PROCEEDINGS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Proc. R. Soc. B 2009 **276**, 4197-4205 first published online 9 September 2009
doi: 10.1098/rspb.2009.0921

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Taxonomic scale-dependence of habitat niche partitioning and biotic neighbourhood on survival of tropical tree seedlings

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In order to differentiate between mechanisms of species coexistence, we examined the relative importance of local biotic neighbourhood, abiotic habitat factors and species differences as factors influencing the survival of 2330 spatially mapped tropical tree seedlings of 15 species of Myristicaceae in two separate analyses in which individuals were identified first to species and then to genus. Using likelihood methods, we selected the most parsimonious candidate models as predictors of 3 year seedling survival in both sets of analyses. We found evidence for differential effects of abiotic niche and neighbourhood processes on individual survival between analyses at the genus and species levels. Niche partitioning (defined as an interaction of taxonomic identity and abiotic neighbourhood) was significant in analyses at the genus level, but did not differentiate among species in models of individual seedling survival. By contrast, conspecific and congeneric seedling and adult density were retained in the minimum adequate models of seedling survival at species and genus levels, respectively. We conclude that abiotic niche effects express differences in seedling survival among genera but not among species, and that, within genera, community and/or local variation in adult and seedling abundance drives variation in seedling survival. These data suggest that different mechanisms of coexistence among tropical tree taxa may function at different taxonomic or phylogenetic scales. This perspective helps to reconcile perceived differences of importance in the various non-mutually exclusive mechanisms of species coexistence in hyper-diverse tropical forests.

Keywords: diversity; logistic regression; lowland tropical rain forest; phylogeny; seedling survival; species coexistence

1. INTRODUCTION

Models of species coexistence in hyper-diverse tropical tree communities emphasize either niche partitioning, density-dependent survival or ecological equivalence (reviewed by Chesson 2000; Wright 2002). These mechanisms have all received partial support in studies of tropical tree communities, but their relative importance is subject to debate. For example, recent research has identified important dimensions of plant trait variation within tropical tree communities (Wright *et al.* 2007; Kraft *et al.* 2008) and these may translate into differential patterns of distribution and demography that hint at abiotic niche partitioning (Harms *et al.* 2001; Russo *et al.* 2005; Comita *et al.* 2007; Queenborough *et al.* 2007*a*). Similarly, demographic analyses have shown that density-dependent mechanisms acting within local biotic neighbourhoods may generate higher survival of locally rare species, in support of the Janzen–Connell hypothesis (Hubbell *et al.* 2001: Uriarte *et al.* 2004, 2005; Queenborough *et al.* 2007*b*; Comita & Hubbell 2009). The null model for evaluating either habitat niche partitioning or negative density dependence is that coexisting species are ecologically equivalent and local community dynamics are governed by dispersal limitation and stochastic ecological drift (Hubbell 2001).

Niche differentiation and negative density dependence are not mutually exclusive. However, these processes are usually examined independently because a simultaneous test would require bringing together spatially explicit information on plant community composition, measurements of the abiotic environment at an appropriate scale and demographic responses for target individuals, all within a common analytical framework. Hence, for tropical tree communities, evidence of negative density dependence has emerged from studies of the sensitivity of seedling survival to the local biotic neighbourhood (Webb & Peart 1999; Gilbert *et al.* 2001; Queenborough *et al.* 2007*b*; Comita & Hubbell 2009), and other studies have examined the dependence of tree demography on the local abiotic environment (e.g. Russo *et al.* 2005), but no study has yet attempted to tease apart the relative importance of both biotic and abiotic drivers of seedling survivorship. In this study we aimed to determine the relative importance of abiotic niche partitioning and negative density dependence by analysing both biotic

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2009.0921 or via http://rspb.royalsocietypublishing.org.

Received 28 May 2009
Accepted 11 August 2009

and abiotic drivers of tree seedling survival within a unified spatially explicit analytical framework.

Niche differentiation and negative density dependence can be specified in statistical models that partition variance in a demographic metric such as growth or survival. Density-dependent growth or survival is commonly modelled as a function of the number, size and identity of individuals in the local biotic neighbourhood (Hubbell *et al.* 2001; Uriarte *et al.* 2004; Queenborough *et al.* 2007*b*; Comita & Hubbell 2009). In this study we extend these models by adding variables that define a signal for niche partitioning, which can be characterized in statistical terms as an interaction of taxonomic identity and the local abiotic environment. Furthermore, because the relatedness between neighbours may have a direct impact on competition and the proportion of shared natural enemies (Webb *et al.* 2006; Gilbert & Webb 2007), we repeated our modelling exercise at two levels of the taxonomic hierarchy (species and genus). This approach enabled us to determine whether the relative importance of abiotic niche partitioning and negative density dependence differed between species and genera. Defining the taxonomic scale at which niche partitioning may occur is important because it has implications for mechanisms of community assembly and implied models of speciation (Webb *et al.* 2002; Emerson & Gillespie 2008). Niche differentiation at the species level is most likely in communities of habitat specialists, in which distributions are determined by intense inter-specific competition along gradients of resource availability (Webb 2000). In contrast, niche differentiation at higher taxonomic levels may occur when regeneration traits are phylogenetically conserved and/or species richness is maintained by density- or frequency-dependent interactions with natural enemies (e.g. Hubbell 2001).

In this paper we test the relative importance of niche differentiation and local biotic neighbourhoods on survival of seedlings of 15 species of Myristicaceae at a site in Amazonian Ecuador. Because there is currently no genus-level phylogeny for the Myristicaceae (Sauquet *et al.* 2003), we infer relatedness from a hierarchical taxonomic classification. Specifically, we tested the prediction that density-dependent effects are more important for intra-specific than intra-generic interactions, while the importance of habitat partitioning shows the opposite trend. We used likelihood methods to differentiate among candidate models of individual seedling survival as a function of the abiotic (light, nutrients and water) and biotic neighbourhoods. We constructed two series of models with an identical list of independent variables, but with focal individuals and their neighbours identified either to species or to genus. We then examined the minimum adequate models to determine whether these included (i) terms for abiotic and biotic neighbourhoods and their relative importance and (ii) an interaction between taxonomic identity and abiotic environmental variables.

2. MATERIAL AND METHODS

(a) *Study site*

A 50 ha permanent forest dynamics plot (FDP; http://www.ctfs.si.edu) is located inside Yasuní National Park (0°41′S, 76°24′W; Valencia *et al.* 2004), a still largely wilderness tropical lowland aseasonal rain forest in eastern Ecuador (Finer *et al.* 2008). Mean annual rainfall is approximately 2800 mm and total monthly rainfall is almost never <100 mm. Mean monthly temperature is 25–27°C (Valencia *et al.* 2004). The FDP ranges from 216 to 248 m a.s.l. It includes three ridges and an intervening valley that floods for brief periods. From 1995 to 2000, all freestanding stems ≥1 cm in diameter at breast height (dbh at 1.3 m), excluding lianas, in the western 25 ha of the FDP were tagged, mapped and identified (Valencia *et al.* 2004). Four genera of Myristicaceae co-occur within the Yasuní plot: *Compsoneura* (A.DC) Warb. (two species), *Iryanthera* Warb. (three species), *Otoba* (A.DC) Karsten. (one species) and *Virola* Aublet (nine species). Fourteen of these species are dioecious; *Iryanthera juruensis* is andromonoecious (Queenborough *et al.* 2007*c*).

(b) *Seedling plots*

Within the western 25 ha of the FDP, 30 plots of 20 × 20 m, each composed of sixteen 5 × 5 m subplots, were established in February to June 2002 in a stratified random design to sample the three main habitats on the plot with equal intensity (Queenborough *et al.* 2007*b*). All plots were under closed canopy in mature forest. The coordinates of all Myristicaceae plants >1 cm in height and <1 cm dbh were mapped and marked. Species were determined from Estacion Cientifica Yasuni herbarium material and seedlings grown from shadehouse-germinated seeds collected in 2002 to 2003. All plots were recensused in the period 13 June to 3 July 2005. A total of 2330 seedlings were censused.

(c) *Abiotic neighbourhood*

We defined the abiotic neighbourhood using three environmental variables at each seedling plot: light (canopy openness values from four hemispherical canopy photographs per plot), soil nutrient concentrations (interpolated estimates from 300 soil cores throughout the FDP) and water availability (inferred from two measurements of soil matric potential measured at each seedling plot).

(i) *Canopy openness*

In June 2004, a hemispherical canopy photograph was taken from the centre of each quarter of each 20 × 20 m plot ($n = 4$ per seedling plot). Photographs were taken 1 m above the ground, in uniformly overcast conditions in the early morning or late afternoon, using a levelled Nikon Coolpix 4500 camera body and Nikon FC-E8 Fisheye Converter lens, saved as black and white JPEGs (2272 × 1704 pixels). Images were analysed using a Gap Light Analyzer 2.0 (http://www.rem.sfu.ca/forestry/). Mean canopy openness was 5.0 per cent ± 0.8 (s.d.), and the range was 2.8 to 7.4 per cent. Raw values were centred and standardized by subtracting the mean and dividing by the standard deviation.

Soil nutrient availability

In the period May to June 2004, 50 g of topsoil (0–10 cm depth) was collected from a regular grid of points every 50 m. At each alternate grid point, soil was also sampled from a location 2, 8 or 20 m in a random compass location from the grid. Soils were therefore sampled at 300 locations throughout the 50 ha Yasuní FDP. Exchangeable cations (Al, Ca, Cu, Fe, K, Mg, Mn, Zn) and P were extracted from 2.5 g of fresh soil and the concentration of cations and P were determined (for details see John *et al.* 2007). Spatial predictions for 10 × 10 m blocks were obtained using geostatistical methods (see appendix S1 in the electronic supplementary

material). Because soil nutrient concentrations are often correlated, we derived orthogonal composite variables by computing principal components (PCs) on the block-kriged values of soil nutrients. We used the first three PCs because higher axes individually accounted for <25 per cent of the variation.

(ii) *Soil matric potential*

Soil matric potential was estimated twice for each seedling plot using the filter paper method (Deka *et al.* 1995; Daws *et al.* 2002). On 2 and 11 June 2002, soil from a depth of 0–10 cm was collected from a randomly selected location in each seedling plot. The samples were placed immediately in direct contact with a filter paper (Whatman No. 42, diameter 55 mm) in 50 mm tall polyethylene jars (141 cm^3). The jars were then sealed and placed in a thermally insulated box, which was stored at room temperature (to avoid thermal distillation) and allowed to equilibrate for seven days. After equilibration the gravimetric water content of the filter papers was determined. All weights were measured to an accuracy of 0.1 mg. Soil matric potential was calculated from gravimetric water content using the calibration curve in Deka *et al.* (1995).

(d) *Data analysis*

(i) *Overview*

We analysed 3 yr survival data on 2330 Myristicaceae seedlings. First, to determine the taxonomic scale at which biotic and abiotic neighbourhoods influence individual survival, we examined two sets of autologistic regression models of individual-based survival. In the first set each individual and its confamilial neighbours were classified to species, and in the second set each individual and its confamilial neighbours were classified to genus. Using likelihood methods (Burnham & Anderson 2002), we selected the best models at each taxonomic scale, and compared them using the Information Criterion derived by Akaike (AIC). In both sets of models, we looked for (i) the effect of seedling and tree neighbours (the biotic neighbourhood), including the relative effect of seedlings and trees, and differences between conspecific/generic and heterospecific/generic Myristicaceae neighbours and (ii) the effect of soil nutrients, matric potential and canopy openness (the abiotic neighbourhood), including an interaction between taxonomic identity (species or genus) and these abiotic environmental variables, as a proxy for niche differentiation.

(ii) *Predictors of individual-level survival*

We used autologistic regression to estimate the probability of a seedling surviving from July 2002 to July 2005 as a function of a spatial autocorrelation covariate, taxonomic identity, and the biotic and the abiotic neighbourhoods. Autologistic regression is a modified form of logistic regression that includes a covariate to account for the spatial autocorrelation in the binary response variable, in this case survival (see Hubbell *et al.* 2001; Dormann *et al.* 2007 for a detailed description and mathematical presentation of the technique). Spatial autocorrelation occurs when the values of variables measured at nearby locations are not independent. The assumptions of most regression models, that the errors are independent and normally distributed with constant variance, are therefore violated if spatial autocorrelation exists, and this can lead not only to underestimation of the parameter variances and confidence limits (Hubbell *et al.* 2001), but also the parameter estimates themselves (Dormann *et al.* 2007). Therefore, traditional significance testing is invalid, and model selection methods are now commonly used (Diniz-Filho *et al.* 2008). Although previous studies have used likelihood methods without accounting for spatial autocorrelation (e.g. Uriarte *et al.* 2005), AIC values are related to unexplained variance of the models, which can be affected by the presence of spatial autocorrelation, and can possibly lead to different most likely models (Hoeting *et al.* 2006; Diniz-Filho *et al.* 2008).

Table 1. Parameters present in models of Myristicaceae seedling survival at Yasuní.

	data		
parameter	range	mean	median
canopy openness (% $\log_{10}$)	2.8–7.4	5.2	5.1
soil matric potential (−MPa)	−0.46–1.03	0.75	0.78
soil nutrients (*PCA axes*)			
PC1	−3.74–3.49	0.75	0.24
PC2	−3.30–2.01	0.20	0.60
PC3	−3.16–1.73	0.22	0.03
seedling density (*within 5 m*)			
conspecific	0–58	3.42	0
heterospecific	0–50	0.53	0
congeneric	0–59	3.71	0
heterogeneric	0–10	0.25	0
adult basal area (m^2, *within 10 m*)			
conspecific	0–1.67	0.14	0
heterospecific	0–1.77	0.20	0.02
congeneric	0–1.67	0.19	0.01
heterogeneric	0–1.67	0.15	0.01

We accounted for spatial autocorrelation in survival by using the proportion of surviving seedling individuals within 5 m of focal seedlings as the autocovariate (Hubbell *et al.* 2001). In a previous study spatial autocorrelation in seedling survival was significant to 5 m from focal individuals (Queenborough *et al.* 2007*b*). In the simplest model, seedling survival depended solely on this autocovariate term. To examine evidence for abiotic niche partitioning, we compared this simple model to a set of models including soil matric potential (per seedling plot) and soil nutrients and canopy openness (per quarter seedling plot), as well as a taxonomic identifier (species or genus). As a proxy for inter-specific niche partitioning, we included interaction terms between the taxonomic term and these abiotic variables.

In order to examine the biotic neighbourhood, we compared these density-independent models to models including the seedling and tree neighbourhood. In the full model, seedling survival depended on the autocovariate, the taxonomic term, the three abiotic variables and their interactions with the taxonomic term, and the number of conspecific (Scon) and heterospecific (Shet) seedlings within 5 m of the focal seedling, and the total basal area m^{-2} of all conspecific (Acon) and heterospecific (Ahet) Myristicaceae trees $\geq$1 cm dbh within 10 m of the focal seedling (table 1). We compared this full model to models in which conspecifics and heterospecifics were pooled, and to models in which only seedling or only tree effects were included. In total we compared 29 models, in three classes: (i) density-independent abiotic models, (ii) models in which the effects of overall seedling and tree neighbours are included, but conspecific and heterospecific neighbours were not differentiated, and (iii) models in which the effects of conspecific and heterospecific neighbours were

Table 2. AIC and Δ_{AIC} values of models of 3-year individual-level Myristicaceae seedling survival (autologistic regression) for two taxonomic identifiers: species and genus. The most likely models are shown in bold. See figures 1 and 3 for odds ratios of the most likely models and figures 2 and 4 for graphical representation of seedling survival versus the biotic and abiotic neighbourhoods. AIC values for logistic regressions models for the same parameters are detailed in table S1 in the electronic supplementary material. Scon, seedling conspecifics/generics; Shet, seedling heterospecifics/generics; Acon, adult conspecifics/generics; Ahet, adult heterospecifics/generics.

	species		genus	
candidate models	AIC	Δ_{AIC}	AIC	Δ_{AIC}
spatial only				
spatial	3065.40	139.12	3066.21	97.18
density independent				
spatial + taxa	2936.75	10.48	3001.01	31.98
spatial + light + soils + water	3053.86	127.58	3054.35	85.32
spatial + taxa + light + soils + water	2939.14	12.87	2994.00	24.97
spatial + taxa × (light + soils + water)	2953.91	27.63	2988.34	19.31
density-dependent het = con				
spatial + Stot	3028.42	102.14	3029.15	60.13
spatial + Atot	3062.07	135.79	3062.77	93.74
spatial + Stot + Atot	3026.69	100.42	3027.71	58.68
spatial + taxa + light + soils + water + Stot	2928.93	2.65	2975.96	6.94
spatial + taxa + light + soils + water + Atot	2940.27	13.99	2994.57	25.54
spatial + taxa + light + soils + water + Stot + Atot	2930.30	4.02	2977.08	8.05
spatial + taxa × (light + soils + water) + Stot	2947.15	20.87	2971.36	2.33
spatial + taxa × (light + soils + water) + Atot	2954.72	28.44	2988.28	19.25
spatial + taxa × (light + soils + water) + Stot + Atot	2948.09	21.82	2971.83	2.80
density-dependent het ≠ con				
spatial + Scon + Shet	3027.76	101.48	3031.05	62.02
spatial + Scon + Shet + Atot	3026.63	100.35	3029.44	60.41
spatial + Acon + Ahet	3046.22	119.94	3042.11	73.08
spatial + Acon + Ahet + Stot	3025.49	99.21	3020.51	51.48
spatial + Acon + Ahet + Scon + Shet	3024.90	98.62	3022.49	53.46
spatial + taxa + light + soils + water + Scon + Shet	2926.28	**0.00**	2975.33	6.30
spatial + taxa + light + soils + water + Scon + Shet + Atot	2928.00	**1.72**	2976.75	7.73
spatial + taxa + light + soils + water + Acon + Ahet	2940.85	14.57	2991.73	22.70
spatial + taxa + light + soils + water + Acon + Ahet + Stot	2932.21	5.94	2977.51	8.48
spatial + taxa + light + soils + water + Acon + Ahet + Scon + Shet	2929.84	3.56	2976.86	7.84
spatial + taxa × (light + soils + water) + Scon + Shet	2944.85	18.58	2969.03	**0.00**
spatial + taxa × (light + soils + water) + Scon + Shet + Atot	2946.22	19.95	2969.99	**0.96**
spatial + taxa × (light + soils + water) + Acon + Ahet	2955.66	29.38	2985.25	16.22
spatial + taxa × (light + soils + water) + Acon + Ahet + Stot	2949.82	23.54	2972.06	3.03
spatial + taxa × (light + soils + water) + Acon + Ahet + Scon + Shet	2947.90	21.62	2969.92	**0.89**

differentiated. We used these models to address the two questions defined above as follows. (1) To test the relative importance of the biotic and abiotic neighbourhoods, we compared models that included (i) only the biotic, (ii) only the abiotic, and (iii) both the biotic and abiotic neighbourhoods. (2) To examine the taxonomic scales at which the local neighbourhood influenced survival, we compared model selection when individuals were identified to species (conspecific or heterospecific) or to genus (congeneric or heterogeneric) in the description of the biotic neighbourhoods. Models differing by an AIC of less than 2 were judged equally valid (Burnham & Anderson 2002). We also provide AIC values for the equivalent logistic regression models (see table S1 in the electronic supplementary material), which makes clear that major conclusions are not affected by choice of approach.

Interpretation

Odds ratios measure the partial effect of each variable on the odds of survival and were calculated by taking the exponential of the estimate of each coefficient. Odds ratios >1 indicate positive effects on survival and ratios <1 indicate negative effects. Significance is inferred when the confidence interval does not include 1. All analyses were conducted using the software package R 2.8.1 (R Development Core Team 2008), the package CTFS 1.00 (Hall 2006), and function 'plot.logi.hist' (de la Cruz Rot 2005).

3. RESULTS

(a) *Abiotic versus biotic predictors of seedling survival*

Models of 3 yr survival of 2330 Myristicaceae seedlings showed wide variation in AIC values (table 2). When 'species' was assigned as the taxonomic identifier, two most likely models were apparent. Both these models included the effects of abiotic variables and seedling neighbours (differentiating between conspecific and heterospecific seedlings), and one model included total adult

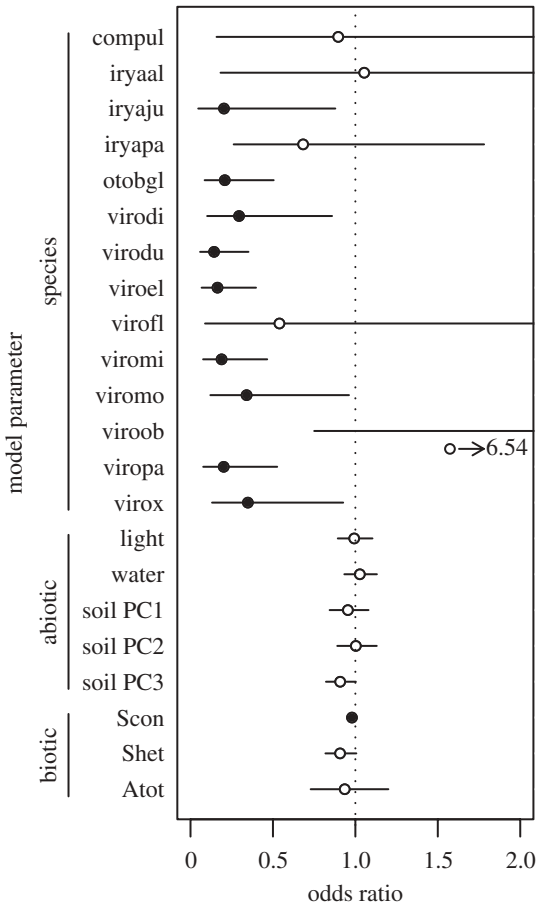

Figure 1. Odds ratios of survival of seedlings compared to *Compsoneura capitellata* for the fullest most likely model in table 2. Here, all seedlings are assigned to SPECIES. The parameters in the model included species, abiotic and biotic neighbourhood variables (see text for details). Circles show odds ratios for each parameter, with 95% confidence limits (CL) indicated by horizontal lines. Odds ratios significantly different from 1 (95% CL do not overlap 1) are indicated by filled circles. The large odds ratio for *Virola obovata* is indicated by the arrow.

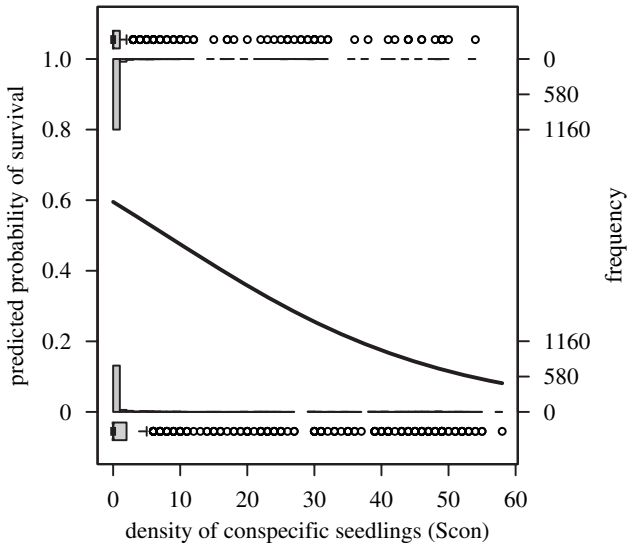

Figure 2. Fitted logistic regression curve for the probability of seedling survival as a function of the number of conspecifics within 1 m. Histograms and boxplots indicate the distributions of dead (bottom) and surviving (top) individuals. Note the very low numbers of seedlings at densities >10.

neighbours. Neither of these best models included an interaction between species and abiotic environmental variables.

Odds ratios for the fullest of the two most likely models showed significant differences in survival between species (figure 1). There was also a significant negative effect of increasing density of conspecific neighbours. Seedlings with no conspecific seedling neighbours had a 0.6 probability of surviving for 3 yr, which declined to <0.2 in areas of high seedling density (figure 2). The presence of heterospecific seedlings and adult trees had non-significant negative effects on focal seedling survival.

When the taxonomic identifier term was set to genus, three most likely models were found (table 2). Again, these models included the effects of abiotic environmental variables and seedling neighbours. All three differentiated between congeneric and heterogeneric seedling neighbours. Two models included adult trees, and one of these differentiated between congeneric and heterogeneric tree neighbours. Furthermore, all these models also included an interaction between genus and all three abiotic environmental variables.

Odds ratios for the fullest of the three most likely models indicated significant negative effects of congeneric and heterogeneric seedling neighbours (figure 3). Seedlings with no congeneric seedling neighbours also had a 0.6 probability of survival, which decreased to <0.2 in areas of high congeneric seedling density. *Otoba* seedlings had significantly higher survival, and *Compsoneura* seedlings had significantly lower survival, in areas of greater canopy openness (figure 4). The model also indicated significantly higher survival of *Iryanthera* seedlings in areas corresponding to high values along soil PC1 (associated with high concentrations of P and low concentrations of Fe, Cu, Zn, Mg and Ca: see figure 4 and table S2 in the electronic supplementary material), as well as significantly lower survival of *Compsoneura* seedlings in areas corresponding to high values of soil PC2 (associated with high concentrations of Al and Fe and low concentrations of Ca, Mg, K and P) (figure 4).

(b) *Summary of taxonomic scale dependence of seedling survival*

The most likely models with species as the taxonomic term included abiotic and biotic neighbourhoods, but no interaction between species and abiotic environmental variables. The most likely models with genus as the taxonomic term included this interaction with the abiotic environmental variables.

4. DISCUSSION

(a) *Relative importance of abiotic and biotic neighbourhoods*

Components of both the biotic and the abiotic environments were important predictors of Myristicaceae seedling survival at Yasuní. When we included variables defining both the abiotic environmental neighbourhood and the biotic neighbourhood in autologistic models of seedling survival, density-dependent effects and habitat variables were significant and pervasive at both taxonomic levels, but the key interaction between taxonomic identifier and habitat (indicative of niche differentiation) was only apparent at the genus level.

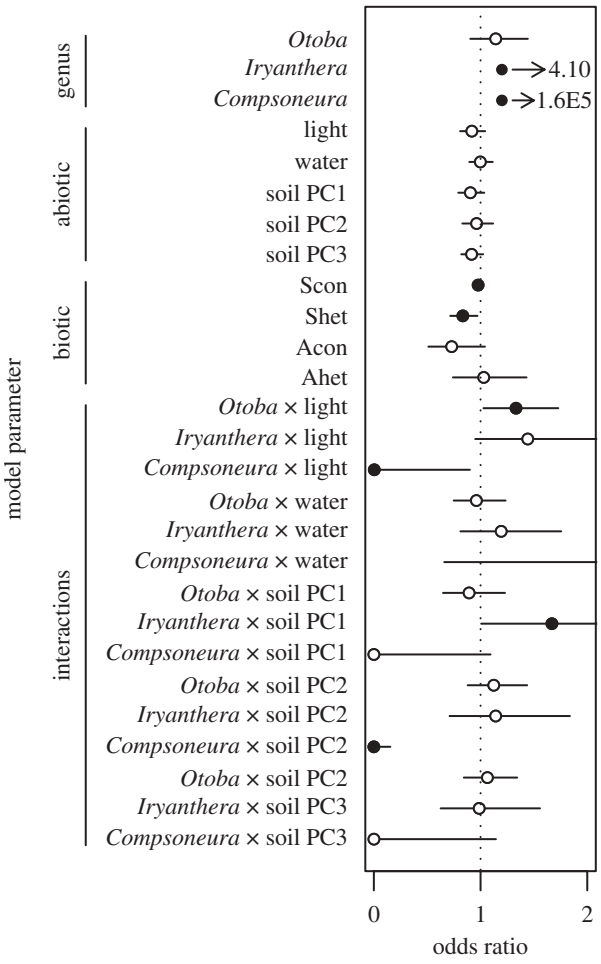

Figure 3. Odds ratios of survival of seedlings compared to *Virola* for the fullest most likely model in table 2. Here, all seedlings are assigned to GENUS. The parameters in the model included genus, abiotic and biotic neighbourhood variables plus interactions (see text for details). Circles show odds ratios for each parameter, with 95% confidence limits (CL) indicated by horizontal lines. Odds ratios significantly different from 1 (95% CL do not overlap 1) are indicated by filled circles. The large odds ratios for *Iryanthera* and *Compsoneura* are indicated by arrows.

Seedlings of the same species or genus had a strong negative influence on focal seedling survival. Therefore, this study provides support for the idea that the negative effects of neighbours are greater for more closely related individuals (Uriarte *et al.* 2005; Webb *et al.* 2006; Comita & Hubbell 2009), which may arise because the likelihood that neighbours share natural enemies increases with their relatedness (Weiblen *et al.* 2006; Gilbert & Webb 2007). However, abundance of adult trees did not affect seedling survival independently of local seedling density. This conclusion is supported by previous work on Myristicaceae seedling demography at Yasuní, which showed that tree abundance was related to seedling survival at the community scale, but not at the local scale (Queenborough *et al.* 2007*b*).

Abiotic environmental variables differentially impacted seedling survival of Myristicaceae tree genera at Yasuní. *Virola* and *Compsoneura* showed declining probability of survival in response to increasing canopy openness, while *Otoba* and *Iryanthera* showed the opposite pattern. These trends generated marked rank-reversals in survival among genera along the natural gradient of light availability represented on our sample of plots. They are indicative of inter-generic variation in seedling shade tolerance, which was manifested across a narrow range of relatively low light conditions that excluded canopy gaps. These responses might have important implications for seedling and sapling distributions across forest light environments (Montgomery & Chazdon 2002; Bloor & Grubb 2003).

Seedlings of the four Myristicaceae genera had differential likelihood of survival along the two most important gradients of soil nutrient availability on the Yasuní plot. *Iryanthera* showed increasing probability of survival in areas of higher P and lower Fe, Cu, Zn, Mg and Ca concentrations (soil PC1), whereas *Virola* and *Otoba* showed the opposite pattern. *Compsoneura* showed declining probability of survival at higher concentrations of Al and Fe, whereas *Virola* had higher survival in areas of high concentrations of these cations. These rank reversals in seedling survival along gradients of soil nutrient availability might translate into non-random distributions of tree genera, but not species, at the 50 ha scale. Seedlings of most Myristicaceae species are widely distributed across the Yasuní plot and few species show significant topographic habitat associations (Queenborough *et al.* 2007*b*). This pattern persists among adult Myristicaceae trees (Queenborough *et al.* 2007*a*), many other species at Yasuní (Valencia *et al.* 2004; John *et al.* 2007), as well as elsewhere (Comita *et al.* 2007). Analyses of tree distributions at higher taxonomic levels and for an entire community at one site might therefore prove fruitful.

The absence of evidence of strong abiotic niche partitioning at the species level in our study supports previous work suggesting that a relatively low proportion of neotropical tree species show strong associations to topographic habitats or soil resource gradients at the local scale of a 25 or 50 ha plot (Harms *et al.* 2001; Valencia *et al.* 2004; John *et al.* 2007). At larger, meso- and landscape scales there is strong evidence that abiotic environments contribute to species distribution limits in neotropical forests (Clark *et al.* 1999; Phillips *et al.* 2003). The limited role for habitat niche partitioning at local scales contrasts with strong evidence that a high proportion of tree species on neotropical forest plots are influenced by the neighbourhood density of trees, over distances >50 m for saplings (Hubbell *et al.* 2001; Uriarte *et al.* 2004), or much shorter distances for seedlings (Queenborough *et al.* 2007*b*). Taken together, these studies suggest that local-scale seedling and sapling demography is more sensitive to the biotic neighbourhood than the local abiotic environment, whereas abiotic niche partitioning becomes increasingly important at greater spatial scales and higher taxonomic ranks.

(b) *Implications for community assembly*

The taxonomic scale dependence of abiotic niche partitioning and negative density dependence has important implications for mechanisms of species coexistence and community assembly. Communities composed of habitat specialists partitioning abiotic resources should manifest niche differentiation at the species level.

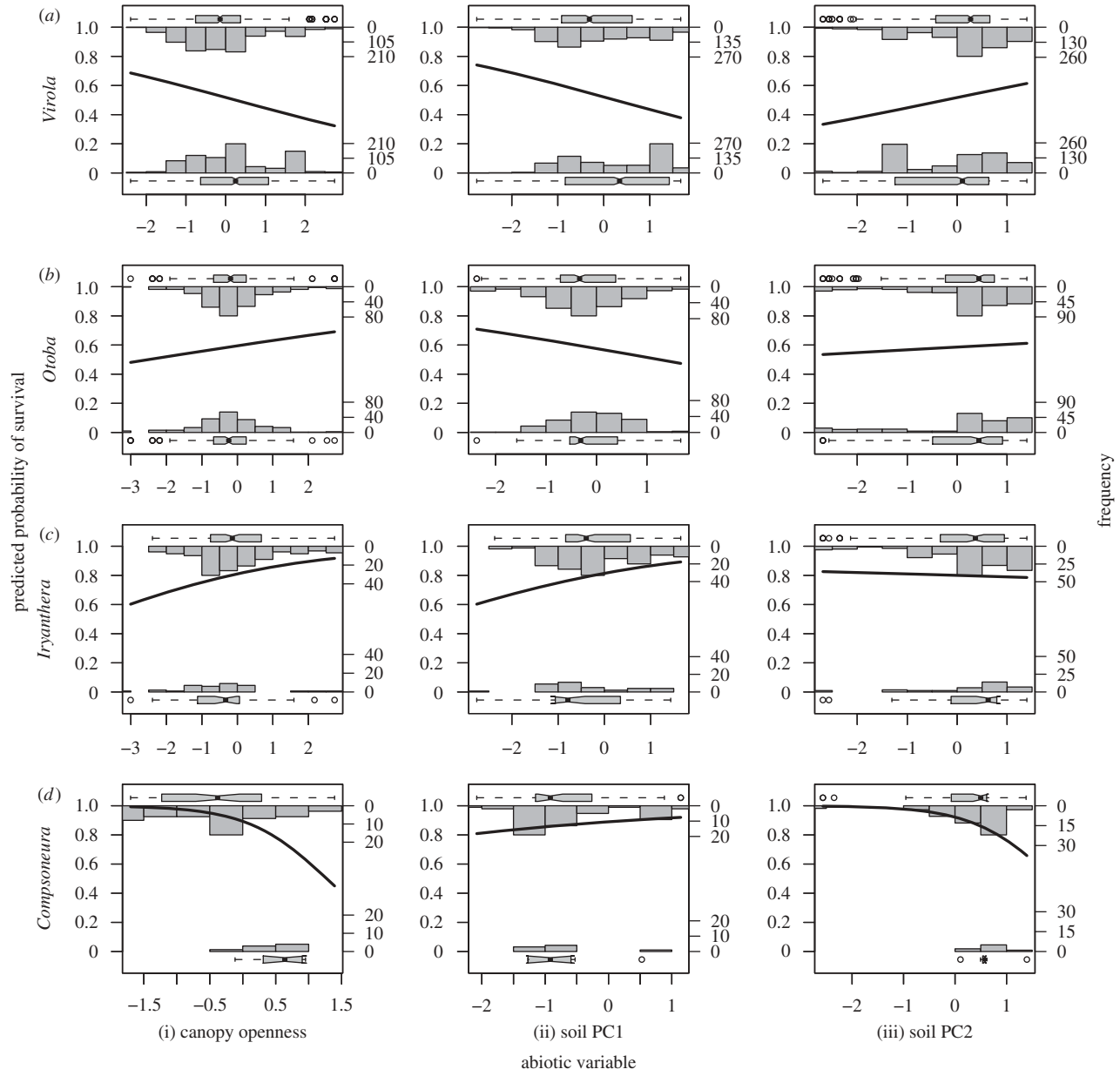

Figure 4. The interaction of genus with three abiotic variables. Each column details one interaction; rows show figures for each genus. Within each graph, the solid line describes the fitted logistic regression curve for the probability of seedling survival as a function of the abiotic variable, and histograms and boxplots indicate the distributions of dead (bottom) and surviving (top) individuals.

Conversely, if species differentiate along other (or no) niche axes, abiotic niche partitioning may occur at higher taxonomic scales or not at all. Although many studies have examined how high numbers of *species* coexist, no previous study has examined how coexistence mechanisms might vary at different ranks of the taxonomic hierarchy. In this study we showed that individuals of different genera had differential survival according to variation in abiotic environmental variables. This implies that groups of taxonomically related species partition the abiotic environment. These groups are likely to be phylogenetically related, and possess similar (conserved) niches (Prinzing *et al.* 2001). Potential mechanisms of species coexistence within genera include density-dependent survival, differentiation with respect to other components of the regeneration niche (Grubb 1977; Daws *et al.* 2002), and dispersal limitation (Hubbell 2001). Future work should examine this finding in more detail for a wider suite of species. Highly resolved species-level molecular phylogenies would help to determine the exact taxonomic and phylogenetic scale over which different mechanisms function. In particular, determining the phylogenetic scale at which significant niche autocorrelation disappears should be a key goal.

(c) *Caveats*

The patterns we described are likely to be highly context- (or ecosystem-) dependent. For example, had our sample included species from many different families but poor representation of inter-generic variation within families (the case for many local floras outside the tropics), niche effects might have been most apparent at the species

level. Similarly, different outcomes might have arisen had we selected a different family for analysis, because of contrasts in evolutionary history and biogeographic origins at the family level. This context dependency highlights the importance of phylogenetic community structure for the mechanisms of species coexistence that may appear to be important at any one site. We also note that the subjective partitioning of individuals into a hierarchy that is unlikely to be an accurate reflection of the evolutionary relationships between them may unduly influence the results, either because the genera may be paraphyletic (unlikely for the Myristicaceae, Sauquet *et al.* 2003) and/or because genera and species within genera may be of different ages, and thus not representative of comparable 'levels' in a taxonomy. These problems will only be solved by the creation of more detailed and resolved dated molecular phylogenies. In this study we have attempted to minimize their importance by restricting the scope of our analysis to a single family.

(d) *Conclusions*

In a hyper-diverse rain forest in western Amazonia, we found evidence that both abiotic niche partitioning and density-dependent mechanisms promote the coexistence of 15 species of Myristicaceae. In common with previous work on multiple species, we found evidence for stronger effects of seedling biotic neighbourhoods than the local abiotic environment on individual seedling survival. However, at the genus scale, niche partitioning along axes of variation in canopy openness and soil nutrient availability was significant, which suggests that different mechanisms of coexistence among tropical tree taxa may be expressed at different taxonomic scales. This perspective helps to reconcile perceived differences in the importance of the various non-mutually exclusive mechanisms of species coexistence in tropical tree communities.

We thank the Yasuní plot census and data management teams. Fieldwork was assisted by G. Bramley, J. Hallo, A. Humphries, S. Koelen, S. Spehar and M. Zambrano. Analyses were much improved by comments from L. Comita. Soil nutrient data were kindly provided by J. Dalling, R. John, K. Harms, R. Stallard and J. Yavitt (NSF DEB 021104, 021115, 0212284, 0212818 and OISE 0314581). Soil matric potential data were kindly provided by L. Hayes, who was funded by the UK Natural Environment Research Council. Fieldwork by S.A.Q. was funded by a Study Abroad Studentship from The Leverhulme Trust and a grant from the Center for Tropical Forest Science. We thank N. Norden and two anonymous referees for many helpful comments.

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