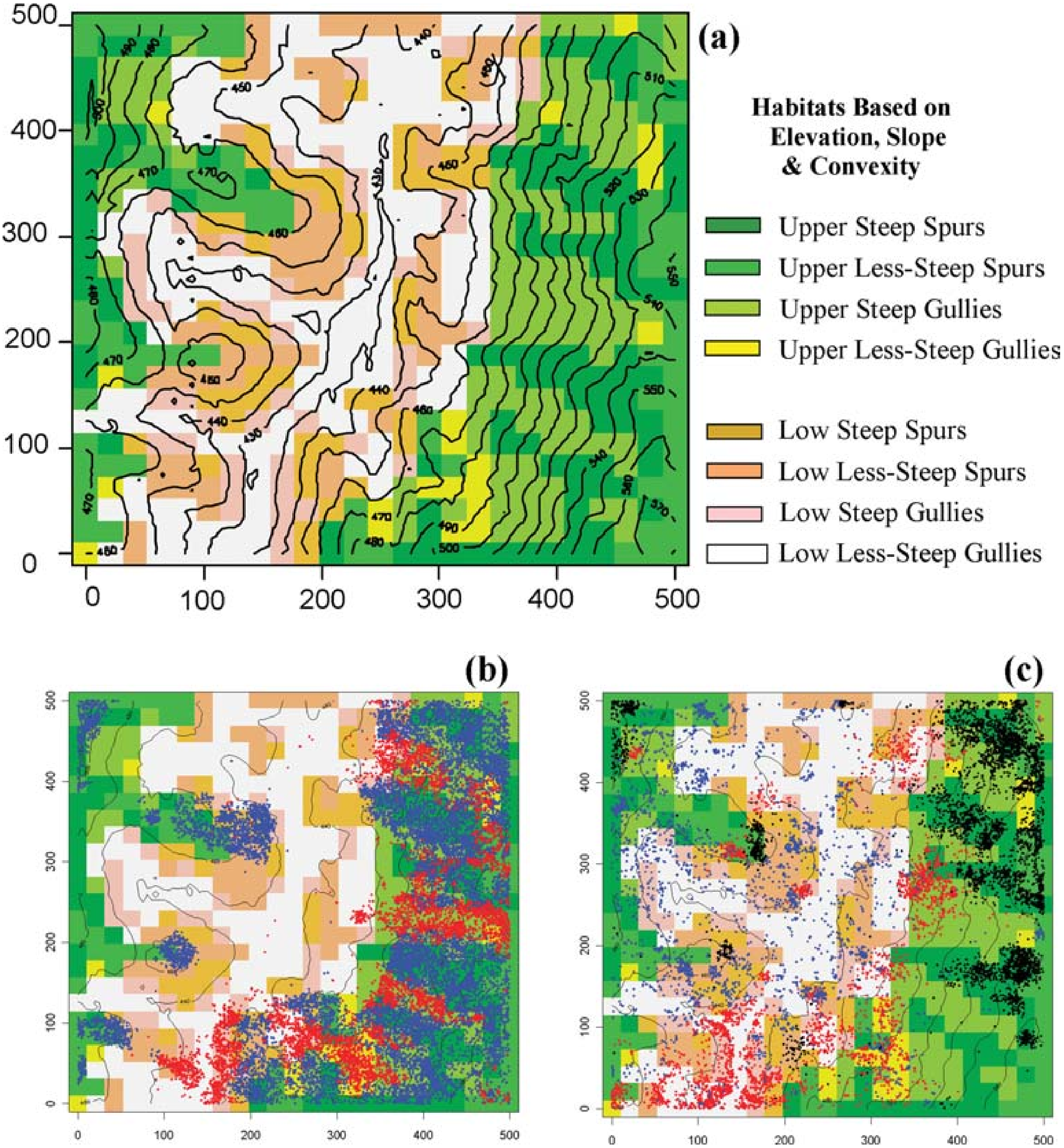

Figure 2. Habitats and selected species distribution patterns within the 25-ha forest dynamics plot in Sinharaja, Sri Lanka. (a) Habitats based on elevation, slope and convexity, each at two levels. Distribution patterns of (b) *Mesua nagassarium* (blue) found predominantly on upper-elevation steep spurs and *Mesua ferrea* (red) found predominantly on upper steep and less-steep gullies. Distribution patterns of (c) *Shorea worthingtonii* (black) found predominantly on upper steep spurs, *Shorea trapezifolia* (blue) found predominantly on the low-elevation less-steep spurs, and *Shorea megistophylla* (red) found predominantly on the low-elevation less-steep gullies.

Structural and floristic characteristics among habitats

To assess the structural characteristics of the vegetation in the different habitats, the means of density and basal area per quadrat in each habitat were compared. Similarly, species richness and Fisher's alpha diversity per quadrat were calculated and compared among habitats. Significant differences in species richness and Fisher's alpha diversity among habitats were determined using torus-translation tests, described below.

Table 2. Mean and standard error for structural (density and basal area) and floristic (species richness and Fisher's alpha diversity) characteristics per quadrat among habitats in the Sinharaja 25-ha Forest Dynamics Plot. Total number of free-standing species identified in the plot was 205. Significance among the respective values column-wise was tested using two-tailed torus-translation tests, $P < 0.025$ for either tail. An asterisk (*) indicates a significant departure from the null expectation. Abbreviations of habitat categories are explained in Table 1.

Habitat categories	Area (ha)	Mean no. of individuals	Mean basal area (m^2)	Mean no. of species	Mean Fisher's alpha
Upper-elevation habitats					
USS	4.2	409 ± 11*	2.36 ± 0.08	46.7 ± 0.8	14.6 ± 0.4*
ULS	2.7	402 ± 13*	2.26 ± 0.10	47.9 ± 1.2	15.1 ± 0.6
USG	4.3	322 ± 10	1.90 ± 0.07	47.0 ± 0.7	15.5 ± 0.4
ULG	1.3	357 ± 18	1.81 ± 0.11	51.7 ± 1.9	17.2 ± 0.8
Low-elevation habitats					
LSS	2.1	368 ± 14	2.05 ± 0.09	56.9 ± 1.7	20.4 ± 0.9
LLS	2.4	352 ± 18	1.88 ± 0.09	54.0 ± 1.5	19.7 ± 0.8
LSG	1.9	322 ± 17	1.51 ± 0.07	53.4 ± 1.3	19.4 ± 0.8
LLG	6.2	220 ± 6*	1.22 ± 0.04	49.6 ± 0.8	21.1 ± 0.4*

Significant associations of species with habitats

Positive and negative associations of species with habitats were determined by torus-translation tests (Harms *et al.* 2001). The tests assess the similarity between the spatial structure of each focal species population and each habitat. For each species, the observed relative densities of stems in each of the habitats were compared with expected relative densities. To obtain the expected values, the true habitat map was shifted about a two-dimensional torus by 20-m increments to exhaustively produce all possible 20-m translations of the true habitat map in the four cardinal directions. Each of the 625 maps provided an estimate of the expected relative density.

A species was significantly positively associated with a particular habitat if its relative density in the true habitat map was > 97.5% of the values obtained from translated maps. A significant negative association occurred if the relative density in the true map was < 97.5% of the values from translated maps. In the Sinharaja FDP, 205 tree species with stems ≥ 1 cm dbh and 10 species of liana have been identified. For the torus-translation tests, we used the 125 tree species with a density ≥ 100 individuals in the 25-ha plot.

We also used torus-translations to test whether species richness, Fisher's alpha diversity, stem density and basal area differed among habitats. In each case, the observed value for a given habitat was compared with a frequency distribution of expected values generated by an exhaustive set of 20-m incremental torus-translations (analogous to the procedure used to assess species associations).

RESULTS

Spatial distribution of habitats

The most extensive habitat was the LLG (6.2 ha), whereas the least extensive and most fragmented was the ULG (1.3 ha; Table 1, Figure 2a). The remaining habitats ranged from 1.9 to 4.3 ha in extent. USS and ULS were greater in extent (4.2–4.3 ha) than the USG and ULG (1.3–2.7 ha). The extent of the LLG was similar to that of the three remaining low-elevation habitats combined.

Structural and floristic differences among habitats

The LLG had the lowest density of individuals ≥ 1 cm dbh, whereas the USS and ULS had the highest densities (> 400 individuals per quadrat, Table 2); in these cases the densities depart significantly from expectations. The densities of the remaining habitats had values between these extremes. Spurs at both elevations, irrespective of whether they were steep or less steep, had significantly higher densities compared with gullies at the same elevation.

Mean basal area among habitats ranged from 1.22 m^2 in the LLG to 2.36 m^2 in the USS, although no mean value differed significantly from expectations (Table 2). The basal area of the tree community on spurs was higher than that in gullies at each of the two elevations, as with stem density. The value for each upper-elevation habitat was greater than that of the corresponding habitat at lower elevation.

Species richness per quadrat showed little variation among habitats and ranged from 46.7 in the USS to a high of 56.9 in the LSS (Table 2). Species diversity per quadrat (measured using Fisher's alpha) among the habitats ranged from 14.6 to 21.1 (Table 2). In the upper-elevation habitats, where the diversity was at the lower end of the range, spurs showed lower values than gullies. The diversity values of the low-elevation habitats were more or less similar, but among them the LLG had the highest diversity. Diversity was significantly higher in LLG than in USS. The differences among all other values were not statistically significant.

Species–habitat associations using torus-translation tests

Based on torus-translation tests, a total of 175 significant associations (94 positive and 81 negative) were observed

Table 3. Numbers of positive and negative associations observed among the different habitats defined by topographic parameters in the Sinharaja Forest Dynamics Plot, based on two-tailed torus-translation tests, $P < 0.025$ for either tail. Abbreviations of habitat categories are explained in Table 1.

Habitat category	Total no. of significant associations	No. of positive associations in each habitat	No. of negative associations in each habitat
Upper-elevation habitats			
USS	24	3	21
ULS	25	7	18
USG	12	5	7
ULG	5	3	2
Totals in upper-elevation habitats	66	18	48
Low-elevation habitats			
LSS	6	5	1
LLS	13	11	2
LSG	24	13	11
LLG	66	47	19
Totals in low-elevation habitats	109	76	33
Total nos. and (%) of significant associations in all categories	175	94 (54%)	81 (46%)

(Table 3). LLG produced the highest number of significant associations. There were 66 significant associations among the four upper-elevation habitats, of which 18 were positive and 48 were negative. The corresponding values in the four low-elevation habitats totalled 109, with 76 positive and 33 negative (Table 3). In the upper-elevation habitats, spurs had more significant associations (mostly negative) than gullies, but in the lower-elevation habitats the pattern was reversed and the gullies had more associations (mostly positive) than spurs.

Species associated with habitats

Of the 125 species with densities ≥ 100 individuals on the plot, 99 species (79%) were positively or negatively associated with one or more of the different habitats, i.e. they were disproportionately over- or under-represented in some habitats (Appendix 1). The remaining 26 species were not significantly associated with any of the eight habitats and were distributed as expected by chance with respect to these habitats. The five most abundant among these species were *Myristica dactyloides*, *Diospyros acuminata*, *Mangifera zeylanica*, *Shorea stipularis* and *Chaetocarpus coriaceus* with 2694, 1569, 1231, 984 and 861 individuals on the 25-ha plot, respectively. The remaining 19 species each had abundances ranging from 106 to 706 individuals in the plot.

Among the 99 species significantly associated with habitats, 16 were positively associated with one or more of the upper-elevation habitats and 12 of these 16 were also negatively associated with either one or both lower-elevation gullies (Appendix 1). The number of species that was positively associated with the lower-elevation habitats was 65; 28 of them were also negatively associated with one or two of the upper-elevation habitats (Appendix 1). Species that were positively associated with one habitat type and negatively associated with a contrasting habitat are exemplified by the USS-associated species *Mesua nagassarium*, *Shorea worthingtonii*, *Agrostistachys intramarginalis* and the ULS-associated species *Humboldtia laurifolia* and *Memecylon arnottianum*. Examples of species significantly positively associated with a lower-elevation habitat and significantly negatively associated with the upper-elevation steep slope habitat include *Bhesa ceylanica*, *Palaquium canaliculatum* and *Urophyllum ellipticum*. Among the 18 species that showed only negative associations, 11 including *Shorea disticha*, *Shorea affinis* and *Shorea congestiflora* were biased against the lower-elevation habitats and seven, including *Anisophyllea cinnamomoides* and *Cullenia ceylanica*, were biased against the upper-elevation habitats (Appendix 1).

Distribution patterns of abundant and less-abundant species

Species with > 800 individuals representing the quartile of most abundant species within the Sinharaja FDP were considered abundant; less-abundant species had 100–800 individuals (Table 4; Appendix 1). The percentage of species positively and negatively associated with habitats hardly differed between abundant and less-abundant species (Table 4). Among the 33 positively associated abundant species, 10 (including *Mesua nagassarium*, *Palaquium petiolare*, *Hydnocarpus octandra*) were positively associated with one or two of the upper-elevation habitats, while the other 23 (including *Palaquium canaliculatum* and *Urophyllum ellipticum*) were positively associated with one or two of the lower-elevation habitats (Table 4, Appendix 1). Among the 48 positively associated less-abundant species, the corresponding values were 6 and

Table 4. Proportions of positively and negatively associated abundant (> 800 individuals) and less abundant (100–800 individuals) species among habitats, defined by topographic parameters in the Sinharaja Forest Dynamics Plot, based on two-tailed torus-translation tests, $P < 0.025$ for either tail. The number of significantly associated species in each abundance class is indicated within parentheses and these were used to calculate the percentages shown in the last row (for details refer to Appendix 1). Abbreviations of habitat categories are explained in Table 1.

	No. of species positively associated with each habitat		No. of species negatively associated with each habitat	
Habitat category	Abundant spp. (41)	Less-abundant spp. (58)	Abundant spp. (41)	Less-abundant spp. (58)
Upper-elevation habitats				
USS	3	0	6	15
ULS	2	5	6	12
USG	4	1	0	7
ULG	3	0	0	2
Subtotals	10	6	10	26
Low-elevation habitats				
LSS	3	2	0	1
LLS	4	7	1	1
LSG	5	8	5	6
LLG	18	29	13	6
Subtotals	23	42	13	10
Total no. and (%) of significantly associated species in each category	33 (80%)	48 (83%)	23 (56%)	36 (62%)

42, respectively. Some species in these habitats were also negatively associated with one of the remaining habitats, indicating that they were significantly underrepresented in them. A total of 18 species, eight abundant and 10 less-abundant, were only negatively associated with certain habitats; they failed to show any positive associations. Among these negatively associated species, seven were biased against upper-elevation habitats and eleven were biased against lower-elevation habitats (Appendix 1).

Twenty-four species out of the total of 99 were positively associated with spurs (Appendix 1). Among them, 10 species (five abundant and five less-abundant species) were positively associated with upper-elevation spurs and 14 were positively associated with lower-elevation spurs (five abundant and nine less-abundant species). Only five abundant and one less-abundant species were positively associated with the upper-elevation gullies. In contrast, 19 abundant and 33 less-abundant species were positively associated with the lower-elevation gullies (Appendix 1).

Habitat associations of species in different life-forms

The 125 species tested represented 19 canopy, 34 subcanopy, 30 understorey tree and 42 treelet and shrub species (Table 5; Appendix 1). Among the canopy, subcanopy and treelet and shrub species tested, 84–86% were significantly associated with the different habitats in the 25-ha plot; among the understorey tree species, 60% were significantly associated. The proportions of significant species with respect to both the abundant and less-abundant species in these growth forms also followed a similar trend.

Table 5. Proportions of significantly associated species in each growth form among the abundant (> 800 individuals) and less abundant (100–800 individuals) species, based on two-tailed torus-translation tests, $P < 0.025$ for either tail.

Abundance/growth categories	No. tested	Number significant	% significant in each growth form
Abundant species			
Canopy species	13	11	85
Subcanopy species	14	12	86
Understorey tree species	8	5	63
Shrub/treelet species	13	13	100
All growth forms	48	41	85
Less-abundant species			
Canopy species	6	5	83
Subcanopy species	20	17	85
Understorey tree species	22	13	59
Shrub/treelet species	29	23	79
All growth forms	77	58	75
All species			
Canopy species	19	16	84
Subcanopy species	34	29	85
Understorey tree species	30	18	60
Shrub/treelet species	42	36	86
All growth forms	125	99	79

DISCUSSION

Forest structure and habitat associations at Sinharaja

The structural and floristic characteristics of the Sinharaja FDP appear to reflect the different micro-environmental conditions prevailing within its elevational range of

151 m. For the three most abundant species (a canopy tree, *Mesua nagassarium*, a treelet, *Agrostistachys intramarginalis*, and an understorey tree, *Humboldtia laurifolia*) in the upper-elevation spurs, their exceptionally high densities (14 880, 18 022 and 22 459 individuals in 25 ha) indicate their differential success in that habitat. Soils are shallower there and more prone to desiccation. These sites may experience lower availability of irradiance at ground level, moisture and nutrients (Ashton 1995, Ashton & Berlyn 1992, Ashton *et al.* 1995, Burslem *et al.* 2001). Data from aerial photographic interpretations (unpublished) revealed that canopy crown densities increase and canopy crown size and canopy porosity decrease from valley to ridge, presumably driven by the hydrology of the site. These observations also suggest that the forest canopy is more compact and uniform on the ridges than in the valley. An experimental study with seedlings of *Mesua nagassarium* that were grown in artificial shelters for 2 y demonstrated their ability to endure deep shade and low soil water availability (Ashton *et al.* 2006).

In the lower-elevation habitats, on the other hand, soils are wetter and light measurements have shown higher mean and variance of irradiance (Ashton & Berlyn 1992). In valleys, larger canopy gaps are found than on ridges because there is a stronger tendency for trees to die in groups (I. A. U. N. Gunatilleke *et al*. pers. obs.). Larger and more frequent openings in the moist valley sites, especially along streams of the lower elevations, support a greater cover of herbaceous species of *Strobilanthes*, *Coleus* and *Ochlandra* (not tallied in the 25-ha plot) sometimes at the expense of woody plants (similar to a pattern observed by Harms *et al*. 2004 for four Neotropical sites). In time, these gaps in different stages of closure provide greater light heterogeneity than those in upper slopes. These lower-elevation gaps support a larger suite of species, adapted to different light intensities, each with lower abundances. The three most abundant species in the lower-elevation habitats are all treelet/shrub species (*Psychotria nigra*, *Urophyllum ellipticum* and *Schumacheria castaneifolia*) each of whose population densities are much lower (6087, 4102 and 3550 individuals, respectively, in 25 ha) than those of the most abundant species in the upper-elevation habitats. Similar patterns of forest structure with lower mean tree density and basal area in valleys compared to mid-slope and upper-ridge sites have been observed in the topographically heterogeneous FDP at Yasuni, Ecuador (Valencia *et al*. 2004) and in Brunei (Ashton 1964).

In the south-western Sri Lankan landscape, forest trees on ridge tops and rocky upper slopes are susceptible to water shortage, particularly during El Niño years, and also to lightning strikes (Ashton *et al.* 2001). The gaps created by these events are often small as the trees die standing and create only small canopy disturbances. Consequently, these habitats also appear to have relatively lower rates of soil disturbance by tip-up mound formation during tree-fall. Furthermore, on these thin soils interspersed with rocky outcrops, the availability of nutrients for tree growth is also limited. These conditions may lead to habitat specialization and canopy dominance by shade-tolerant and slow-growing species that are adapted to regenerate preferentially in smaller gaps (e.g. *Shorea worthingtonii*) and to lower species richness. Mid-slopes on the other hand, are prone to small-scale earth slips and landslides, and the lower slopes with a higher water table have trees with shallow rooting systems. Both of these processes result in multiple tree falls. Wind-throws from sudden downdrafts are also channelled into valleys, and cause relatively greater disturbance both above- and below-ground (Ashton *et al.* 2001). Fast-growing species with a high shoot:root ratio (e.g. *Shorea megistophylla*) establish more successfully in these lower-elevation habitats than in upper slopes and ridge tops, and exhibit both habitat specialization and canopy dominance (Ashton *et al.* 1995). The relatively larger gaps with greater soil disturbance, higher soil nutrient availability, and larger and more frequent canopy openings at lower elevations may result in higher species diversity, and select for abundant species that are mostly shade-intolerant. As a result of the relatively greater extent of canopy and soil disturbance on mid-slopes and valleys, greater opportunities are made available for resource partitioning among species present in the seedling bank. Thus, in the Sinharaja landscape, while topographic and edaphic habitat partitioning appear to play a significant role in the spatial distribution of species, intermediate disturbance conditions may contribute to higher species diversity at lower elevations than in the more stable conditions prevailing at upper elevations (cf. Connell 1978). A greater tree species diversity in low-elevation valley plots than nearby ridge-top plots has also been observed in lowland dipterocarp forests in Sumatra (Rennolls & Laumonier 2000) and Sabah (Nilus 2003). The mechanisms that determine these consistent patterns of tree diversity across topographic gradients have not been fully explored.

Comparisons with other forest dynamics plots

This study shows that nearly four-fifths (79%) of species examined are associated with topographically defined habitats in the Sinharaja FDP. Among the plots examined using comparable methods, Sinharaja stands among those with the highest percentage of species demonstrating significant habitat associations: the plot on Barro Colorado Island, Panama, has 33% of its species significantly associated with habitats, those at Mudumalai in India and Korup in Cameroon have 68% each (Anon. 2003, Harms *et al.* 2001), but that at Lambir in Sarawak – also a topographically heterogeneous plot – has 86.8% of species significantly biased with respect to the habitat gradient of the plot (Davies *et al.* 2005). This study may have underestimated the total percentage of habitat specialists at Sinharaja, however, by arbitrarily confining the analysis only to an elevational and topographic gradient. There are, for instance, aspect-related patterns of species distribution within the plot: for example, *Shorea trapezifolia* and *Syzygium rubicundum* are concentrated on the north-east facing slope, while *Shorea megistophylla*, *S. disticha*, *S. cordifolia* and *S. worthingtonii* are concentrated on the south-west facing slope. These two associations are widespread in the Sinharaja landscape and appear to be correlated with soil depth and possibly occasional large-scale canopy openings (Ashton *et al.* 2001, Gamage *et al.* 2003). Using an index of relative neighbourhood density (a probability density function), Condit *et al.* (2000) observed that in both the Sinharaja and Lambir FDPs, the species distribution patterns followed topographic features resulting in habitat-related patchiness more than in the two more topographically homogeneous Forest Dynamics Plots at BCI and Pasoh. The eight habitat classification appears to have successfully represented much of the topographic variability of the Sinharaja FDP.

Mechanistic basis of habitat specialization

The strong relationships between species distributions and habitats are consistent with ecophysiological, morphological and anatomical studies carried out with seedlings of *Shorea, Mesua, Dipterocarpus* and *Syzygium* species in natural canopy gaps along topographic catenas and in artificial shelters, each over a period of 2 y (Ashton 1995, Ashton & Berlyn 1992, Ashton *et al.* 1995, 2001, 2006, Gamage *et al.* 2003, Gunatilleke *et al.* 1997, Singhakumara *et al.* 2003). For example, seedlings of *Shorea worthingtonii* and *Mesua nagassarium* are more tolerant of shade and drought than their sympatric congeners and these characteristics might explain their strong positive associations with upper-elevation spurs. These species possess relatively small leaves, low leaf surface to volume ratios, low stomatal densities per unit area and low rates of stomatal conductance (Ashton & Berlyn 1992, Ashton *et al.* 2006). Compared to the other *Shorea* species, seedlings of *S. worthingtonii* exhibit the least plasticity in leaf anatomy between shade and sun, higher root allocation and rates of net photosynthesis, and lower mortality in deep shade (Ashton 1995). *Shorea worthingtonii* and *M. nagassarium* showed higher survival and growth in both natural and simulated upper-slope environments, and *S. worthingtonii* experienced the lowest survival and growth rates in open valley habitats in the Sinharaja landscape (Ashton *et al.* 1995, 2006).

Compared to the other species of *Shorea*, seedlings of *S. megistophylla* exhibited the greatest plasticity in growth measures and leaf morphology between shade and sun treatments and the greatest net photosynthetic rates and stomatal conductivity, largest and thickest leaves, largest stomates, thickest cuticles and greatest rates of mass gain in full-sun environments (Ashton 1995, Ashton & Berlyn 1992). Taken together these traits provide a mechanistic explanation for the observation that seedlings of *S. megistophylla* show greatest rates of growth and survival in large canopy gaps in valleys (Ashton *et al.* 1995) and the positive association of stems ≥ 1 cm dbh to LLG (the habitat most clearly describing the valley environment at Sinharaja). *Mesua ferrea*, a species restricted to lower-lying areas along streams, exhibited similar growth attributes to *S. megistophylla* (Ashton *et al.* 2006). Differential patterns of water-use efficiency and shade tolerance among four sympatric species of *Syzygium* also reflect differences in their habitat preferences in the Sinharaja landscape (Gamage *et al.* 2003, Singhakumara *et al.* 2003). Similar experimental investigation of the mechanisms underlying habitat specialization in lowland dipterocarp forest at Lambir National Park, Sarawak, has emphasized the potential importance of differences in water availability between soil types (Palmiotto *et al.* 2004).

Niche-assembly vs. dispersal-assembly mechanisms underlying species distribution

The results from Sinharaja and other CTFS FDPs indicate that with increases in fine-scale topographic and edaphic heterogeneity, there may be a concomitant increase in the proportion of habitat specialists (Harms *et al.* 2001, Potts *et al.* 2004). At Sinharaja, habitat specialists are dispersed by gyration (dipterocarps), ballistic mechanisms (*Agrostistachys*) and large and small animals (most species in Appendix 1; Jayasekara *et al.* 2003). Consequently, this suggests that the role of dispersal agents is relatively less important than that of habitat features in spatial patterning of tree species in the Sinharaja landscape.

Phillips *et al.* (2003) have shown a similarly high degree of association to contrasting substrates among forest trees in Madre de Dios, south-eastern Peru and concluded that substrate-mediated local processes may play a much more important role than distance-dependent processes in structuring forest composition. Likewise, Potts *et al.* (2004) have shown that habitat heterogeneity and niche structure play a more important role than dispersal-based mechanisms in explaining observed species distribution patterns in a NW Borneo mixed dipterocarp forest. A larger-scale study in the Western Amazon by Fine *et al.*

(2005) has shown that edaphic heterogeneity has played an important role in both allopatric and parapatric speciation of taxa within tribe Protieae of Burseraceae. However, in a FDP in *terre firme* forest at Yasuni in Ecuador, most species occurred in all habitats with similar densities from ridge top to valley bottom, suggesting that they might be habitat generalists (Valencia *et al.* 2004). Valencia *et al.* (2004) found little evidence for fine-grained partitioning of the topographic gradient, in contrast to the observed patterns at Sinharaja. Furthermore, Valencia *et al.* (2004) found that habitat specialists were mostly treelets and shrubs, whereas in Sinharaja all growth forms, including most of the abundant and canopy-dominant species are well represented among habitat specialists (Table 5, Appendix 1). These marked differences observed in the patterns of species distribution among forests may relate to their differences in historical and ecological biogeography, or to differences in local topography that create conditions that differentially dictate species distribution patterns (Ashton 1998, Burslem *et al.* 2001, Fine *et al.* 2005, Gamage *et al.* 2003, Phillips *et al.* 2003, Potts *et al.* 2004).

Finally, the neutral theory of community organization postulates that populations take random walks in abundance as they disperse, colonize, advance and retreat across landscapes (Hubbell 2001). The theory was conceived and has been explored on homogeneous landscapes (Hubbell 2001), even though real-world landscapes are heterogeneous (e.g. Figure 1). The extent that species distribution patterns are biased with respect to landscape features is the extent to which predictions made by neutral theory are not met. The present study demonstrates dramatic levels of habitat association that are inconsistent with a strict interpretation of neutrality as applied to tropical forest tree communities.

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Appendix 1. Abundant and less-abundant species, each having ≥ 800 or 100–800 individuals, respectively, in the Sinharaja FDP, showing significant positive (+) and negative (−) associations to different habitats. Abbreviations of habitat categories are explained in Table 1. C = Canopy tree species; SC = Sub-canopy tree species; UT = Understorey tree species; ST = Shrub and treelet species.

Habitat categories	USS	ULS	USG	ULG	LSS	LLS	LSG	LLG
Abundant species showing significant associations								
(+) associations with upper-elevation habitats and with/without (−) associations with lower-elevation habitats								
Agrostistachys intramarginalis (ST)	+						−	−
Mesua nagassarium (C)	+							−
Shorea worthingtonii (C)	+							−
Memecylon arnottianum (ST)		+					−	−
Humboldtia laurifolia (UT)		+					−	−
Hydnocarpus octandra (SC)			+					
Shorea cordifolia (SC)			+					−
Palaquium petiolare (C)			+	+				−
Mesua ferrea (C)			+	+				
Nargedia macrocarpa (UT)				+				
(+) associations with lower-elevation habitats and with/without (−) associations with upper-elevation habitats								
Garcinia hermonii (UT)					+			
Xylopia championii (UT)					+	+		
Memecylon rostratum (ST)					+	+		
Shorea trapezifolia (C)						+		
Gaertnera rosea (ST)	−					+		+
Agrostistachys hookeri (ST)							+	
Semecarpus walkeri (SC)							+	+
Schumacheria castaneifolia (ST)							+	+
Palaquium canaliculatum (SC)	−	−					+	+
Urophyllum ellipticum (ST)		−					+	+
Psychotria dubia (ST)	−	−						+
Bhesa ceylanica (C)	−							+
Semecarpus gardneri (SC)	−							+
Litsea longifolia (UT)		−						+
Leea indica (ST)		−						+
Shorea megistophylla (C)								+
Syzygium neesianum (SC)								+
Mastixia tetrandra (SC)								+
Cryptocarya wightiana (SC)								+
Psychotria nigra (ST)								+
Gaertnera vaginans (ST)								+
Glochidion acuminatum (ST)								+
Allophyllus zeylanicus (ST)								+
(−) associations with either upper- or lower-elevation habitats								
Anisophyllea cinnamomoides (C)	−							
Cullenia ceylanica (SC)		−						
Palaquium thwaitesii (SC)						−		−
Shorea affinis (C)							−	−
Calophyllum thwaitesii (SC)							−	−
Shorea disticha (C)								−
Shorea congestiflora (C)								−
Cullenia rosayroana (SC)								−
Less-abundant species showing significant associations								
(+) associations with upper-elevation habitats and with/without (−) associations with lower-elevation habitats								
Psychotria glandulifera (ST)		+	−					
Isonandra lanceolata (SC)		+					−	
Symplocos cuneata (ST)		+					−	
Prismatomeris tetrandra (ST)		+					−	−
Lasianthus obliquus (ST)		+						−
Madhuca fulva (SC)			+					−
(+) associations with lower-elevation habitats and with/without (−) associations with upper-elevation habitats								
Erythroxylum obtusifolium (ST)	−				+			
Syzygium lissophyllum (SC)	−		−			+		
Carallia calycina (SC)	−		−			+		
Syzygium sylvestre (SC)	−						+	
Dysoxylum binectariferum (C)		−					+	
Aglaia apiocarpa (ST)		−					+	

Appendix 1. Continued.

Habitat categories	USS	ULS	USG	ULG	LSS	LLS	LSG	LLG
Dysoxylum peerisi (C)	–						+	+
Syzygium cylindricum (SC)	–							+
Syzygium wightianum (SC)	–							+
Nothopodites foetida (ST)	–	–					+	+
Psychotria pleurivenia (ST)	–							+
Antidesma pyrifolium (ST)	–							+
Mallotus rhamnifolius (ST	–							+
Euphoria longana (SC)	–	–			–			+
Pometia tomentosa (SC)	–	–						+
Scolopia acuminata (UT)	–	–						+
Symplocos hispidula (ST)		–	–					+
Actinodaphne albifrons (UT)		–	–	–				+
Semecarpus acuminata (ST)		–		–				+
Diospyros insignis (UT)			–					+
Calophyllum bracteatum (SC)					+			
Pseudocarapa championii (C)						+		
Putranjiva tomentosa (SC)						+		
Garcinia spicata (UT)						+		
Gomphia serrata (ST)						+		
Eurya acuminata (ST)						+		
Ptychopyxis thwaitesii (UT)							+	
Pavetta indica (ST)							+	+
Eugenia rivulorum (ST)							+	+
Chaetocarpus castanocarpus (SC)								+
Axinandra zeylanica (SC)								+
Vitex altissima (SC)								+
Cinnamomum capparu-coronde (UT)								+
Cinnamomum dubium (UT)								+
Dillenia retusa (UT)								+
Semecarpus subpeltata (UT)								+
Elaeocarpus subvillosus (UT)								+
Mallotus fuscescens (UT)								+
Thottea siliquosa (ST)								+
Glochidion zeylanicum (ST)								+
Symplocos coronata (ST)								+
Glycosmis pentaphylla (ST)								+
(–) associations with either upper- or lower-elevation habitats								
Dipterocarpus hispidus (C)	–							
Urandra apicalis (SC)		–						
Glenniea unijuga (SC)		–						
Nothopegia beddomei (UT)		–						
Campnosperma zeylanicum (C)			–					
Litsea iteodaphne (ST)						–		–
Syzygium makul (SC)							–	
Memecylon procerum (ST)							–	
Gyrinops walla (UT)							–	–
Goniothalamus hookeri (ST)								–