Habitat niche partitioning by 16 species of Myristicaceae in Amazonian Ecuador

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Abstract The distribution and spatial pattern of
plants in tropical forests have important implications
for how species interact with each other and their
environments. In this article we use a large-scale
permanent census plot to address if the coexistence of
16 co-occurring species of Myristicaceae is aided by
topographic and light gradient niche partitioning. We
used a second order spatial pattern analysis based on
Ripley's K function to describe species' distributions
and associations among species, and a torus transla-
tion procedure to test for associations with three
topographically defined habitats. A majority of
species displayed spatial aggregation and over half
had one or more significant habitat associations. Four
species were associated with the ridge habitat, four
species with slope habitat, and two with valley

habitat. Seven other species showed no habitat
association. Within each habitat group, species
exhibited a variety of distributions in relation to light
availability. However, habitat associations were
largely unexplained by differential rates of mortality,
growth or recruitment over a 5-year interval. We
conclude that although in principle partitioning of the
topographic and light environments may double or
treble the number of species able to coexist, there is
no evidence that partitioning of physical habitats can
explain the coexistence of all 16 of these closely
related species.

Keywords Coexistence · Lowland tropical rain
forest · Species diversity · Yasuní

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Introduction

The lowland tropical rain forests of western Amazo-
nia are among the most diverse plant communities in
the world (Gentry 1982; Valencia et al. 1994; Balslev
et al. 1998). Exploring the mechanisms that explain
the presence of >300 species of tree ha^{-1}, and govern
their distributions over much larger areas has been a
key question in tropical forest ecology for the last two
decades (Gentry 1982; Hubbell 2001; Losos and
Leigh 2004). Attempts to understand the relative
importance of niche differentiation for species coex-
istence have motivated many of these studies
(reviewed by Grubb 1977; Wright 2002), including

several studies of the relationship between plant distribution and physical environmental factors in the western Amazon (e.g. Tuomisto et al. 2003). The abiotic factors that potentially influence species coexistence and distributions include soil chemistry, water availability, topography and light availability; uncoupling these factors and their associated spatial autocorrelation entails careful analyses.

The well-documented contrast in light availability among patches at different successional stages may permit the coexistence of groups of species defined by differential shade tolerance at the seedling stage (Denslow 1987; Clark and Clark 1992). However, the patterns of differentiation of species with respect to soil-borne resource availability and topography are less well known. Examples of clear habitat associations linked to topography have been demonstrated for tree communities in Central America (Clark et al. 1999; Harms et al. 2001; Pyke et al. 2001). In contrast, the majority of lowland Amazonian 'terre firme' forest exists on un-flooded non-podsolised soils and beta-diversity over large areas of forest appears remarkably low (Pitman et al. 1999, 2001). Within this broad forest type, however, species associations with minor variation in topography and soils are apparent (Phillips et al. 2003). Significant non-random distribution of stem density with respect to two or three microhabitats has been demonstrated for 25% of the tree species ≥ 1 cm dbh occurring on a large permanent plot in western Amazonia (Valencia et al. 2004a) and for palms, pteridophytes and species of the Melastomataceae in similar forest (Svenning 1999; Duque et al. 2002; Tuomisto et al. 2002, 2003). However, these studies are correlative and provide no mechanistic understanding of the factors influencing the spatial distributions of tropical trees. A more comprehensive understanding of habitat-related spatial aggregation in tropical tree communities would require evidence that species have improved growth and/or survival in the habitat in which they are aggregated (e.g. Russo et al. 2005).

Although the availability of light and soil-borne resources are known to influence the growth and survival of tropical forest trees, they are usually considered in isolation and by different authors. In order to provide context for recent articles examining seeding dynamics and flowering frequency in the Myristicaceae (Queenborough et al. 2007; in press), we here examine patterns of spatial distribution and

habitat association with respect to both factors for 3,351 individuals of 16 species of Myristicaceae on a permanent large-scale mapped forest plot in a seasonal lowland *terre firme* rain forest in Amazonian Ecuador. We then determine if growth, mortality and recruitment rates over 5 years varied among habitats and thus provide mechanistic explanations for species—habitat associations. We address the following specific questions:

1. Do species of Myristicaceae have aggregated spatial distributions?
2. Do species of Myristicaceae show habitat associations?
3. How important are differences in habitat-specific growth, mortality and recruitment rates in explaining these associations?

Finally, we discuss how habitat associations may limit abundance and promote species coexistence.

Methods

Study site

Yasuní National Park and Biosphere Reserve and the adjacent Huaorani Ethnic Reserve cover 1.6 million ha of forest and form the largest protected area in Amazonian Ecuador. Within the Park, extensive oil reserves are ceded for prospecting and exploitation. Human influences are currently sparse but increasing; currently <3,000 Huaorani indigenous people live in the region, and road and oil sites are localised. Most of the Park is undisturbed wilderness covered by unbroken forest. The Park is nearly level at about 200 m a.s.l., but is crossed by numerous ridges rising 25–40 m above the intervening streams. At wider intervals, large rivers flow east to meet the Napo and Amazon. The canopy is 10–25 m high but punctuated with emergents to 40 and rarely 50 m tall. Rainfall and temperature are aseasonal at Yasuní (Valencia et al. 2004b). The mean annual rainfall is 2,800 mm, and mean monthly rainfall is almost never <100 mm. Mean monthly temperature is 25–27°C.

A 50-ha permanent forest dynamics plot (FDP) is located inside the park (0°41′ S, 76°24′ W), just south of the Tiputini River. It is within 1 km of the Yasuní Research Station of the Pontificia Universidad Católica del Ecuador (Valencia et al. 2004b). There are a

few Huaorani settlements on an oil access road north of the station, and low-intensity hunting occurs near the research station and inside the plot. The 50-ha plot ranges from 216 to 248 m a.s.l: it includes three ridges and an intervening valley that occasionally floods for brief periods.

Plot establishment and measurements

The FDP was fully surveyed in 1995. Between June 1995 and June 2000, all freestanding stems ≥ 1 cm dbh (1.3 m), excluding lianas, were tagged, mapped, and identified to morphospecies in the western half of the 50 ha (Valencia et al. 2004b). All stems ≥ 10 cm dbh were tagged, mapped, and identified in the eastern 25 ha. A second census was undertaken from January 2003 to June 2004. All living stems were re-measured and new recruits mapped, tagged and identified. We used data for the Myristicaceae from both censuses.

Between January 2002 and January 2003 all Myristicaceae stems ≥ 10 cm dbh (for the genus *Iryanthera* stems ≥ 1 cm dbh) were visited and the crown illumination index (CII, Clark and Clark 1992) recorded. CII quantifies the light available to a tree by estimating the exposure of the crown on a scale of 1–5: no vertical light and minimal lateral light (1), no vertical light and medium lateral light (2), crown exposed to some vertical and some lateral light (3), crown exposed to vertical and some lateral light (4), crown completely exposed vertically and laterally (5), CII correlates with canopy openness values obtained from hemispherical photographs (Davies et al. 1998) and is a rapid and repeatable way of estimating light availability on tree canopies (Keeling and Phillips 2007).

Study species

The Myristicaceae is a pan-tropical family and an important component of Amazonian lowland forests (Pitman et al. 2001). It is suitable for investigation of the mechanisms of species coexistence, because large numbers of closely related species of Myristicaceae typically co-occur at one site, and include both rare and abundant species with diverse growth forms and life histories. On the Yasuni FDP, it is ranked tenth in terms of basal area (Valencia et al. 2004b), and a total of 3,351 stems were enumerated in the first plot

census. Habit ranges from understorey to canopy and emergent tree. All members of the family are dioecious, except some species of *Iryanthera* that are monoecious (Smith 1937; Queenborough et al. 2007), and floral morphology in the Myristicaceae conforms closely to the syndrome of dioecy in tropical trees (Bawa and Opler 1975; Bawa 1980). The fruits are woody capsules, each containing a single arillate seed, which are dispersed by various monkeys (*Alouatta seniculus*, *Ateles beelzebuth*, *Lagothrix lagotricha*, *Pithecia monochus*), toucans (*Ramphastos tucanus*), guans (*Penelope jacquacu* and *Pipile pipile*) and motmots (*Baryphthengus martii*) (Howe 1983; Roosmalen et al. 1996; DiFiore and Link pers. comm. 2004; Queenborough unpublished).

Sixteen species in four genera of Myristicaceae co-occur in the Yasuní FDP: *Compsoneura capitellata* (A.DC.) Warb., *C. sprucei* (A.DC.) Warb., *Iryanthera grandis* Ducke, *I. juruensis* Warb., *I. hostmannii* (Benth.) Warb., *Otoba glycycarpa* (Ducke) W.A. Rodrigues & T.S. Jaram., *Virola dixonii* Little, *V. duckei* A.C.Sm., *V. elongata* (Benth.) Warb., *V. flexuosa* A.C.Sm., *V. mollissima* (A.DC.) Warb., *V. multinervia* Ducke, *V. obovata* Ducke, *V. pavonis* (A.DC.) A.C.Sm., *V.* 'microfuzzy', *V.* cf. *calophylla*. Nomenclature follows Rodrigues (1980). A complete set of collections from the plot is held in the Herbarium of the Pontificia Universidad Católica del Ecuador, Quito.

Data analysis

Total abundance of a species was defined as the number of individuals ≥ 1 cm dbh in the western half of the plot (the eastern half was only censused to 10 cm dbh). The frequency of 20 m × 20 m subplots in which a species occurred assessed the extent of its distribution, and was expressed as a percentage of all subplots ($N = 625$). We also calculated median and maximum density in the subplots. Using these four measures one can distinguish among widespread but rare species, and locally common but spatially restricted species, both of which may have equal total abundance within the plot.

The spatial distribution of individuals of each species was tested for non-randomness with a method of univariate second-order spatial pattern analysis based on Ripley's K function, corrected for edge

effects (Ripley 1976). Methods were implemented using SPPA 2.0.3 (Haase 1995). $K(d)$ was calculated separately for each distance d from 0 to 250 m in 5-m increments. The test statistic used was $L(d) = \sqrt{[(K(d)\pi) - d]}$ and results are displayed as a plot of $L(d)$ vs. d. To test for significant deviance away from a random distribution, Monte Carlo computer-generated data were used to construct a 99% confidence envelope for comparison to the sample statistic. A sample statistic that exceeded the confidence envelope was inferred to show an aggregated distribution if positive and a regular or over-dispersed distribution if it was negative. Values of $L(d)$ that remained within the confidence envelope showed that individuals were distributed randomly. One analysis was run for each species, for all individuals ≥ 1 cm dbh on the western 25 ha of the FDP.

A similar method of analysis was used to test for spatial association among the distributions of each pair of species using a bivariate form of Ripley's K. When $L(d)$ exceeded the confidence envelope with positive values the distributions were inferred as significantly associated, and with negative values were inferred as significantly complementary. The number of significant inter-specific interactions was summed for each species.

Annual growth rates were calculated as

$$[\text{dbh}_1 - \text{dbh}_0]/[\text{time}_1 - \text{time}_0]$$

where subscripts 0 and 1 refer the initial and re-census respectively.

The annual mortality rates were calculated as

$$1 - [1 - (N_0 - S)/N_0]^{1/t}$$

where N_0 is the number of individuals alive in the first census, S is the number of surviving individuals of N_0 in the second census, and t is the mean census interval (in years) for all N_0 individuals (Sheil et al. 1995). *Virola obovata* and *V.* cf. *calophylla* were combined in this analysis as individuals died before correct determination could be made. The confidence limits for the number of survivors were calculated by assuming a binomial distribution around S survivors out of N_0 individuals.

Annual recruitment rates were calculated as

$$1 - (1 - n_r/N_1)^{1/t}$$

where N_1 is the number of stems at the end of interval, and n_r is the number of recruits. Recruitment represents growth of pre-existing plants <1 cm dbh, rather than growth of newly germinated seedlings.

Habitat associations were calculated using a randomisation method to account for spatial autocorrelation in stem distributions (Harms et al. 2001; Debski et al. 2002). Habitats were defined with topographic information only and were based on elevation estimated at each point on a 20 m × 20 m grid by the survey team. Quadrats were placed into one of three topographic habitats, splitting the plot around median values of elevation and slope and around zero convexity (Valencia et al. 2004a):

– valley (slope < 12.8°, elevation < 227.2 m);
– slope (slope $\geq$ 12.8°, elevation < 227.2 m, or slope $\geq$ 12.8°, elevation $\geq$ 227.2 m, convexity < 0);
– ridge (slope $\geq$ 12.8°, elevation $\geq$ 227.2 m; convexity > 0, or slope < 12.8°, elevation $\geq$ 227.2 m, convexity > 0).

The torus-translation procedure consisted of generating a null distribution of stem densities in each habitat by shifting the true habitat map about a two-dimensional torus by 20-m increments in the four cardinal directions. For the tests of association, each simulated map was overlain by the observed distributions of trees and the relative density of each species was calculated for each habitat. Evaluation of these maps gave frequency distributions of relative-density estimates for each species. For further details of this method and an illustration of the distributions of habitats in the Yasuní FDP see Harms et al. (2001) and Valencia et al. (2004a). Torus-translation procedures were carried out for all trees $\geq$ 1 cm dbh within the western 25 ha.

We examined differences in light environments by calculating the percentage of stems in each CII class for each species. Differences among species were compared using a Kruskal–Wallis test.

In order to test whether differences in the spatial distributions of species could be explained by differential growth, mortality or recruitment rates, we examined differences in these rates among the three habitat types. For growth we used analysis of covariance (ANCOVA) in which annual growth rate

in mm year^{-1} was the response variable and the explanatory variables were species, habitat (categorical: ridge/slope/valley), CII (categorical) and initial dbh (continuous). For mortality we used logistic ANCOVA where the response variable was binary (either alive or dead) with the same explanatory variables. The ANCOVA tested the null hypotheses that (i) accounting for differences in dbh, trees in different habitats had equal mean growth/mortality rates, and (ii) the relationship between growth/mortality rate and dbh were equal among habitats (i.e. there was no interaction among habitat and dbh).

We tested the association of new recruits with habitats and female trees using a randomisation approach. We allocated each recruit to either (i) a random quadrat in the FDP, or (ii) a random conspecific female. We then calculated the number of recruits per female in each of the three habitat types. We repeated this procedure 1,000 times, and compared the distribution of ratios with that of the true recruit:female ratio. This test evaluated the null hypotheses (i) that recruitment per unit ground area was equal among habitats and (ii) that recruitment per female tree was equal among habitat types.

Results

Species abundance and clumping

The abundance of Myristicaceae species on the 25 ha plot ranged from only 23 individuals of *Virola multinervia* to 838 of *Iryanthera hostmannii* (Table 1). There was no marked local (i.e. subplot) clustering of stems (all species except *I. hostmannii* had a median subplot density of one) and common species were spread throughout the plot, with high percentage abundance relative to rare species. However, the more abundant species occurred in larger groups than less abundant species.

There was marked variation in the spatial structure of species populations on the plot (Table 2). Eight out of the 16 species (7–8 and 10–15, Table 2) displayed little or no spatial pattern at all spatial scales. All were in the genus *Virola* and ranged in abundance from 23 to 212 individuals. Three species showed some degree of aggregation at nearly all spatial scales (3–4 and 16, Table 2). The remaining five species

were aggregated at small to medium spatial scales (5–100 m) but became random or over-dispersed at larger spatial scales. Interestingly, four of the species showing aggregation were randomly distributed at very small spatial scales (5–30 m) (1–3 and 9, Table 2).

Species and habitat associations

Using the bivariate Ripley's K analysis, we identified the number of significant pair-wise associations for each species (Appendix 1). *Virola* cf. *calophylla* had nine significant associations with other species out of a potential 15. Two of these were positive and seven were negative. The remaining species had fewer significant associations. Four species had only one association, and *V. flexuosa* had no significant pair-wise associations. Pair-wise comparisons of *Compsoneura capitellata*, *C. sprucei*, *Iryanthera hostmannii*, *I. juruensis* and *Virola elongata* generally showed positive association at distances <150 m, but were complementary at distances >180 m.

Sixteen significant ($p < 0.05$) topographical habitat associations (seven negative and nine positive) out of a possible 48 were found for stems ≥ 1 cm dbh among the 16 species and three habitats (Table 3). Two species had significant complementary associations with all three habitats: *Compsoneura capitellata* was positively associated with ridge habitat and negatively with slope and valley habitat and *Otoba glycycarpa* was negatively associated with ridge and positively with slope and valley. *Iryanthera juruensis* was significantly negatively associated with valley and slope and marginally significantly associated with ridge habitat. *Otoba glycycarpa* was the only species to have a positive association with two habitats. Seven species showed no significant habitat associations at all. For each habitat, we found 6–7 significant or marginally significant associations. Four species were negatively associated with valley, and two positively; four species were positively associated with slope habitat, and two species negatively; and two species were positively associated with ridge habitat (two others marginally significantly so) and one species had a negative association (two others marginally significantly so).

Comparing species associations and habitat associations (Table 4) we found that species with many significant species associations (Groups A and B)

Table 1 Size distributions and abundance data for all 16 species of Myristicaceae occurring on 25 ha of the Yasuní FDP

Species	FDP species code	Size class (dbh)			Total abundance	Deaths	Frequency (%)	Subplot density	
		1–10 cm	10–30 cm	30+ cm				median	max
Otoba glycycarpa	otobgl	170	117	86	373	41	41.6	1	5
Compsoneura capitellata	compca	75	35	0	110	4	15.4	1	3
Compsoneura sprucei	compsp	38	6	0	44	1	6.4	1	2
Iryanthera grandis	iryagr	37	21	3	61	5	8.8	1	2
Iryanthera juruensis	iryaju	128	8	0	136	11	15.5	1	4
Iryanthera hostmannii	iryaho	832	6	0	838	40	66.7	2	9
Virola dixonii	virodi	65	9	0	74	2	10.4	1	2
Virola duckei	virodu	58	40	25	123	11	18.1	1	3
Virola elongata	viroel	65	9	4	78	10	10.6	1	4
Virola flexuosa	virofl	48	20	7	75	5	11.5	1	2
Virola 'microfuzzy'	viromi	58	7	6	71	4	10.7	1	2
Virola mollissima	viromo	43	6	3	52	3	7.8	1	2
Virola multinervia	viromu	19	4	0	23	1	3.5	1	1
Virola obovata	viroob	65	17	1	83	*	12.5	1	2
Virola pavonis	viropa	150	46	16	212	10	29.4	1	3
Virola cf. *calophylla*	viroca	199	15	10	224	31*	25.8	1	4

Subplots are 20 × 20 m (N = 625). Subplot density values are for each species within a subplot. Deaths is the number of indivduals that died in the inter-census interval. Frequency is the proportion of subplots in which the species occurs

V. obovata and *V.* cf *calophylla* data for mortality are grouped together

Table 2 Results of univariate Ripley's K spatial pattern analysis of stems ≥ 1 cm dbh of 16 species of Myristicaceae on 25 ha Yasuní FDP

Species	Spatial pattern			L(d)		
	aggregated	random	over-dispersed	d = 5	Intermediate max. or min.	d = 250
1. *Compsoneura capitellata*	15–140	5–10; 145–190	195–250	−1.4	13.9	−13.2
2. *Compsoneura sprucei*	35–80	5–30; 85–250	–	−5.0	17.0	1.8
3. *Iryanthera grandis*	20–250	5–15	–	1.5	51.1	36.9
4. *Iryanthera juruensis*	5–225	230–250	–	2.8	34.4	−1.3
5. *Iryanthera hostmannii*	5–160	165–180	185–250	1.3	5.8	−9.3
6. *Otoba glycycarpa*	10–90	95–250	–	0.6	3.3	0.8
7. *Virola dixonii*	5–15	20–250	–	7.1	−3.3	5.6
8. *Virola duckei*	–	5–250	–	2.2	3.6	−2.2
9. *Virola elongata*	20–155	5–15; 160–215	220–250	5.2	21.0	−20.6
10. *Virola flexuosa*	–	5–250	–	−5.0	–	7.2
11. *Virola* 'microfuzzy'	105–145	5–100; 150–250	–	0.6	13.6	9.0
12. *Virola mollissima*	–	5–50; 70–250	55–65	−5.0	−10.4	−4.3
13. *Virola multinervia*	–	5–250	–	−5.0	17.0	−8.5
14. *Virola obovata*	–	5–250	–	−0.2	4.2	−2.7
15. *Virola pavonis*	–	5–250	–	−1.2	3.0	0.9
16. *Virola* cf. *calophylla*	5–250	–	–	3.1	21.6	16.3

Values show the distances over which aggregated, random or over-dispersed distributions were found. Range values of L(d) over d (distance from focal individual) indicated (from minimum to maximum d, with any intermediate peak); d = 0–250 m

Table 3 Habitat associations and densities in three habitats for stems ≥ 1 cm dbh of 16 species of Myristicaceae on the Yasuní 25 ha FDP, using a torus translation procedure

Species	Valley		Slope		Ridge		Total N
	density ha^{-1}	p	density ha^{-1}	p	density ha^{-1}	p	
1. *Compsoneura capitellata*	0.01	−−	0.04	0	0.12	++	109
2. *Compsoneura sprucei*	0.00	−	0.02	0	0.05	0	45
3. *Iryanthera grandis*	0.01	0	0.05	++	0.03	0	61
4. *Iryanthera juruensis*	0.01	−−	0.03	−−	0.18	++	136
5. *Iryanthera hostmannii*	0.29	0	0.40	0	0.66	0	839
6. *Otoba glycycarpa*	0.18	++	0.24	++	0.18	−−	372
7. *Virola dixonii*	0.03	0	0.04	0	0.04	0	74
8. *Virola duckei*	0.03	−	0.09	++	0.08	0	125
9. *Virola elongata*	0.03	0	0.03	0	0.08	0	89
10. *Virola flexuosa*	0.05	+	0.03	0	0.04	0	75
11. *Virola* 'microfuzzy'	0.04	0	0.04	0	0.04	0	78
12. *Virola mollissima*	0.02	0	0.04	0	0.03	0	52
13. *Virola multinervia*	0.00	0	0.00	−	0.03	+	23
14. *Virola obovata*	0.03	0	0.06	+	0.05	0	83
15. *Virola pavonis*	0.10	0	0.10	0	0.14	0	211
16. *Virola* cf. *calophylla*	0.07	0	0.11	0	0.18	0	224

Habitats follow combined habitats of Valencia et al. (2004a). N = number of stems within habitat type. Associations are positive (+), negative (−) or absent (0): +/− $p < 0.05$, ++/−− $p < 0.01$

Table 4 The relationship between species associations (bivariate Ripley's K, Appendix 1) and habitat associations (torus translation procedure, Table 3) for 16 species of Myristicaceae on the Yasuní FDP

Habitat associations (significant or marginally significant positive associations)	Species associations [number of significant associations]				
	Group A (widely associated species) [9]	Group B (strongly associated species) [4-6]	Group C (weakly associated species) [2-3]	Group D (very weakly assocated species) [1]	Group E (not associated with other species) [0]
Ridge species	–	iryaju (136) compca (110) compsp (44)	viromu (23)	–	–
Slope species	–	–	virodu (123) viroob (83) iryagr (61)	otobgl (373)	–
Valley species	–	–	–	otobgl (373)	virofl (75)
No speciality (not +ly associated with one of 3 habitats)	viroca (224)	iryaho (838) viroel (78)	viromi (71)	viromo (52) viropa (212) virodi (74)	–

Numbers after species codes indicate number of stems ≥ 1 cm dbh on the 25 ha FDP

tended to be associated with ridges or were common widespread species. Species with few species associations (Groups C, D and E) preferred valley or slope habitats or were less common widespread species. Pair-wise species associations among specialists of different habitats were negative or showed no associations. Ridge specialists were generally positively associated with each other, but the few species associations present among slope and valley specialists were generally negative.

Canopy light environment

In all species, most individuals were in CII class 3 or lower, but a higher proportion were in CII classes 1 and 2 for subcanopy species such as *Iryanthera hostmannii* and *I. juruensis* than canopy species such as *Virola duckei* and *V. multinervia*. Both mean CII (range 1.5–3.3) and the proportion of trees in each CII class varied significantly among species (Fig. 1, Kruskal–Wallis test: $p < 0.001$), although each species occurred in at least three classes.

Effects of light availability and habitat on growth, mortality and recruitment

There was no effect of topographic habitat, light availability or tree size on mortality of trees between the period of the two plot censuses (Table 5, see Table 1 for numbers of trees that died). Growth rates of individuals, however, depended on species and amount of light received. When we accounted for tree size, individuals of different species, in different habitats and/or different CII classes showed significant differences in growth rates, and there were also significant interactions among species, habitat and light availability. Species in different habitats and CII classes had significantly different growth rates.

Topographic habitat was also a significant factor in the recruitment rates of five species. Three species had significantly different numbers of recruits per unit ground area than expected (Table 6, Method 1). Both *Iryanthera hostmannii* and *Virola elongata* had more recruits per unit area in ridge habitat; *I. hostmannii* also had fewer recruits per unit area in valley and slope habitats. *Virola* 'microfuzzy' had more recruits in valley habitat and less in slope habitat.

Eight species had significantly different numbers of recruits per female than expected among habitats (Table 6, Method 2). In three rare species (*Compsoneura sprucei*, *Iryanthera grandis* and *I. juruensis*), females were only present in one habitat type, but there were no recruits in this habitat—all recruitment occurred in a different habitat. In three other species (*Virola. elongata*, *V.* 'microfuzzy' and *V. obovata* cf. *calophylla*), recruitment per female was less than expected in ridge habitat, and in two species (*V.* 'microfuzzy' and *Otoba glycycarpa*), recruitment per female was greater than expected in valley habitat. *Iryanthera hostmannii* had fewer recruits per female in slope habitat and more recruits per female in ridge habitat. Curiously, *Virola elongata* in ridge habitat showed a higher recruit:female ratio, but fewer recruits per female than expected.

Discussion

Abundance and spatial distribution

Most tropical tree species populations have aggregated or random distributions (Connell et al. 1984; He et al. 1996; Condit et al. 2000; Debski et al. 2000, 2002). This study provides further evidence of clumping over at least some spatial scales for 11 out of the 16 Myristicaceae species. Evidence of a regular, or over-dispersed distribution was found for only four species, and in three of these a regular distribution was noted only at distances >180 m, below which they were aggregated. These results imply that clumps of these species were over-dispersed, and are likely to be correlated with the two ridge systems at the northern and southern ends of the plot. Aggregated distributions can be caused by many factors. For the Myristicaceae, clumped seed dispersal by toucans and primates is the most likely explanation (Howe 1993; Russo and Augspurger 2004).

Associations with habitat variables such as topography (Newbery et al. 1996; Harms et al. 2001), soil nutrients (Gartlan et al. 1986), light (Lieberman et al. 1995), or interactions of all three (e.g. Palmiotto et al. 2004) can also lead to patchy or restricted distributions. For example, *Virola surinamensis* on Barro Colorado Island, Panama (BCI) is strongly positively associated with moist slopes and streamsides (Fisher
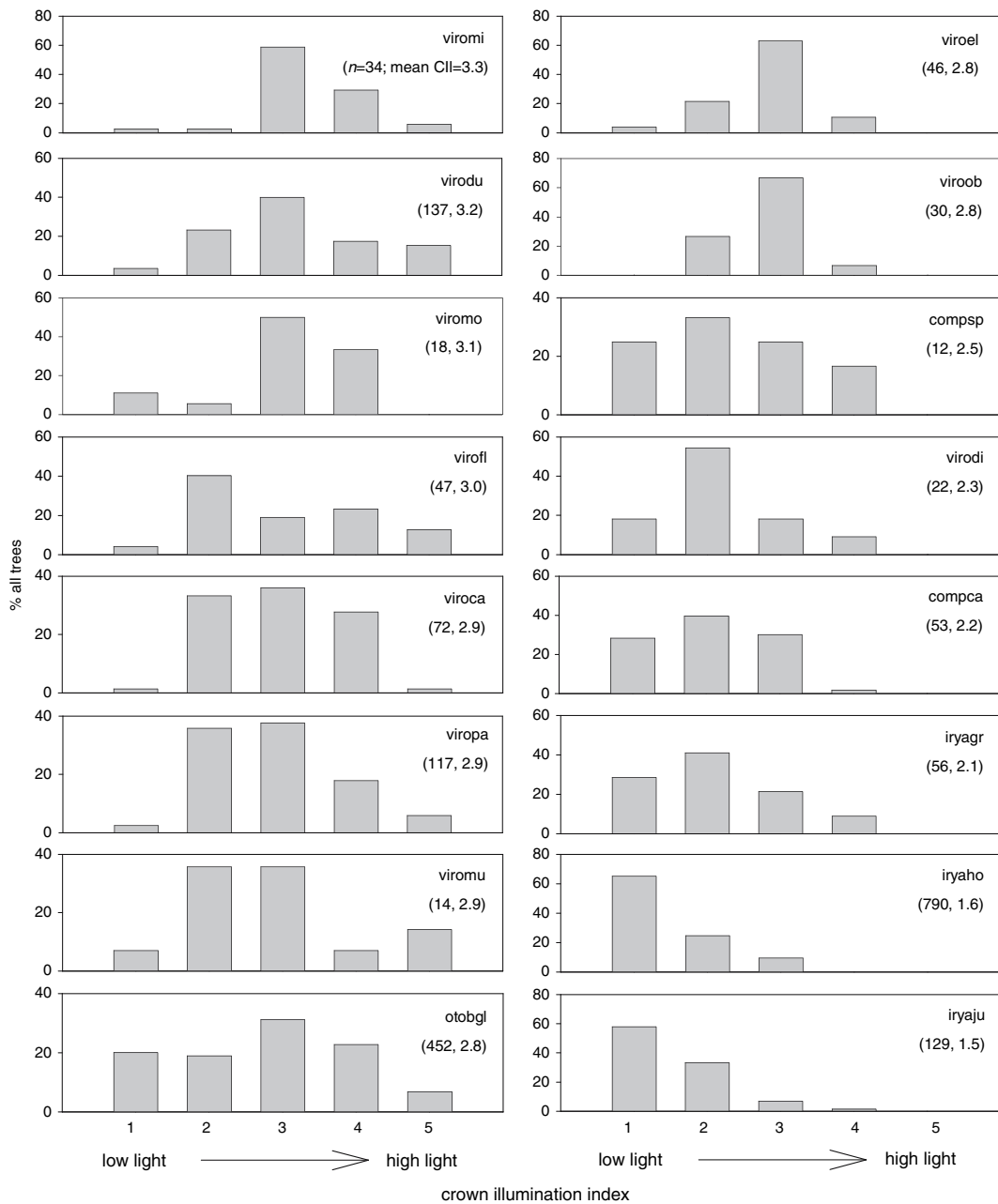
Fig. 1 The percentage of individuals occurring in each of five crown illumination index (CII) classes for 16 Myristicaceae species on the Yasuni FDP. Species are arranged in decreasing order of CII, with sample size for CII estimates and mean CII in parentheses

et al. 1991; Howe 1990; Harms et al. 2001). However, water availability may be less likely to influence *terre firme* species distributions in aseasonal forests such as Yasuní compared to seasonal ones such as BCI.

At least one significant habitat association, however, was found for half the Myristicaceae species studied at Yasuní. This frequency is lower than for the whole tree community on BCI, where

Table 5 The effects of topographic habitat, light availability and tree size on annual growth rates and mortality in 16 species of Myristicaceae on the Yasuní FDP

Model parameter	(i) Growth					(ii) Mortality
	df	Sum Sq	Mean Sq	p	p	p
Species	15	0.038980	0.002599	15.8211	***	ns
Habitat	2	0.000785	0.000393	2.3897	ns	ns
CII	6	0.007314	0.001219	7.4218	***	ns
Dbh	1	0.013361	0.013361	81.3447	***	ns
Species:habitat	30	0.006123	0.000204	1.2426	ns	ns
Species:CII	65	0.017120	0.000263	1.6035	**	ns
Habitat:CII	12	0.001567	0.000131	0.7948	ns	ns
Species:dbh	15	0.007435	0.000496	3.0176	***	ns
Habitat:dbh	2	0.003073	0.001536	9.3539	***	ns
CII:dbh	6	0.002413	0.000402	2.4486	*	ns
Species:habitat:CII	74	0.027492	0.000372	2.2618	***	ns
Species:habitat:dbh	30	0.018424	0.000614	3.7389	***	ns
Species:CII:dbh	44	0.020412	0.000464	2.8244	***	ns
Habitat:CII:dbh	12	0.011495	0.000958	5.8321	***	ns
Species:habitat:CII:dbh	51	0.012520	0.000245	1.4946	*	ns
Residuals	1758	0.288760	0.000164			

Table shows (i) results for the full interaction ANCOVA models for annual growth rates (mm/yearr) and (ii) summary results for a binomial ANCOVA for mortality with dbh for the covariate. Significance is indicated by asterisks: *$p < 0.05$, **$p < 0.01$, *** $p < 0.001$, ns = not significant

Table 6 Recruitment of Myristicaceae in three different habitats on the Yasuní FDP

Species	Recruits per female			p (Method 1) random location			p (Method 2) random female		
	Valley	Slope	Ridge	Valley	Slope	Ridge	Valley	Slope	Ridge
Compsoneura capitellata	1.00	1.00	0.78	ns	ns	ns	ns	ns	ns
Compsoneura sprucei	0.00	NA	NA	ns			− − −		
Iryanthera grandis	NA	2.00	NA		ns			− − −	
Iryanthera juruensis	NA	NA	0.60			ns			− − −
Iryanthera hostmannii	0.58	0.46	1.18	− − −	−	+++	ns	− − −	+++
Otoba glycycarpa	1.36	0.57	0.43	ns	ns	ns	++	ns	ns
Virola duckei	NA	0.75	0.57		ns	ns		ns	ns
Virola elongata	NA	13.00	9.33		ns	+		ns	− − −
Virola flexuosa	NA	NA	NA						
Virola 'microfuzzy'	21.00	1.50	1.80	+++	− −	ns	+++	−	− − −
Virola mollissima	3.00	3.00	4.00	ns	ns	ns	ns	ns	ns
Virola obovata/cf. *calophylla*	NA	7.75	3.11		ns	ns		ns	− − −
Virola pavonis	9.00	10.00	5.00	ns	ns	ns	ns	ns	ns

Values show observed number of recruits >1 cm dbh per females within each habitat on the 25 ha plot. p values are calculated from two methods of 1,000 bootstrapped calculations of this ratio (1) with recruit location assigned at random within the FDP, and (2) with recruits assigned at random to females within the FDP. The true recruit:female can be within (ns), lower (−) or higher (+) than confidence intervals of the bootstrapped values. Significance is indicated by the number of symbols: ± $p < 0.05$, ±± $p < 0.01$, ±±± $p < 0.001$, ns = not significant. NA indicates no females or recruits present in that habitat. *V. obovata* and *V.* cf. *calophylla* are grouped together due to confusion in the determination of new recruits

64% of 171 species with >65 stems had at least one significant association (Harms et al. 2001), and lower than in Malaysia, where 15 out of 17 species of understorey *Aporosa* at Lambir, Sarawak, Borneo, and all 11 species at Pasoh, Negri Sembilan, Peninsular Malaysia had significant associations with topography (Debski et al. 2002), and eight out of ten species of Sterculiaceae at Lambir showed a significant habitat association (Yamada et al. 2006).

Habitat preferences by female trees will impact on the distribution of a dioecious species. Females of *Otoba glycycarpa* have a positive association with valleys (Queenborough et al. 2007), but the species as a whole also shows a positive association with slopes, which implies fairly extensive dispersal uphill. In three other species (*Compsoneura sprucei*, *Iryanthera grandis* and *I. juruensis)*, no recruits were found in the same habitat as female trees, which also implies active dispersal away from parent trees.

Habitat differentiation and population dynamics

Short-term growth, mortality and recruitment rates explained little of the observed spatial distribution of Myristicaceae species at Yasuní. Mortality of trees ≥ 1 cm dbh over a 5-year interval did not significantly modify the distribution of any species in relation to habitat. Local habitat variables are more likely to affect seedling survival and earlier stages in the life history of a plant, such as during germination and establishment (Dalling et al. 1998; Dalling and Hubbell 2002; Daws et al. 2005), than be a cause of death in established trees. Seedlings are often much more widely distributed than saplings and adults (Webb and Peart 2000), and refining of this distribution may give rise to habitat associations as adults.

Local topographic habitat had a subtle effect on growth rates. Differences in growth among habitats may be caused by unequal light availability, because trees on slopes and ridges will have less lateral and overhead light obscured by neighbours than trees in valley habitat. We found a strong interaction between habitat and CII on growth at Yasuní, which indicates that this mechanism might be occurring. Water and mineral nutrient availability may also influence tree distributions, but are hard to disentangle, because

mineral nutrient availabilities are also often correlated with topography (John et al. 2007) and may be influenced by tree species (e.g. Villela and Proctor 1999).

The seedlings of all the species of Myristicaceae studied here are shade-tolerant. However, there were marked differences in the distribution of established tree stems with respect to light availability, even though all species had most of their stems in relatively low-light environments (mean CII ≤ 3). The relationships between forest structure and physical environments defined by topography and edaphic factors have not been determined at Yasuní, although soil type and topography may influence disturbance regimes and canopy structure in tropical lowland forests elsewhere (e.g. Gunatilleke et al. 2006). The contributions of these interactions to habitat partitioning of Yasuní Myristiaceae awaits further investigation.

The pattern of recruitment in different habitats did not provide strong evidence for or against dispersal limitation. Higher than expected recruitment within a habitat occurred in three species, but only in *Otoba glycycarpa* was this correlated with the habitat association of established trees and of females (Queenborough et al. 2007). Both *Iryanthera hostmannii* and *Virola* 'microfuzzy' had strong (opposing) patterns of recruitment in ridge and valley habitats, but showed no significant habitat associations.

Implications for coexistence of Myristicaceae species at Yasuní

We have shown that species of Myristicaceae show patterns of spatial partitioning at Yasuní. Our analyses of short-term demographic data suggest that where habitat associations exist the survival and growth of established trees has no detectable impact. Our findings agree with other recent work at Yasuní suggesting that topographic niche partitioning is not fine-grained (Valencia et al. 2004a). Species of Myristicaceae are partitioned between two major habitat types: ridge habitat (four species), or valley and slope habitats (five species), or they showed no habitat association (seven species). However, negative associations among the widespread species *Virola* cf. *calophylla*, *V.* 'microfuzzy' and *V. pavonis* hint at other possibilities for niche differ-

entiation. Differentiation with respect to light adds another dimension to the habitat niche, which may substantially increase the scope for species to coexist within a single topographic habitat. For example, the four ridge specialists are arrayed along a spectrum from *Iryanthera juruensis*, which has most of its crowns in deeply shaded sites (CII 1 and 2) to *Virola multinervia*, which occupies sites with intermediate canopy exposure (>50% in CII 3 and above). A well-documented trade-off exists in seedlings between growth in high light and survival in deep shade (Kitajima 1994; Pacala et al. 1996). This trade-off remains unexplored for the Myristicaceae at Yasuní, but all 16 species are unlikely to have similar responses. Tree size also can be used to partition species within a forest (Turner 2001; King et al. 2006). These three factors (topography, light and size) may provide three major axes of environmental niche partitioning (Fig. 2). Within each
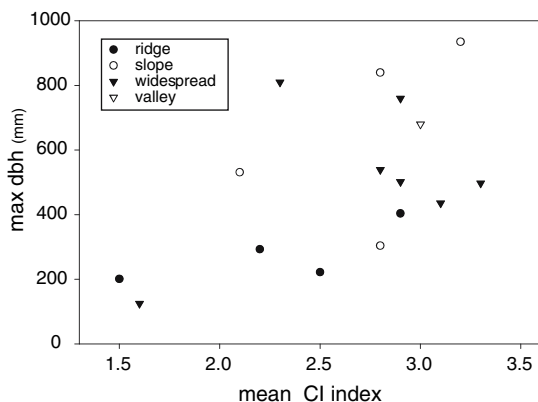
topographic habitat, species are distributed along gradients of both light availability and maximum size. Very few species cluster together and those that do are separated by other factors: for example, *Virola elongata* and *V*. cf. *calophylla* are both widespread species with similar mean CII and maximum sizes, but seed size is an order of magnitude greater in *V*. cf. *calophylla* (Queenborough et al. in press). Thus on the basis of only a limited number of axes, resource partitioning may permit more species to coexist than if the topographic component of the habitat niche is considered in isolation.

Conclusion

Although microhabitat specialisation is important for some groups, such as palms (Svenning 1999), and is very striking in some genera such as *Matisia* Bombacaceae and *Rinorea* Violaceae (Valencia et al. 2004a), our work supports the general conclusion that topographic niche differentiation and habitat associations make a relatively minor contribution to the maintenance of high species diversity in neotropical forests (Harms et al. 2001; Svenning 2001; Wright 2002). However, the interactions among niche axes such as light and soil nutrient availability and their relationships to topography deserve further study and may reveal intriguing opportunities for coexistence of species in these high-diversity forests.

Fig. 2 Partitioning of three niche axes by 16 species of Myristicaceae on the Yasuní FDP. Species were assigned a topographic niche according to significant habitat associations using a randomisation procedure (Table 4), mean crown illumination index was calculated from CII assigned to all trees on the FDP (Fig. 1), and maximum tree size (dbh) was calculated from plot census data

Appendix

Table A1 Results of bivariate Ripley's K analysis for pair-wise comparisons among species

Species	Significant pair-wise comparisons		Pair-wise comparisons among species															
	Number	Group	viroca	iryaju	iryaho	compca	viroel	compsp	viromi	iryagr	viroob	viromu	virodu	otobgl	virodi	viropa	viromo	virofl
V. cf. calophylla	9	A	*	+	−	−	0	0	−	+	−	−	−	0	0	0	−	0
I. juruensis	6	B		*	±	±	+	±	−	0	0	0	0	0	0	0	0	0
I. hostmannii	6	B			*	±	+	±	0	−	0	0	0	0	0	0	0	0
C. capitellata	5	B				*	±	+	0	0	0	0	0	0	0	0	0	0
V. elongata	5	B					*	−	0	0	0	0	0	−	0	0	0	0
C. sprucei	4	B						*	0	0	0	0	0	0	0	0	0	0
V. 'microfuzzy'	3	C							*	0	0	0	0	0	0	−	0	0
I. grandis	3	C								*	−	0	0	0	0	0	0	0
V. obovata	3	C									*	0	0	0	−	0	0	0
V. multinervia	2	C										*	−	0	0	0	0	0
V. duckei	2	C											*	0	0	0	0	0
O. glycycarpa	1	D												*	0	0	0	0
V. dixonii	1	D													*	0	0	0
V. pavonis	1	D														*	0	0
V. mollissima	1	D															*	0
V. flexuosa	0	E																*

Species pairs showing a significant spatial relationship over at least some distance are shown by the following: species pairs are aggregated (+) or complementary (−), or aggregated at distances <150 m and complementary at distances >150 m, (±), or have no spatial relationship (0), and are ordered by the number of significant pair-wise comparisons

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