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A test of the hypothesis of ecological equivalence in an Australian subtropical rain forest

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ABSTRACT. We tested the hypothesis that tree species in a subtropical rain forest in south-east Queensland are ecologically equivalent and therefore have identical environmental requirements for their regeneration. We assessed the evidence that juveniles of species differed in their distributions in treefall gap microsites and along gradients of light availability, soil pH, soil PO_4-P availability and soil NO_3-N availability. Pairwise comparisons were made on a subset of the common species selected on the basis that they showed a relatively high level of positive association, and would therefore, a priori, be expected to have similar regeneration requirements. Detailed comparisons between the species failed to demonstrate evidence for species differentiation with respect to their tolerance of the disturbance associated with gap microsites or to the gradient of NO_3-N availability. However, species differed markedly in their distributions along the soil pH gradient and along the gradients of light availability and soil PO_4-P availability. The overall level of ecological differentiation between the species is high: seven out of the 10 possible species pairings showed evidence for ecological differentiation. Such niche differentiation amongst the juveniles of tree species may play an important role in maintaining the species richness of rain-forest communities.

KEY WORDS: *Doryphora sassafras*, gap microsites, light environment, niche differentiation, nitrogen, *Orites excelsa*, pH, phosphorus, *Polyosma cunninghamii*, *Sarcopteryx stipata*, *Sloanea woollsii*, species co-existence, treefall gaps

INTRODUCTION

The role of niche differentiation in species-rich rain-forest communities has been a subject of much debate (Hubbell & Foster 1986*a*, Kobe 1999, Lieberman *et al.* 1995). It has long been recognized that rain-forest tree species differ in

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their ability to tolerate shade, and this led to a simple dichotomous classification of rain-forest trees into pioneer and climax or non-pioneer (Swaine & Whitmore 1988, Whitmore 1975). More recent studies have recognized additional groups, including shade specialists, intermediate or gap-edge specialists, and gap specialists (Hubbell & Foster 1986*b*, Welden *et al.* 1991). However, the observation that most tree species in rain forests are apparently generalists whose distributions appear to be unrelated to canopy openness (Hubbell & Foster 1986*b*), and the apparent lack of evidence for finer-scale partitioning of the light environment within these broad regeneration guilds, has led a number of authors to question the importance of niches for the co-existence of rain-forest tree species (Hubbell & Foster 1986*a*, Lieberman *et al.* 1995).

There is evidence, however, to suggest that environmental factors other than light availability could provide opportunities for niche differentiation within rain-forest communities. In most cases these environmental gradients have been studied at the landscape level, using areas in different topographic locations. For example, Hubbell & Foster (1986*c*) recognized several guilds of edaphic and topographic specialists amongst the species at Barro Colorado Island, Panama. More recently, Clark *et al.* (1998) found differences between Costa Rican tree species with respect to their abundance in areas of contrasting soil type, topographic position and slope angle. Topography and soil type also appear to be important in defining the niches of a variety of palm species and understorey species in the neotropics (Clark *et al.* 1995, Kahn & de Castro 1985, Svenning 1999, Tuomisto & Ruokolainen 1993). Similar patterns of topographic and edaphic influence have also been observed for rain forests on other continents (Baillie *et al.* 1987, Gartlan *et al.* 1986, Itoh 1995).

Ecological specializations likely to contribute to species co-existence may operate at a variety of scales. That is, niches that are defined by environmental gradients operating at a landscape scale (such as topography, soil type etc.) may only partially account for species co-existence in rain forests. There may also be additional mechanisms that explain the co-existence of the many species within the guilds adapted to each habitat type. The identification of these requires the investigation of environmental factors that vary over comparatively short distances (1–100 m), i.e. within habitat types. Although numerous studies have compared the distributions of rain-forest species along gradients of canopy openness, species differentiation along other environmental gradients has rarely been examined at this fine scale.

In contrast to these explanations of species richness based on niche differentiation, several authors have suggested that species might actually coexist for long periods if they were ecologically equivalent (Aarssen 1983, Connell 1978, Goldberg & Werner 1983, Hubbell & Foster 1986*a*, Pacala 1988, Sale 1977, Shmida & Ellner 1984, Shmida & Wilson 1985). In the absence of forces to maintain the species composition, the population of each species would ‘drift in a random walk’, ultimately to local extinction (Hubbell & Foster 1986*a*).

However, as Hubbell (1979) and Wright & Hubbell (1983) have argued, the time for this to occur could be extremely long and, in fact, be comparable to the time scale at which speciation might occur (Hubbell & Foster 1986*a*).

More recently, it has been suggested that recruitment limitation (the failure of species to regenerate in suitable sites) might allow species to persist for long periods even if they differ in competitive ability (Brokaw & Busing 2000, Hubbell *et al.* 1999, Tilman 1999). Although there is evidence for strong recruitment limitation in tropical forests (Hubbell *et al.* 1999), the evidence from theoretical studies that any such recruitment limitation plays a significant role in allowing species to coexist is less clearcut. For example, species persistence in a model developed by Hurtt & Pacala (1995) depends on the unrealistic assumption that *per capita* fecundity is constant across all species. Chesson & Huntly (1989) have criticized Hubbell's original model of coexistence amongst ecologically equivalent species (Hubbell 1979) because it also depends on similar assumptions for long-term coexistence.

This study explores the hypothesis of ecological equivalence by investigating the gap-microsite specializations and differentiation in shade tolerance within a group of subtropical rain-forest tree species. We have also looked at differentiation between species with respect to their distribution along fine-scale soil pH and nutrient gradients. In keeping with Grubb's (1977) recognition that the opportunities for niche differentiation in plant species are greater during regeneration, we have focused our investigation on the extent of differentiation between juveniles rather than mature trees.

Attempts to compare the distributions of a group of species along various environmental gradients can result in an excessive number of comparisons being made. This presents a statistical problem because the overall probability of making Type I errors will increase as the number of comparisons increases. To reduce the number of comparisons, we identified a subset of the species that we would expect, a priori, to show a relatively low degree of ecological differentiation. The approach we took was to measure the level of association between species and use cluster analysis to identify a group of species that showed the greatest level of interspecific association, on the assumption that species with relatively similar regeneration requirements will be the most highly associated (Ludwig & Reynolds 1988). Subsequent interspecific comparisons were then restricted to this final group of species. Evidence for a high level of niche differentiation amongst this group would indicate a significant level of niche differentiation amongst the wider community of tree species.

METHODS

Site description and vegetation sampling

All field work was carried out in Gambubal State Forest (28°14′S, 152°24′E), which is located on the western escarpment of the Main Range (part of the Great Dividing Range), 35 km east of Warwick, in south-east Queensland, Australia. The study was carried out in a 2.25-ha area of relatively undisturbed subtropical rain forest (notophyll vine forest *sensu* Webb 1959, 1978) on a gently sloping shelf approximately 100 m below the summit of Bald Mountain (1196 m asl). The soil at the research site is a red rough-ped earth (Northcote *et al.* 1975) overlying basalt parent material (Grenfell 1984). More detailed descriptions of the geology, climate and vegetation of the site can be found in Penfold & Lamb (1999) and Debski *et al.* (2000).

A survey of tree seedlings and saplings (hereafter collectively referred to as juveniles) in the rain-forest understorey was carried out between June 1993 and July 1994. In total, 604 quadrats (each 1 m^2) were established throughout the 2.25-ha area. The survey was stratified such that half of the quadrats were placed within 18 canopy gaps (all created by limbfalls or the uprooting of single trees), while the other half were placed in intact forest areas around these gaps. In this study gaps were defined as openings in the canopy extending down to within 2 m of the ground. Recently created gaps might still contain individuals which, although intolerant of the changed environmental conditions, have yet to respond to them. To reduce the risk of sampling such individuals the study was restricted to gaps which were at least 2–3 y old. Within each gap or intact forest area, the quadrats were located randomly. Each of the quadrats was given an identification number and the density of juveniles (individuals with more than four leaves or leaf pairs and less than 30 cm GBH) of each tree species was noted. The upper size limit was chosen to fit in with the lower size limit of a tree survey that was also conducted in the area. In practice, the number of individuals in the juvenile survey that were greater than 1 cm in diameter was inconsequential, and the majority were also below 1 m in height. These forests contain about 58 canopy tree species but only 14 species were found in at least 10 quadrats, and these were used in the analyses described below. The abundance of these 14 species and their authorities are given in Penfold & Lamb (1999).

Interspecific association

The degree of association between species was assessed using the Phi (ϕ) coefficient (Fleiss 1981), which is an association measure for presence/absence data and is derived from χ^2. It ranges from -1 (complete negative association) to 1 (complete positive association). Species distributed randomly with respect to each other would have a ϕ of zero. To identify a group of species that showed a relatively high level of positive association, cluster analysis was performed using a distance measure derived directly from ϕ thus:

$$D = 2 - (1 + \phi) \tag{1}$$

Species that tend to be found together will have a low D (< 1), whereas species that tend not to be found together will have a higher D (> 1).

Gap microsites

Each of the 302 1-m^2 quadrats placed in treefall gaps was assigned to one of three microsite types: the soil mound and pit at the base of the fallen tree (root-throw zone), the area covered by the crown of the fallen tree (crown zone), or undisturbed zone (equivalent to the bole zone *sensu* Brandani *et al.* 1988, Núñez-Farfán & Dirzo 1988).

Differentiation between species with respect to their tolerance of gap microsites was examined for each species pairing amongst the group of species identified by the cluster analysis technique described above. For each species pair we calculated the frequency of each species in each microsite and the ratio of the frequency of the first species to the frequency of the second species. If the two species are ecologically equivalent we would expect this ratio to be similar for species favouring each of the gap microsites and for species favouring undisturbed areas. Although the frequency of the species might vary considerably from one type of microsite to another or between the gap microsites and undisturbed areas, we would expect the frequency of each species to vary in a similar manner, and therefore the ratio of their frequencies would remain constant across the range of environments.

To test this prediction concerning the ratio of species frequencies in different microsites we used a sampled randomization test (Sokal & Rohlf 1995). Due to the small number of quadrats that fell in root-throw zones (14 quadrats), our analyses were restricted to a comparison of the ratio of species frequencies in crown zones *vs* undisturbed areas. For each species pair we calculated the difference between the ratio of frequencies in crown-zone quadrats and the ratio of frequencies in undisturbed quadrats (only the 302 quadrats located in treefall gaps were used in these analyses). This observed difference was then compared with the distribution of values expected under the hypothesis of ecological equivalence to determine if it was significantly deviant. The distribution of expected values was determined as follows. Initially we identified the quadrats that contained one or both of the species being compared. Each species was then randomly reassigned to these quadrats such that the total frequency of each species was maintained. The frequency of each species in crown-zone and undisturbed quadrats was recalculated, as was the corresponding ratio of frequencies for each type of quadrat. This process of random reassignment was replicated from 1000 to 5000 times and the proportion of replicates where the difference between the ratios was greater than or equal to the observed difference was recorded.

Per cent sky visible

As an index of the quantity of light reaching each quadrat, the per cent sky visible above the quadrat was estimated using a concave spherical densiometer (Lemmon 1956, 1957). The densiometer was chosen because it provides a rapid means of estimating the light environment at a large number of points, and because it can be used effectively in any cloud conditions. Measurements were taken at 110 cm above ground level (a little above waist height) so that the amount of light reaching the majority of individuals in each quadrat could be estimated. Four measurements were taken (looking north, south, east and west) and averaged.

Differentiation between species with respect to their distribution along the gradient of per cent sky visible was detected by comparing the distributions of species along the gradient. These differences were tested using a sampled randomization test as follows. The values of percentage sky visible were first transformed to $ln(0.5 + \%$ sky visible$)$ to provide a gradient with a more even distribution of values. The gradient was then split into three equal width classes and the frequency of each species in each class was calculated. The class boundaries were determined in such a way that the classes covered the full range of percentage sky visible values as evenly as possible, and also there was a minimum of about 30 quadrats in each class that contained at least one of the species from each pairing. Randomization tests were carried out in a similar way to those used to analyse the differentiation of species with respect to their tolerance of gap microsites, except that all 604 quadrats were used, and the standard deviation (SD) of the ratios calculated for the three classes was used in place of the difference between the ratios in crown zones and undisturbed areas. Under the null hypothesis of ecological equivalence we would expect the ratio of the species frequencies to be constant across the three classes and therefore that the standard deviation would tend towards zero. Between 1000 and 10 000 replicates were used, depending on the extent to which the observed standard deviation deviated from this expected value.

Soil pH, phosphate phosphorus and nitrate nitrogen

To determine soil pH, a 20-g soil sample was collected from the top 5 cm of each of the 604 quadrats. Samples were frozen on the day of collection and analysed within two days. The pH of field moist samples was determined using a 1:5 ratio of soil weight to distilled water volume.

The availability of phosphate phosphorus (PO_4-P), and nitrate nitrogen (NO_3-N) was assessed using an ion exchange resin (IER) bag technique (Binkley & Matson 1983, Hübner *et al.* 1991, Stewart *et al.* 1993). IER bags were constructed by placing 5 g fresh weight of mixed bed resin (DOWEX MR-3) in a 6-cm × 7-cm nylon mesh bag (365 μm mesh size). One IER bag was buried to a depth of 5 cm in each of the understorey vegetation survey quadrats. The IER bags were left in the field for approximately 1 mo, between 17 March and 18 April 1994. This incubation period was at the end of summer and was chosen to provide an assessment of nutrient availability at a time of year when soil moisture availability and temperature were both high, and conditions were, therefore, favourable for soil microbial activity. Rainfall during this period was approximately 100 mm (Lindsay Hutley, unpubl. data). Eight IER bags could not be relocated after the incubation period, thereby reducing the number of quadrats sampled to 596. After collection the resin was air dried, removed from the bags and eluted for 30 minutes with 20 ml 1 M KCl. After stirring, the eluate was decanted. The resin was then eluted a further 4 times, the eluate being decanted and retained each time. The bulked eluates were then filtered (Whatman No. 42) and frozen until analysed. PO_4-P concentration in the extracts was determined using the ascorbic acid-molybdate method (Murphy & Riley 1962, Olsen & Sommers 1982, Watanabe & Olsen 1965). NO_3-N was first reduced to nitrite by cadmium, and then nitrite concentration was determined (Sloan & Sublett 1966).

Differentiation between species with respect to their distribution along these soil environmental gradients was detected by comparing the distributions of species along each gradient. The technique used was identical to that used for the gradient of percentage sky visible. Values of PO_4-P were transformed to $ln(0.5 + PO_4\text{-P})$ and values of NO_3-N were transformed to $ln(NO_3\text{-N})$ prior to analysis.

RESULTS

Interspecific association

On the whole, the species showed no evidence of either strong positive or negative associations. *Sarcopteryx stipata* and *Polyosma cunninghamii* showed the highest level of association, but even these species were only rather weakly associated ($\phi = 0.29$). Nevertheless, two small groups of positively associated species could be identified from the cluster analysis (Figure 1). The cluster analysis was conducted using a range of linkage methods, including single linkage, average linkage and complete linkage. The same two groups of species were identified by each of the linkage methods. They were also identified when the cluster analysis was repeated using a distance metric derived from Jaccard's coefficient of similarity (van Tongeren 1987), which is a measure of association with very different properties to ϕ. It was decided to select a group of five species, from the larger of the two groups indicated by the cluster analyses, for use in all subsequent pairwise comparisons. This group of species (indicated with an asterisk in Figure 1) consistently displayed a relatively high level of positive association in all analyses and provided a sufficient number of species for use in the pairwise comparisons, whilst still restricting the number of comparisons to a manageable level.

Gap microsites

The degree of differentiation between species with respect to their tolerance of the disturbance associated with crown zones was investigated further for the group of five species identified by cluster analysis. For each of the ten possible species pairings we calculated the ratio of the species frequencies in undisturbed and crown-zone quadrats (Figure 2). As expected, differences between the ratios in undisturbed and crown zones were greatest when the two species

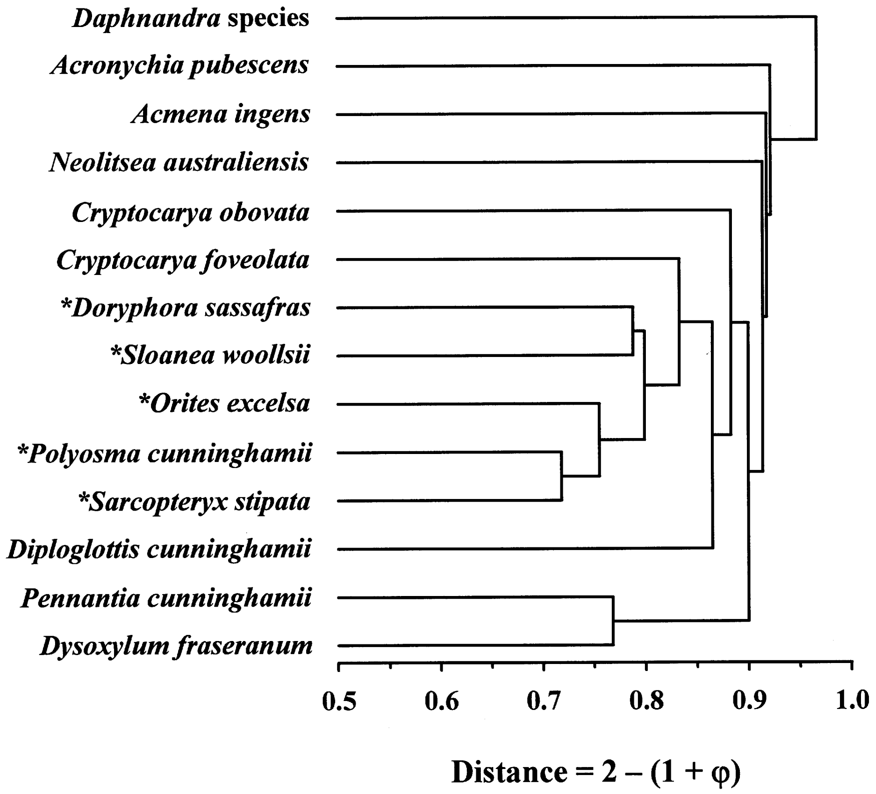

Figure 1. Dendrogram showing the results of cluster analysis (average linkage) using the distance measure derived from ϕ. Species selected for detailed comparisons are marked with an asterisk.

that showed the strongest evidence for a reduction in frequency in crown zones (*Sloanea woollsii* and *Sarcopteryx stipata*) were compared with the other three species. Differences between the ratios in disturbed and undisturbed quadrats were tested using sampled randomization tests. To maintain an experimentwise alpha level of 0.05, we used a Bonferroni correction (Sokal & Rohlf 1995) and set the alpha level for individual pairwise comparisons at $P = 0.005$. None of the species pairings produced significantly different abundances in disturbed and undisturbed quadrats at this alpha level (Table 1).

Per cent sky visible

The degree of species differentiation in respect to their distribution along the gradient of per cent sky visible was explored further with the group of five species identified by cluster analysis. For most of the species pairings the ratio of species abundances showed little variation along the gradient (Figure 3). However, two of the species pairings showed a considerable shift in the ratio of their frequencies along the gradient. The ratio of *Sarcopteryx stipata* frequency to *Sloanea woollsii* frequency was much higher at low levels of per cent sky

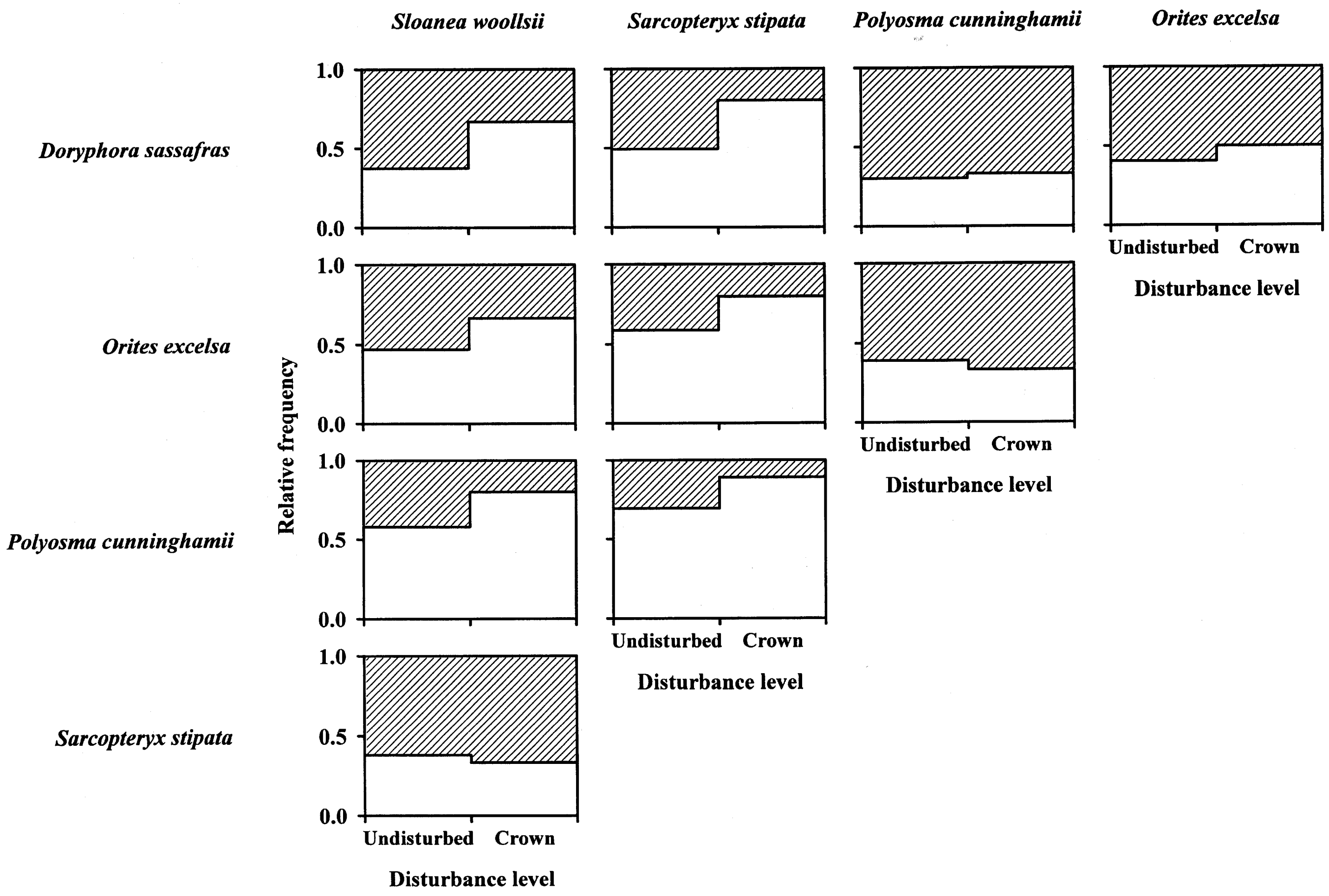

Figure 2. Comparison of species frequencies in crown-zone microsites and undisturbed areas of treefall gaps. For each graph, the unshaded area represents the frequency of the species listed to the left of the graph, and the shaded area represents the frequency of the species listed above the graph. Frequency values have been scaled so that the sum of the species frequencies in each class = 1.

Table 1. Difference in relative abundance in disturbed and undisturbed areas of treefall gaps for each species pair. Values shown are: total number of quadrats containing either species, observed difference between frequency ratios, number of replicates used in each sampled randomization test, and the proportion of replicates where the difference in relative abundance was greater than or equal to the observed difference. The frequency of each species is shown in parentheses after the species name.

Species pairing	Quadrats	Observed difference	Replicates	Proportion
Doryphora sassafras (40) – *Sloanea woollsii* (62)	83	0.292	5000	0.012
Doryphora sassafras (40) – *Sarcopteryx stipata* (38)	70	0.307	5000	0.048
Doryphora sassafras (40) – *Polyosma cunninghamii* (91)	110	0.031	1000	0.80
Doryphora sassafras (40) – *Orites excelsa* (57)	81	0.096	1000	0.43
Orites excelsa (57) – *Sloanea woollsii* (62)	95	0.198	1000	0.17
Orites excelsa (57) – *Sarcopteryx stipata* (38)	79	0.211	1000	0.12
Orites excelsa (57) – *Polyosma cunninghamii* (91)	112	0.056	1000	0.56
Polyosma cunninghamii (91) – *Sloanea woollsii* (62)	122	0.220	5000	0.043
Polyosma cunninghamii (91) – *Sarcopteryx stipata* (38)	103	0.197	5000	0.052
Sarcopteryx stipata (38) – *Sloanea woollsii* (62)	83	0.048	1000	0.68

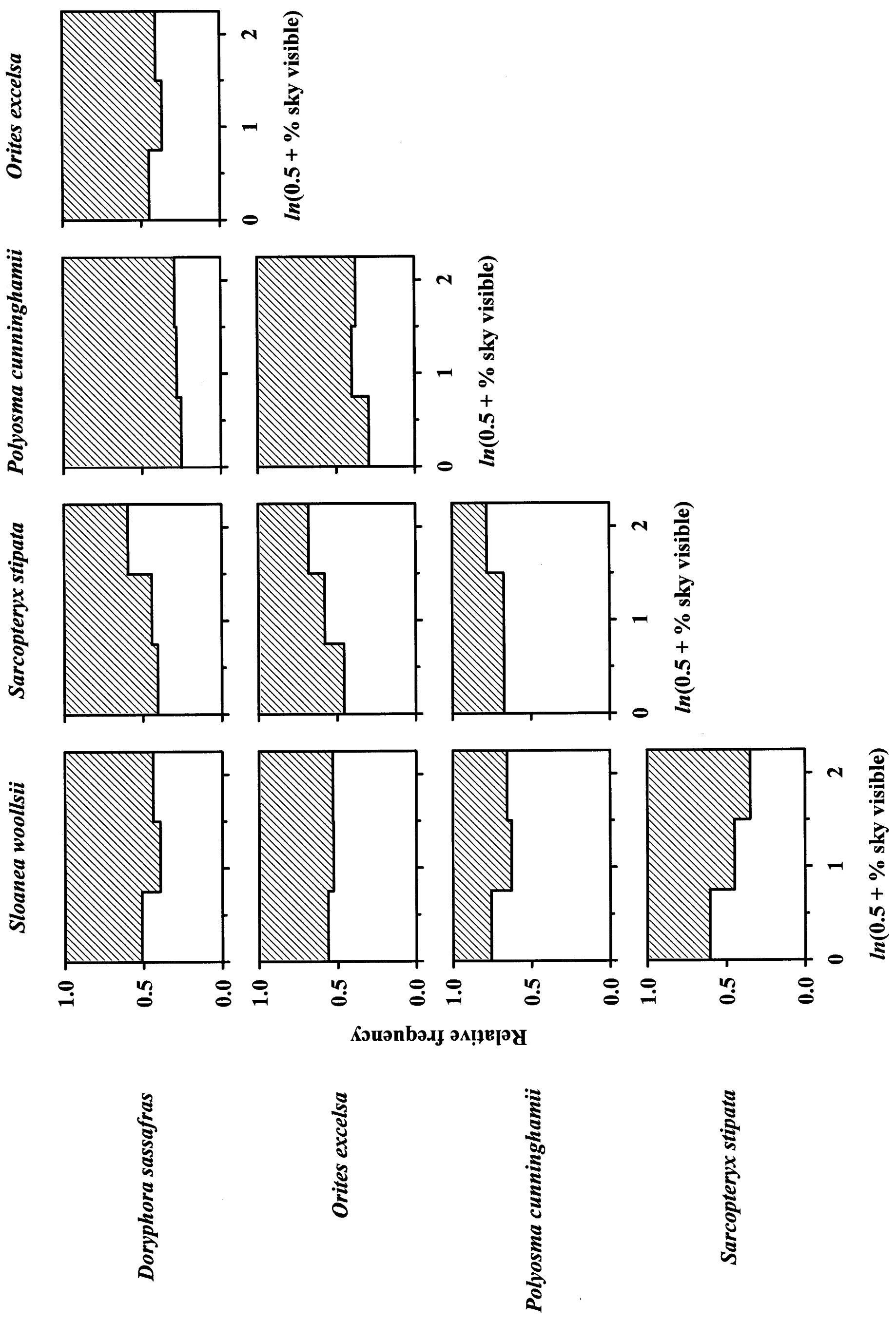

Figure 3. Comparison of species frequencies at different locations along the gradient of per cent sky visible. See legend of Figure 2 for more details.

visible than it was at high levels. The ratio of *Orites excelsa* frequency to *Sarcopteryx stipata* frequency increased in quadrats with relatively high values of per cent sky visible. The results of sampled randomization tests suggest that for these two species pairings, the observed variation in abundance ratios deviates considerably from expected values (Table 2).

Soil pH, phosphate phosphorus and nitrate nitrogen

For each of the possible pairings of the five species we examined the ratio of their abundances at different points along each environmental gradient. The results for the soil pH gradient are shown in Figure 4. Several of the species pairs showed considerable variation in the ratio of their abundances along the pH gradient. Of the 10 possible pairwise comparisons, six were found to be significantly deviant ($P < 0.005$) based on the results of sampled randomization tests (Table 3). The frequency of both *Doryphora sassafras* and *Sloanea woollsii* tended to increase, relative to the frequency of the other three species, at higher pH values. The ratio of the abundance of *Doryphora sassafras* to the abundance of *Sloanea woollsii* remained constant along the pH gradient. The other three species, *Orites excelsa*, *Polyosma cunninghamii* and *Sarcopteryx stipata*, were similarly undifferentiated with respect to their distributions along the pH gradient.

Only one of the species pairings indicated differentiation with respect to distributions along the PO_4-P gradient (Figure 5 and Table 4). The abundance of *Doryphora sassafras* tended to increase relative to *Orites excelsa* in quadrats with intermediate and (to a lesser extent) low levels of soil PO_4-P. *Sloanea woollsii* and *Polyosma cunninghami* showed a similar trend to *Doryphora sassafras* but the level of variation was not significantly different ($P = 0.011$ and $P = 0.008$ respectively).

There was no evidence for differentiation with respect to species distributions along the gradient of soil NO_3-N (Figure 6). The abundance of *Doryphora sassafras* showed a slight tendency to increase relative to the abundance of some of the other species (*Sloanea woollsii*, *Polyosma cunninghamii* and *Orites excelsa*) at low levels of soil NO_3-N (Figure 6). However, this variation was not significantly different ($0.05 > P < 0.005$, Table 5).

DISCUSSION

Evidence for ecological equivalence

A number of species pairs appeared to be differentiated with respect to their tolerance of the disturbance associated with crown zones. For example, the ratio of *Doryphora sassafras* frequency to *Sloanea woollsii* frequency was much lower in undisturbed quadrats in gaps than it was in crown-zone quadrats. However, the probability of obtaining the observed difference ($P = 0.012$) was sufficiently high that, given the number of pairwise comparisons, it could have arisen by chance rather than reflect a genuine difference between the species.

Table 2. Variation in relative abundance along a gradient of per cent sky visible for each species pair. Values shown are: total number of quadrats containing either species, observed SD of frequency ratios, number of replicates used in each sampled randomization test, and the proportion of replicates where the SD was greater than or equal to the observed SD. The frequency of each species is shown in parentheses after the species name.

Species pairing	Quadrats	Observed SD	Replicates	Proportion
Doryphora sassafras (76) – *Sloanea woollsii* (98)	146	0.048	1000	0.18
Doryphora sassafras (76) – *Sarcopteryx stipata* (87)	144	0.081	5000	0.011
Doryphora sassafras (76) – *Polyosma cunninghamii* (200)	240	0.017	1000	0.71
Doryphora sassafras (76) – *Orites excelsa* (114)	166	0.033	1000	0.41
Orites excelsa (114) – *Sloanea woollsii* (98)	176	0.015	1000	0.81
Orites excelsa (114) – *Sarcopteryx stipata* (87)	168	0.091	10000	0.0009
Orites excelsa (114) – *Polyosma cunninghamii* (200)	249	0.046	5000	0.039
Polyosma cunninghamii (200) – *Sloanea woollsii* (98)	250	0.056	5000	0.014
Polyosma cunninghamii (200) – *Sarcopteryx stipata* (87)	230	0.051	5000	0.036
Sarcopteryx stipata (87) – *Sloanea woollsii* (98)	158	0.105	10000	0.0004

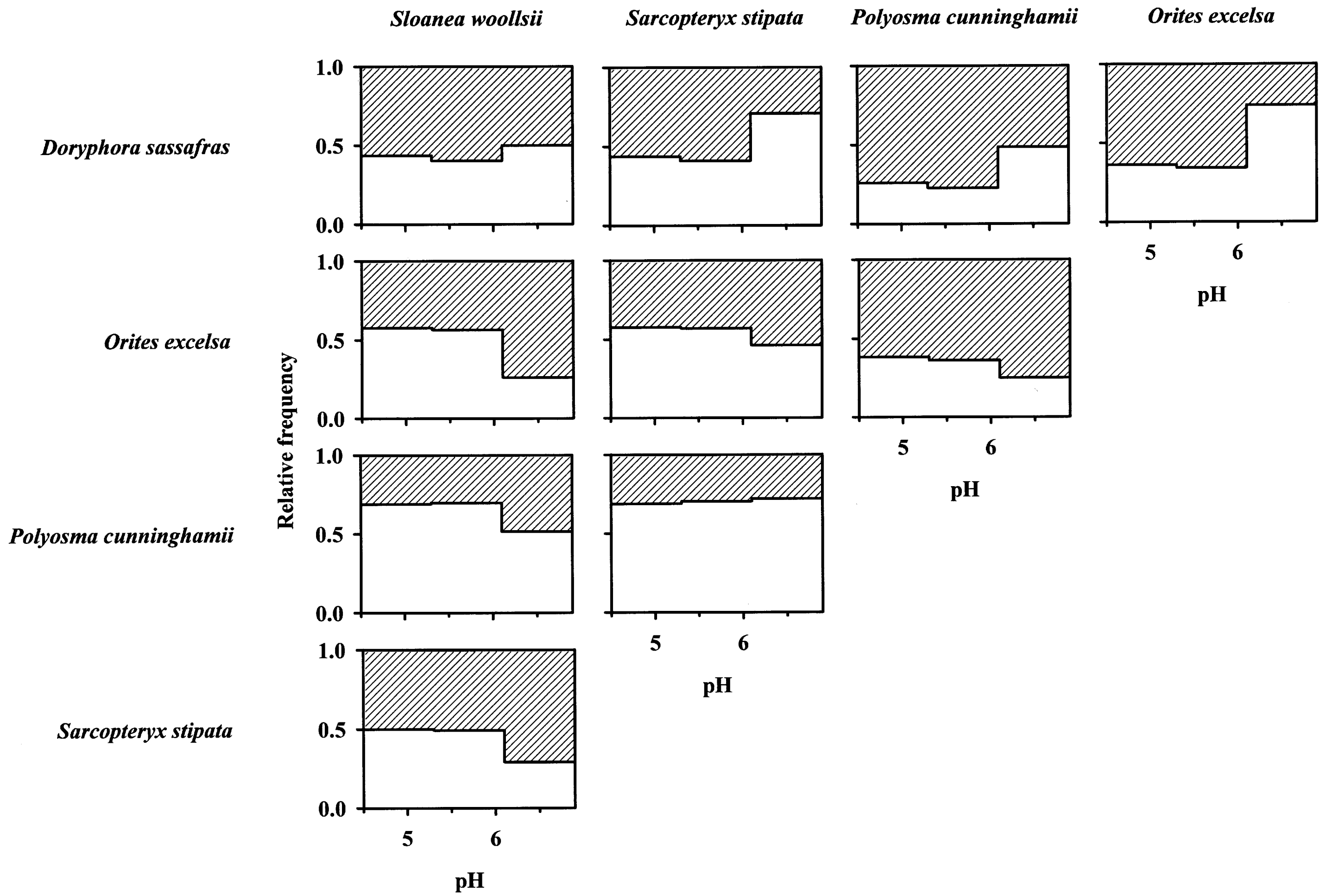

Figure 4. Comparison of species frequencies at different locations along the soil pH gradient. See legend of Figure 2 for more details.

Table 3. Variation in relative abundance along a gradient of soil pH for each species pair. See legend of Table 2 for more information about the values shown.

Species pairing	Quadrats	Observed SD	Replicates	Proportion
Doryphora sassafras (76) – *Sloanea woollsii* (98)	146	0.040	1000	0.28
Doryphora sassafras (76) – *Sarcopteryx stipata* (87)	144	0.135	10000	0.0005
Doryphora sassafras (76) – *Polyosma cunninghamii* (200)	240	0.115	10000	0.0002
Doryphora sassafras (76) – *Orites excelsa* (114)	166	0.183	10000	0.0000
Orites excelsa (114) – *Sloanea woollsii* (98)	176	0.146	10000	0.0002
Orites excelsa (114) – *Sarcopteryx stipata* (87)	168	0.053	1000	0.26
Orites excelsa (114) – *Polyosma cunninghamii* (200)	249	0.058	5000	0.058
Polyosma cunninghamii (200) – *Sloanea woollsii* (98)	250	0.084	10000	0.0015
Polyosma cunninghamii (200) – *Sarcopteryx stipata* (87)	230	0.013	1000	0.84
Sarcopteryx stipata (87) – *Sloanea woollsii* (98)	158	0.097	10000	0.0033

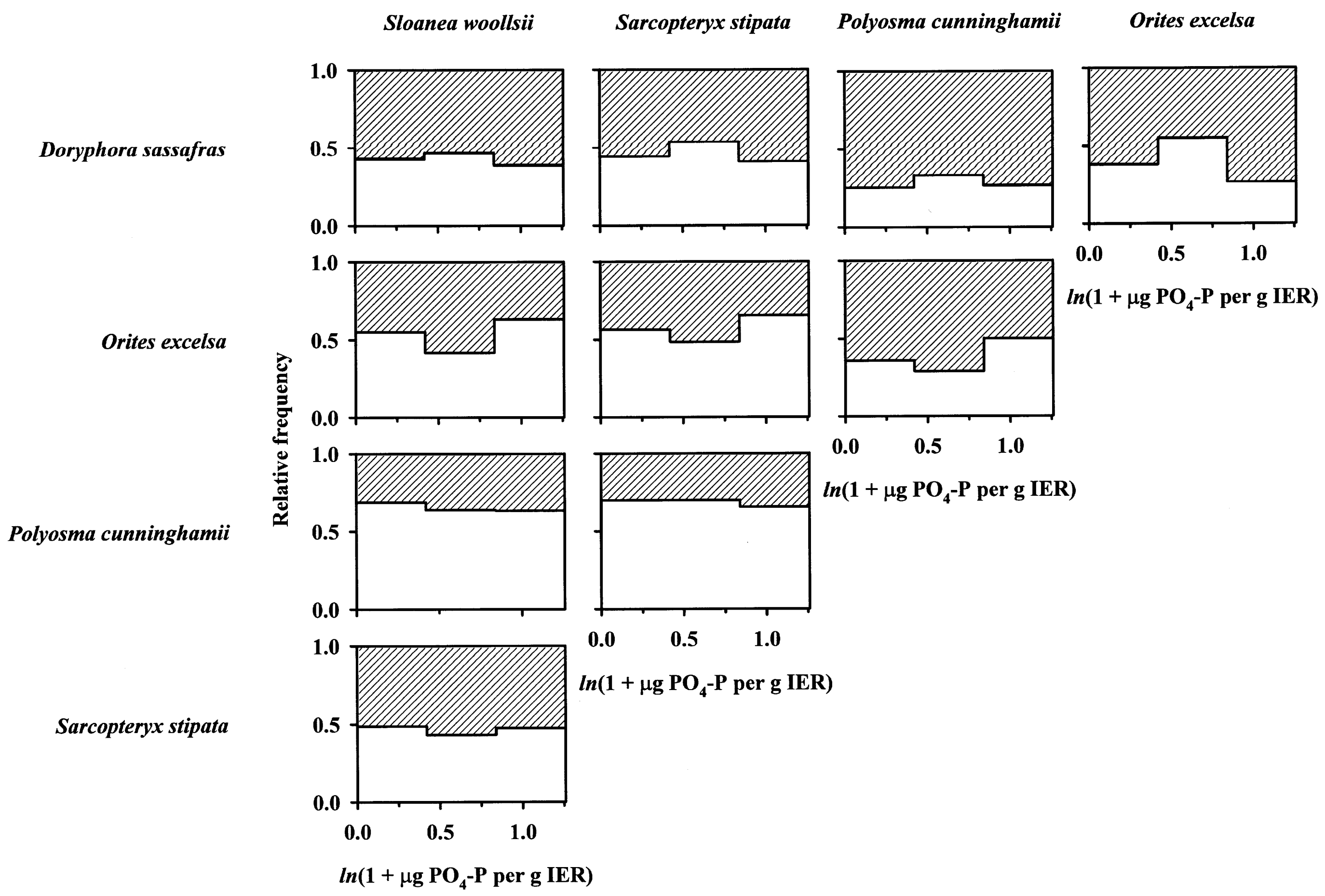

Figure 5. Comparison of species frequencies at different locations along the soil PO_4-P availability gradient. An index of PO_4-P availability was provided by measuring PO_4-P adsorption by ion-exchange resin (IER) buried in nylon mesh bags. See legend of Figure 2 for more details.

Table 4. Variation in relative abundance along a gradient of soil PO_4-P for each species pair. See legend of Table 2 for more information about the values shown.

Species pairing	Quadrats	Observed SD	Replicates	Proportion
Doryphora sassafras (76) – *Sloanea woollsii* (98)	146	0.025	1000	0.64
Doryphora sassafras (76) – *Sarcopteryx stipata* (86)	143	0.041	1000	0.38
Doryphora sassafras (76) – *Polyosma cunninghamii* (198)	238	0.033	1000	0.34
Doryphora sassafras (76) – *Orites excelsa* (112)	164	0.099	10000	0.003
Orites excelsa (112) – *Sloanea woollsii* (98)	174	0.077	10000	0.011
Orites excelsa (112) – *Sarcopteryx stipata* (86)	165	0.066	5000	0.053
Orites excelsa (112) – *Polyosma cunninghamii* (198)	245	0.067	10000	0.008
Polyosma cunninghamii (198) – *Sloanea woollsii* (98)	248	0.022	1000	0.60
Polyosma cunninghamii (198) – *Sarcopteryx stipata* (86)	227	0.004	1000	0.98
Sarcopteryx stipata (86) – *Sloanea woollsii* (98)	157	0.023	1000	0.71

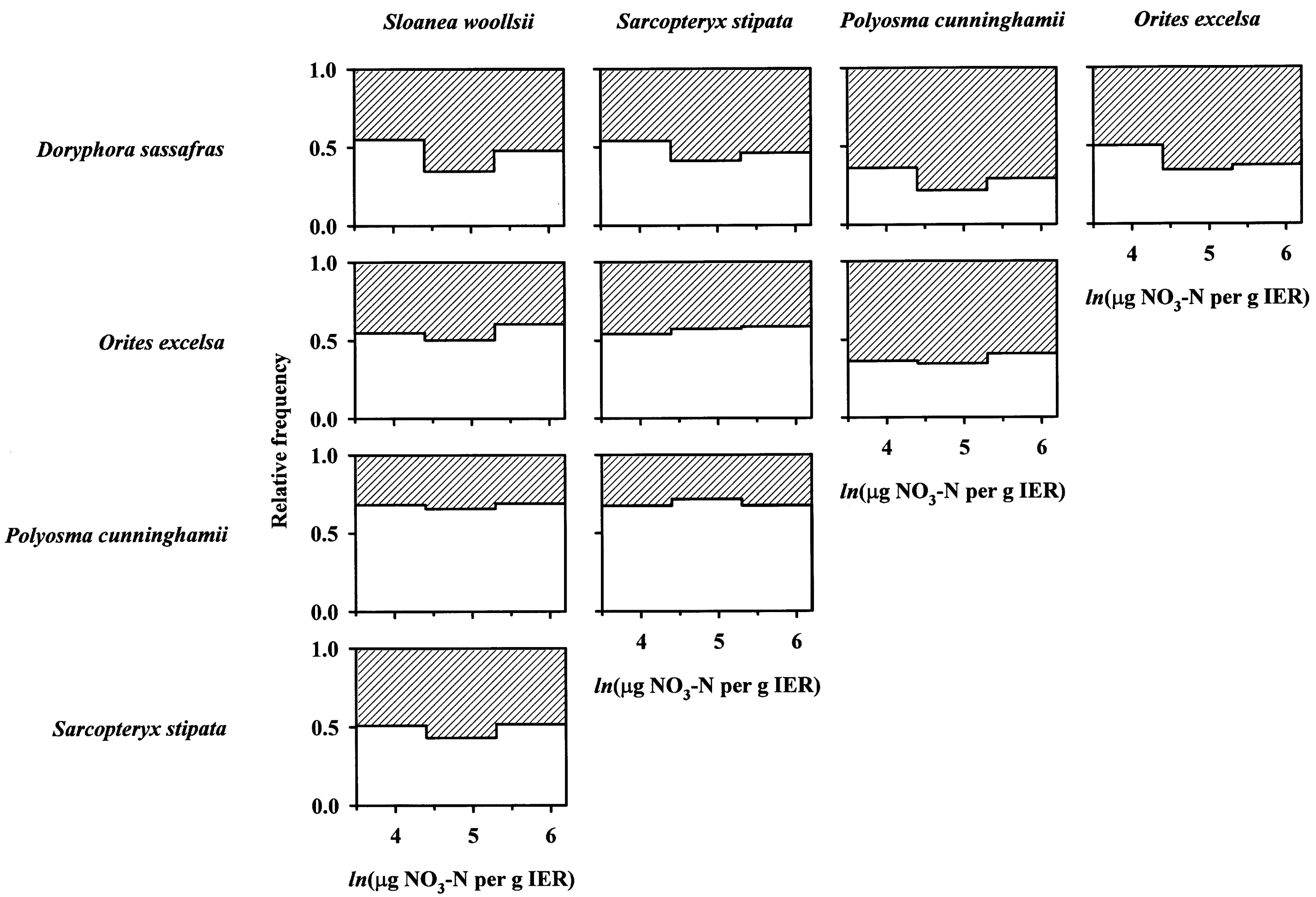

Figure 6. Comparison of species frequencies at different locations along the soil NO_3-N availability gradient. An index of NO_3-N availability was provided by measuring NO_3-N adsorption by ion-exchange resin (IER) buried in nylon mesh bags. See legend of Figure 2 for more details.

Table 5. Variation in relative abundance along a gradient of soil NO_3-N for each species pair. See legend of Table 2 for more information about the values shown.

Species pairing	Quadrats	Observed SD	Replicates	Proportion
Doryphora sassafras (76) – *Sloanea woollsii* (98)	146	0.084	5000	0.016
Doryphora sassafras (76) – *Sarcopteryx stipata* (86)	143	0.053	1000	0.20
Doryphora sassafras (76) – *Polyosma cunninghamii* (198)	238	0.059	5000	0.035
Doryphora sassafras (76) – *Orites excelsa* (112)	164	0.067	5000	0.048
Orites excelsa (112) – *Sloanea woollsii* (98)	174	0.042	1000	0.25
Orites excelsa (112) – *Sarcopteryx stipata* (86)	165	0.020	1000	0.73
Orites excelsa (112) – *Polyosma cunninghamii* (198)	245	0.026	1000	0.41
Polyosma cunninghamii (198) – *Sloanea woollsii* (98)	248	0.014	1000	0.78
Polyosma cunninghamii (198) – *Sarcopteryx stipata* (86)	227	0.020	1000	0.64
Sarcopteryx stipata (86) – *Sloanea woollsii* (98)	157	0.039	1000	0.37

It should be noted, however, that the statistical power of the randomization tests used to analyse differentiation with respect to tolerance of the disturbance associated with crown zones was lower than for the other analyses because of the smaller number of quadrats involved.

Pairwise comparisons of the abundance of these species at different points along the percentage-sky-visible gradient only indicated significant ecological differentiation between *Sarcopteryx stipata*, a species that exhibits a high degree of shade specialization, and two species that are known to be more abundant at intermediate light levels, *Sloanea woollsii* and *Orites excelsa* (Penfold 1996).

Comparisons between the five species selected for detailed analysis suggest that a factor associated with soil pH may define an important niche axis and we were able to reject the hypothesis of ecological equivalence in 6 out of the 10 possible pairwise comparisons. Comparisons of species along the PO_4-P and NO_3-N gradients suggest that these may be less important for co-existence. For the PO_4-P gradient we were able to reject the hypothesis of ecological equivalence in only one of the pairwise comparisons. This is comparable to the number obtained for the gradient of per cent sky visible. The hypothesis of ecological equivalence was accepted for all 10 pairwise comparisons of species distributions along the NO_3-N gradient.

The spatial variation in soil pH is most probably caused by trees being uprooted during windstorms and bringing subsoil to the surface. Unpublished data show that pH declines rapidly with soil depth in this forest. However, we do not know the factor associated with soil pH that might be responsible for the observed differences between species. Sollins (1998) has identified aluminium, which increases in availability at low pH, as being one of the soil factors most likely to influence the composition of tropical lowland rain forest. Whilst aluminium toxicity might influence the distribution of some of the species at Gambubal, the five species selected for pairwise comparisons were all apparently tolerant of low pH. Rather, they differed in their abundance in quadrats at the higher end of the pH gradient. Potential factors that might lead to an apparent intolerance of areas of high pH include iron availability. The availability of iron (and other micro-nutrients such as zinc and manganese) is generally greater between pH 4 and pH 6 than it is at higher pH levels, and this may limit the growth of susceptible species in soils above pH 6 (Troeh & Thompson 1993).

The demonstration of relationships between juveniles and edaphic factors is an important step towards understanding the co-existence of rain-forest tree species. However, we accept that experimental studies will be needed to confirm that these relationships represent the influence of soil factors on juvenile distributions and not the influence of juveniles on soil conditions. A range of studies have demonstrated that standing vegetation can influence soil properties both through root activity and the decomposition of leaf litter (Gibson 1988, Grubb *et al.* 1969, Jarvis & Duncan 1976, Leeper & Uren 1993, Pigott

1970, Zinke 1962). However, we would argue that in rain-forest communities the impact of mature trees on soil conditions might be much greater than the impact of juveniles.

Another potential problem with observational studies such as ours is that for many species the juveniles are likely to be clumped around adult trees. Poor dispersal, in association with broad-scale environmental gradients and patchy adult tree distributions, could produce the appearance of environmental specializations in the juveniles, even where none exist. In the current study we consider this to be unlikely. We have found no evidence of significant environmental gradients across the study area (Penfold 1996). Moreover, although at a broader scale many tree species had adults which showed some degree of clumping, adults of the five species used in the detailed comparisons were all widely distributed across the area in which the juveniles were surveyed (Penfold 1996).

In this study we have analysed the distribution of tree species along five potential niche axes: gap microsites, light availability, soil pH, PO_4-P availability and NO_3-N availability. What is the combined evidence from these analyses that the tree species at Gambubal are ecological equivalents? Of the ten pairwise comparisons that can be made between the five species selected for detailed comparisons, only three species pairs (*Doryphora sassafras* – *Sloanea woollsii*, *Orites excelsa* – *Polyosma cunninghamii* and *Sarcopteryx stipata* – *Polyosma cunninghamii*) were found to be undifferentiated along all of the five environmental gradients (with $\alpha = 0.005$). However, the first of these species pairs showed some indication that the species might be differentiated along the gradient of NO_3-N or in their ability to tolerate the disturbance associated with the crown zones of treefall gaps. The second pair (*Orites excelsa* – *Polyosma cunninghamii*) showed some evidence for differentiation along the PO_4-P gradient ($P = 0.008$). All of the other species pairings indicated some degree of differentiation between the species along at least one of the gradients, and some (such as *Doryphora sassafras* – *Orites excelsa* and *Sloanea woollsii* – *Sarcopteryx stipata*) were differentiated along two of the five gradients.

We must exercise some caution in interpreting these results because the pairwise comparison of five species along five environmental gradients requires 50 statistical tests, some of which will be expected to appear statistically significant by chance alone. To maintain an experimentwise alpha level of 0.05 we can apply a Bonferroni correction (Sokal & Rohlf 1995) and use an alpha level of 0.001 for individual tests. This is likely to result in an unduly conservative test with an increased probability of making Type II errors, i.e. concluding that species are undifferentiated when in fact they are. However, even at this alpha level, six of the ten possible pairwise comparisons showed evidence for differentiation between the species. Overall, the evidence suggests that the five species selected for detailed pairwise comparisons showed a high level of differentiation along the environmental gradients we investigated. This result is particularly significant given that the five species also showed a relatively high level of interspecific association. We would expect the level of differentiation between positively associated species to be lower than the level of differentiation found in the community as a whole.

The role of niche differentiation in rain-forest tree co-existence

Our results suggest that niche differentiation amongst juveniles may have an important role to play in the co-existence of rain-forest tree species. Rather than finding undifferentiated generalist species as predicted by Hubbell & Foster (1986*a*, *c*) our investigation has revealed that the majority of the more common tree species at Gambubal show evidence for a high degree of ecological differentiation. Hubbell & Foster (1986*c*) provided a two-way classification of species at Barro Colorado Island based on their gap regeneration requirements and their habitat (e.g. topographic) specializations. Our study has shown that this scheme is inadequate to describe the level of differentiation occurring between species at Gambubal. We have demonstrated that species with similar gap requirements can exhibit fine-scale differentiation along edaphic gradients, even in an area with a uniform soil type and topography. For example, *Sloanea woollsii* and *Orites excelsa* were completely undifferentiated with respect to their distributions along a gradient of per cent sky visible, but were significantly differentiated along the pH gradient. Our conclusion, that fine-scale edaphic gradients need to be taken into account when defining the niches of rain-forest tree species supports the results of Davies *et al.* (1998) who found differentiation between sympatric *Macaranga* species in their distributions along a soil-texture gradient.

Although we have made some progress towards determining the extent of niche differentiation among the rain-forest trees at Gambubal, there are several ways in which we could improve on our characterization of niches, and there are a number of other questions that remain unresolved. Firstly, we have concentrated exclusively on the role of spatial environmental heterogeneity in defining plant niches. A more complete characterization of niches would need to include some consideration of species-specific responses to environmental fluctuations over time, for example asynchrony in the regeneration of species in relation to short-term (1–10 y) climatic variation (Chesson 1986, Chesson & Warner 1981, Shmida & Ellner 1984). In addition, we were only able to assess the role of a very small number of edaphic gradients in the current study and clearly it would be useful to investigate other potential spatial niche axes to determine the extent of differentiation between species. The endless search for additional niche dimensions has attracted criticism (Mahdi *et al.* 1989, Silvertown & Law 1987). However, we would argue that our understanding of species co-existence is unlikely to progress without studies of species differentiation along environmental gradients. Moreover, these studies should try to maximize the number of environmental gradients and the number of species studied. There are a number of potential niche axes that we were unable to incorporate into the current study, but which have been shown to be significant in other studies in a range of plant communities. Two of particular interest are the role of soil moisture availability (Grubb 1984) and litter depth (Molofsky & Augspurger 1992, Sydes & Grime 1981).

The accuracy of the species–environment relationships observed in the current study was constrained by the use of quadrat-based sampling. The light and soil environment of 1-m^2 quadrats is not uniform, and individuals within the quadrats are likely to experience slightly different growing conditions. A more accurate method of characterizing species–environment relationships would be to use individual seedlings as sampling points. Such an approach would also have the advantage of allowing uncommon species to be targeted – a group of species for which we currently have little information.

To fully assess the role of niches in species co-existence we need to be able to evaluate the realized niche of each species, that is the environmental conditions to which the species is restricted through interactions with other species (Hutchinson 1957). Moreover, we need to characterize the realized niche of each species separately for each of the species with which we wish to compare it. The characterization of species niches by determining their distributions along environmental gradients falls short of achieving this. Rather, the resulting definition is likely to be intermediate between the fundamental niche and the realized niches – individuals might persist in areas outside of the species' realized niche simply because they have not encountered potential competitors. It is possible, therefore, that in some cases our results may have over-estimated the degree of overlap between species niches.

A more serious criticism of the current study is that although we have demonstrated variation in the balance between species abundances along various environmental gradients (and therefore that they are not ecologically equivalent in the strict sense), we have not demonstrated that each species has an area of the environmental gradient in which it will be more likely to recruit than the other species. Although information from static distributions can provide a basic index of recruitment probability (Condit *et al.* 1992) it cannot take into account subsequent differences between species in growth or mortality rates, and data from repeated censuses provide a much more reliable measure of recruitment. A consideration of each of the above points suggests that subsequent studies of ecological equivalence/niche differentiation should aim to determine the fate of individuals of each species, growing in contrasting environments, and both alone and in the presence of a range of potential competitors.

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