Developmental changes in habitat associations of tropical trees

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Summary

1 Recent studies have documented local-scale associations between tree species and topographic and edaphic habitat types in forests worldwide. To determine whether such associations form at early life stages, we compared species' positive associations with five habitat types (high plateau, low plateau, slope, streamside, and swamp) at two life stages for 80 tree and shrub species in a Panamanian lowland forest.

2 Nineteen significant, positive habitat associations were detected at the small tree stage (seedlings and saplings $\geq$ 20 cm tall and < 1 cm d.b.h.), and 18 at the large tree stage (individuals $\geq$ 1 cm d.b.h.), according to results of torus-translation randomization tests. The majority of species did not show consistent associations at the two stages. Of the 30 species significantly associated with a habitat, only five were associated with the same habitat at both stages. Overall, more species were associated with the wetter slope habitat at the large tree stage compared with the small tree stage.

3 For a subset of species, we examined the relationship between observed habitat associations and seed dispersal and seedling establishment patterns by using species-specific seed dispersal kernels to predict seed rain into each habitat.

4 Two-thirds of species associated with a habitat at the large tree stage had higher predicted seed densities in the associated habitat relative to other habitat types, indicating that limited seed dispersal acts to reinforce habitat associations for most species. In contrast, only one-third of the species associated with a habitat at the large tree stage showed evidence of higher seedling establishment rates in the associated habitat compared with other habitats, and an equal number of species appeared to have lower rates of establishment in the habitat that large trees of the species were associated with.

5 Overall, our results indicate that habitat associations of large trees typically do not form at early life stages. Rather, many species appear to exhibit different ecological habitat preferences across life stages. Future studies of species' habitat associations should therefore include multiple life stages in order to detect developmental shifts in ecological preferences.

Key-words: dispersal limitation, edaphic specialization, environmental heterogeneity, habitat preference, regeneration niche, tropical tree seedlings

Introduction

Non-random species distributions with respect to environmental gradients have been documented at various scales in numerous plant communities worldwide. Such observations have led biologists to invoke niche differentiation with respect to resources as an explanation for the maintenance of local diversity in multispecies communities (Ashton 1969; Tilman 1982). Theoretical models predict species coexistence in heterogeneous environments where each species is best suited to a particular habitat (Tilman & Pacala 1993). However, all plant species depend on the same

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handful of resources and acquire them in similar ways, making it difficult to explain coexistence through niche differentiation, especially in species-rich communities such as tropical forests (Silvertown 2004). The paucity of resources on which adult trees can specialize led Grubb (1977) to propose that habitat partitioning is most likely during early life stages and that coexistence is possible through the partitioning of the 'regeneration niche'.

Studies of regeneration niche differentiation in tree communities initially focused on species' partitioning along gradients of light availability (Denslow 1980, 1987; Canham 1989; Clark *et al*. 1993; Kobe 1999; Brokaw & Busing 2000). More recently, numerous studies have revealed species' associations with topography and soil water and nutrient availability on local scales in forests worldwide (e.g. Clark *et al*. 1998; Davies *et al*. 1998; Svenning 1999; Plotkin *et al*. 2000; Webb & Peart 2000; Harms *et al*. 2001; Tateno & Takeda 2003; Aiba *et al*. 2004; Cannon & Leighton 2004; Valencia *et al*. 2004; Gunatilleke *et al*. 2006). If niche differentiation is most likely to take place during regeneration, then observed associations with edaphic factors are expected to arise during early life stages, such as seed germination and seedling establishment. However, most community-level analyses of species' habitat associations are based on static distributions of large saplings and trees. Studies of seedling habitat associations and comparisons of species' habitat associations at multiple life stages are rare (Webb & Peart 2000). Thus, it remains unclear when observed species' habitat associations form and whether such associations reflect regeneration niche differences. In addition, physiological requirements and selective pressures may change with size, such that a species' ecological preferences may differ from one life stage to the next (Werner & Gilliam 1984; Schupp 1995). Assessments of species' habitat associations at a single life stage are insufficient to detect such developmental changes in ecological preferences.

Even when data on both seedling and adult tree distributions with respect to habitat are available, comparisons of associations at the two stages may be confounded by the fact that seedling distributions are strongly influenced by seed dispersal patterns (Webb & Peart 2000). Typically, most seeds fall close to parent trees, and the density of seeds will therefore tend to be higher in the preferred habitat of adult trees compared with other habitats. Thus, seedlings may show associations with the same habitat as adults, even when seedlings have no true habitat preference. High seed densities near parent trees may also mask low rates of seedling establishment and survival in the preferred habitat of adults, which can result from different resource requirements of seedlings or from negative density dependence during the seed-to-seedling transition (e.g. Harms *et al*. 2000; Lambers *et al*. 2002). Alternatively, species may show consistent habitat preferences across life stages, indicated by a contraction of the species' distribution from the seed to juvenile to adult stage due
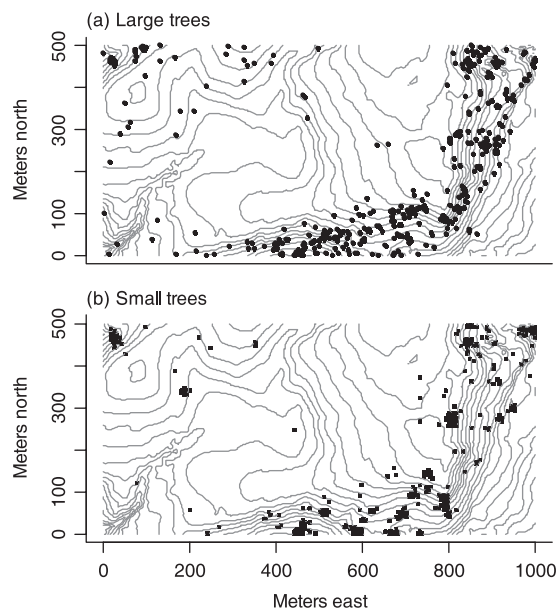

Fig. 1 Distribution of large trees (≥ 1 cm d.b.h.) and small trees (≥ 20 cm height – < 1 cm d.b.h.) of the slope specialist *Ocotea whitei* (Lauraceae) in the Barro Colorado Island 50-ha Forest Dynamics Plot. In panel (a), circles represent individuals ≥ 1 cm d.b.h. In panel (b), squares represent 1-m^2 seedling plots that were occupied by one or more *O. whitei* individuals. *O. whitei* was significantly associated with the slope habitat at both life stages.

to consistently lower survival outside of the preferred habitat.

In order to differentiate between these possibilities, information on seed dispersal patterns is needed, in addition to spatially explicit data on both seedling and adult tree distributions across habitats. Here we compare topographic habitat associations across two different life stages for 80 common tree and shrub species in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama (BCI FDP; Fig. 1), where a previous study of large saplings and trees found that many species are positively associated with one or more habitats (Harms *et al*. 2001). In addition, using published species-specific dispersal functions generated from data on seed rain into seed traps within the BCI FDP (Muller-Landau 2001), we simulate seed dispersal across the landscape and compare seedling distributions with predicted seed rain into different habitat types. Using this information, we ask: (i) Do species show similar habitat associations across different life stages? (2) Are observed associations related to higher seedling establishment and survival in a habitat or limited seed dispersal away from parent trees?

Methods

STUDY SITE

The study was conducted in the 50-ha Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI), Panama

(9°9′ N, 79°51′ W). Detailed descriptions of the climate, geology, flora and fauna of BCI can be found in Croat (1978), Leigh *et al.* (1982), Leigh (1999) and Losos & Leigh (2004). Established in 1980, the 50-ha FDP is situated in the middle of BCI and consists of mainly old growth lowland moist forest, with the exception of a 2-ha area of secondary forest along the north-eastern edge of the plot. Elevation on the FDP ranges from 120 to 155 m above mean sea level (Hubbell & Foster 1983). Although the FDP sits mainly on a level plateau, the edges of the plot also include slopes with up to 20° inclination (Fig. 1). In a previous analysis of species' habitat associations, Harms *et al.* (2001) divided the BCI FDP into 1250 20×20 m quadrats and assigned each quadrat to one of five habitat types: high plateau (< 7° inclination, ≥ 152 m elevation; 170 quadrats), low plateau (< 7° inclination, < 152 m elevation; 620 quadrats), slope (≥ 7° inclination; 284 quadrats), streamside (30 quadrats), and seasonal swamp (32 quadrats). Sixty-six 20×20 m quadrats contained more than one habitat type and were excluded from further analysis, as were 48 quadrats located in the 2-ha area of secondary forest.

In the BCI FDP, an andesitic cap beneath the plateau accumulates water and creates springs along the slopes (Leigh *et al.* 2004). The slopes therefore remain wetter than plateaus and experience a shorter duration of drought during the annual 4-month dry season (Becker *et al.* 1988; Daws *et al.* 2002). The high plateau is the driest area of the BCI FDP, having lower dry season soil water availability than slopes or the low plateau (B. M. J. Engelbrecht & L. S. Comita, unpublished data). At the other extreme is the seasonal swamp, a 1.5-ha area that is inundated during the 8-month wet season (Harms *et al.* 2001). Finally, streamside habitats are steeply sloped areas adjacent to seasonal streams, located in the north-east and south-west corners of the FDP, that tend to contain water into the dry season (Hubbell & Foster 1986; Condit 1998; Harms *et al.* 2001).

DATA COLLECTION

All saplings, shrubs and trees ≥ 1 cm d.b.h. in the BCI FDP were mapped, identified to species, and measured between 1982 and 1983 (Hubbell & Foster 1983; Condit 1998). Recensuses of stems ≥ 1 cm d.b.h. have been conducted at 5-year intervals between 1985 and 2005. Here we use data from the 2000 recensus (data available for download at http://ctfs.si.edu). In 2001, we established a permanently marked 1-m² seedling plot in the centre of each 5×5 m subquadrat of the 50-ha FDP, for a total of 20 000 plots (Comita *et al.* 2007). Between January and October 2001, all woody plants ≥ 20 cm in height and < 1 cm d.b.h. were tagged, mapped and identified to species within each 1-m² plot. Individuals were not censused in 366 seedling plots to avoid pre-existing research plots within those areas. For simplicity, we hereafter refer to seedlings and small saplings ≥ 20 cm in height and < 1 cm d.b.h. as *small trees*, and all individuals ≥ 1 cm d.b.h. as *large trees*.

ANALYSES OF HABITAT ASSOCIATIONS

We tested for positive associations with the five habitat types (high plateau, low plateau, slope, streamside, swamp; defined above) at both the small and large tree stages for 80 species having ≥ 50 individuals in both the small and large tree censuses. We tested whether species density was significantly higher in one or more habitats using torus-translation tests of habitat association, which take into account the spatial autocorrelation inherent in both plant distributions and habitats (Harms *et al.* 2001). Torus-translation tests compare observed densities of a species in each habitat with densities predicted under a null model in which the species is distributed randomly with respect to habitat. In order to facilitate comparisons between habitat associations at the two different life stages, we deviated slightly from the methods described in Harms *et al.* (2001) in that we tested only for positive associations and used the absolute stem density of each species in a 20×20 m quadrat rather than the density of the focal species relative to overall stem density within that quadrat.

In each 20×20 m quadrat, large tree density was calculated from the total number of stems ≥ 1 cm d.b.h. within the quadrat and small tree density was averaged over the 1-m² seedling plots located within the quadrat. We used 20×20 m blocks because habitat types were assigned at that scale and because spatial autocorrelation is strongest at scales < 20 m in many tropical forests (Condit *et al.* 2000). Thus, 20×20 m quadrats should represent independent sample units (Valencia *et al.* 2004). The predicted (null) densities were generated by conserving the spatial locations of stems and the spatial distribution of habitats, but shifting the habitat map by 20-m increments in each of the four cardinal directions to generate a total of 1249 unique, random estimates of species density in each habitat. *P*-values were calculated based on the number of times the observed stem density in a habitat was higher than the stem density in that habitat in the torus-translated maps. For example, if the observed density of a species in a given habitat was higher than the density in that habitat for 99% of the torus-translated maps (i.e. 1237 out of the 1249 false maps), the species was positively associated with the habitat with a *P* of 0.01.

Because of the large number of species included in the analysis, we used randomization to calculate the expected number of false positives and determine the appropriate value of *P* to use as a cut-off for significance. We randomly shuffled the species identity assigned to each *xy*-coordinate of all stems in the 50-ha plot. We then tested for significant positive associations between the five habitat types and the 80 focal species. We repeated this 100 times for each life stage and calculated the mean number of significant associations detected in the randomized data sets (Table 1). For both life stages, in nearly all habitats a cut-off of *P* = 0.01 yielded less than 0.8 false positives out of the 80 species tested (i.e.

Table 1 Mean number of false positives detected in tests of habitat association for 80 species with five habitat types, based on 100 randomized data sets created by shuffling the species identities assigned to *xy*-coordinates of stems in the Barro Colorado Island 50-ha plot

Significance level	Mean number of false positives				
	High plateau	Low plateau	Slope	Stream	Swamp
Large tree stage					
$P < 0.05$	0.81	26.2	2.88	1.17	0.04
$P < 0.01$	0.13	9.24	0.45	0.09	0.01
$P < 0.005$	0.05	5.34	0.26	0.03	0
$P < 0.001$	0.02	1.57	0.05	0.01	0
$P < 0.0005$	0	0.76	0.04	0	0
Small tree stage					
$P < 0.05$	3.58	0.77	2.29	0.83	0.94
$P < 0.01$	0.34	0.11	0.27	0.07	0.16
$P < 0.005$	0.13	0.02	0.16	0.04	0.07
$P < 0.001$	0.02	0	0.04	0.01	0.04
$P < 0.0005$	0	0	0.02	0.01	0.02

less than 1% of the 80 tests result in a false positive). The one exception was the low plateau habitat, where a number of false positives were estimated to occur at the large tree stage (Table 1). Therefore, in tests of association with the low plateau at the large tree stage, we used the more conservative cut-off of $P = 0.0005$, the highest value at which the mean number of false positives was less than 0.8. Out of the 400 tests conducted at each stage (80 species × 5 habitats), using these cut-offs for significance we expect only one to two false positive associations at the large tree stage and less than one false positive at the small tree stage.

Torus-translation tests determine only whether species are significantly associated with a habitat. To assess the strength of associations, we calculated the adjusted stem density of each species for each habitat type at the small and large tree stages by dividing the density of the species in the focal habitat by the total density of the species across the entire 50-ha plot. This measure allows for a comparison among life stages and among habitats as it adjusts for differences in overall stem density and the area of each habitat. Values of adjusted stem density > 1 suggest a species' positive association with the habitat, while values < 1 suggest that the species avoids that habitat type.

SEED DISPERSAL SIMULATIONS

To determine the degree to which habitat associations result from seed dispersal vs. differential seedling establishment and survival among habitats, we predicted patterns of seed arrival across the BCI FDP using species-specific dispersal kernels published in Muller-Landau (2001). Using 13 years of data on seed rain into seed traps located throughout the BCI FDP, Muller-Landau (2001) employed inverse modelling techniques (e.g. Ribbens *et al.* 1994) to determine the best model to describe patterns of seed arrival in the BCI FDP as a function of the distance to, and basal area of,

surrounding reproductive adult trees. We used the best-fit parameter values reported by Muller-Landau (2001) for constrained Weibull dispersal kernels with negative binomial errors to simulate seed dispersal across the BCI FDP.

Inverse modelling techniques represent an improvement over previous methods used to characterize seed dispersal patterns (Nathan & Muller-Landau 2000), but nonetheless have several limitations. For example, fitted dispersal kernels are based on the assumption that an individual's fecundity is determined solely by its basal area. In addition, seed dispersal is often spatially patchy, particularly for animal dispersed species, making it difficult to accurately predict seed arrival into small plots (e.g. 1-m²). However, in the present study we sum predicted seed rain within 20 × 20 m quadrats (see below), presumably smoothing over much of the small-scale variation. There has also been debate in the literature about which dispersal kernel function provides the most accurate description of true seed dispersal patterns (Clark *et al.* 1999; Nathan & Muller-Landau 2000; Greene *et al.* 2004). This debate has largely focused on the ability of different functions to correctly capture the tail of the dispersal kernel. Here, however, differences in the frequency of long distance dispersal events are unlikely to effect our conclusions, as such events are rare and therefore make a negligible contribution to seed density estimates. Thus, for our purposes seed dispersal simulations can provide a reasonably accurate description of seed rain patterns in the absence of empirical data. Nonetheless, as with any analysis based on predicted rather than observed data, we interpret the results with caution.

Species-specific dispersal kernels were available for 42 out of the 80 species that we tested for small and large tree habitat associations. For those species significantly associated with a habitat (based on the analyses described above), we used information on the spatial location and d.b.h. of reproductive-sized adults (as

defined in Muller-Landau 2001) from the 2000 census of stems ≥ 1 cm d.b.h. to predict seed rain into each 1-m² seedling plot. We then summed the total predicted number of seeds in the 16 1-m² seedling plots located within each 20 × 20 m quadrat. We eliminated 20 × 20 m quadrats on the border of the FDP, leaving 1104 non-edge quadrats, as a high proportion of seeds dispersing into edge quadrats were likely to have come from trees located outside of the plot. As we did for small and large trees, we calculated the adjusted density of seeds in each habitat type. We then bootstrapped 95% confidence intervals around the adjusted seed density measures by randomly drawing 1104 20 × 20 m quadrats 1000 times with replacement. Adjusted seed density values significantly > 1 indicate higher seed arrival in the favoured habitat compared with other habitats. We also inferred whether seedling establishment rates were higher or lower in the favoured habitat by testing whether the adjusted density of small trees fell outside of the 95% confidence intervals around the adjusted density of seeds. All analyses were carried out using the software package R version 2.1.0 (R Development Core Team 2005).

Results

SMALL AND LARGE TREE HABITAT ASSOCIATIONS

A total of 30 out of the 80 species examined were significantly and positively associated with one or more of the five habitat types at the small or large tree stage. Nineteen significant species–habitat associations were detected at the small tree stage, and 18 at the large tree stage. (Exact *P*-values and adjusted densities for all species can be found in Appendix S1 in Supplementary Materials.) Species were typically associated with only a single habitat at a given life stage, with the exception of *Trichilia tuberculata*, which was associated with both the high plateau and swamp habitats at the small tree stage.

Few species exhibited extremely strong habitat associations, as indicated by adjusted density values. Only eight species had adjusted densities > 3 in the habitat that they were significantly associated with (see Appendix S1). The most strongly associated species was *Psychotria graciliflora*, with adjusted density values of 26.7 and 30.4 at the small and large tree stages, respectively. In contrast, most species exhibited weaker associations, with 17 species having adjusted densities ≤ 2 and seven species having adjusted densities between 2 and 3 in their associated habitat types.

For most of the species exhibiting significant habitat associations, the associations were not consistent at the two life stages. Twelve species were associated with a habitat only at the large tree stage and another 12 only at the small tree stage. Only five species were associated with the same habitat at both the small and large tree stages: one species with the low plateau, two with the
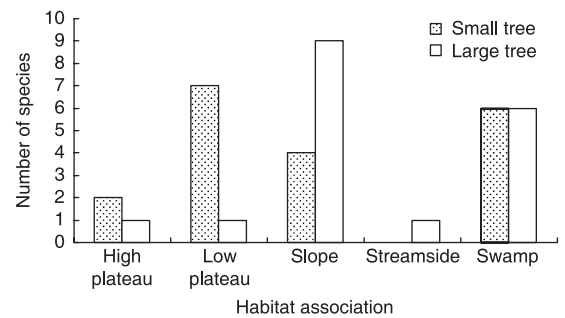

Fig. 2 Number of species associated with each of five habitat types at the small and large tree stages in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama. Torus-translation randomization tests were used to assess the significance of habitat associations for 80 tree and shrub species (see text for details).

swamp, and two with the slope habitat (Fig. 1). One species, *Tabebuia rosea*, was significantly associated with different habitats at the small and large tree stages (small tree stage, slope; large tree stage, swamp). Overall, the number of associations with each habitat type also differed between the small and large tree stages (Fig. 2). More than twice as many species were associated with the slope habitat at the large tree stage compared with the small tree stage. There were also more significant associations with the low plateau at the small, rather than large, tree stage (Fig. 2). However, it must be remembered that a more conservative cut-off of *P* = 0.0005 was used to test for significance in the low plateau at the large tree stage due to the large number of expected false positives (Table 1).

Despite differences in habitat associations at the two stages, comparisons of the adjusted densities of small and large trees in each habitat revealed that species with high large tree density in a habitat tended also to have high small tree density in that habitat, and vice versa (Fig. 3; see Appendix S1). In general, the similarity in adjusted density values at the two life stages suggests that most species do not experience large shifts in distribution with respect to habitat type between the small and large tree stages. However, some species did show large differences in adjusted density between the two stages, particularly in the swamp and streamside habitats (Fig. 3e,f). For example, four species (*Cecropia insignis*, *Faramea occidentalis*, *Trichilia tuberculata* and *Stylogyne turbacensis*) were positively associated with the swamp habitat at one life stage, but had adjusted densities of < 1 in the swamp at the other stage.

SEED DISPERSAL PATTERNS

Simulations of seed rain suggest that when a species is associated with a habitat at the large tree stage, seed density is often significantly higher in the associated habitat compared with other habitats. Specifically, we found that, of the 12 cases where a species was significantly associated at the large tree stage and seed
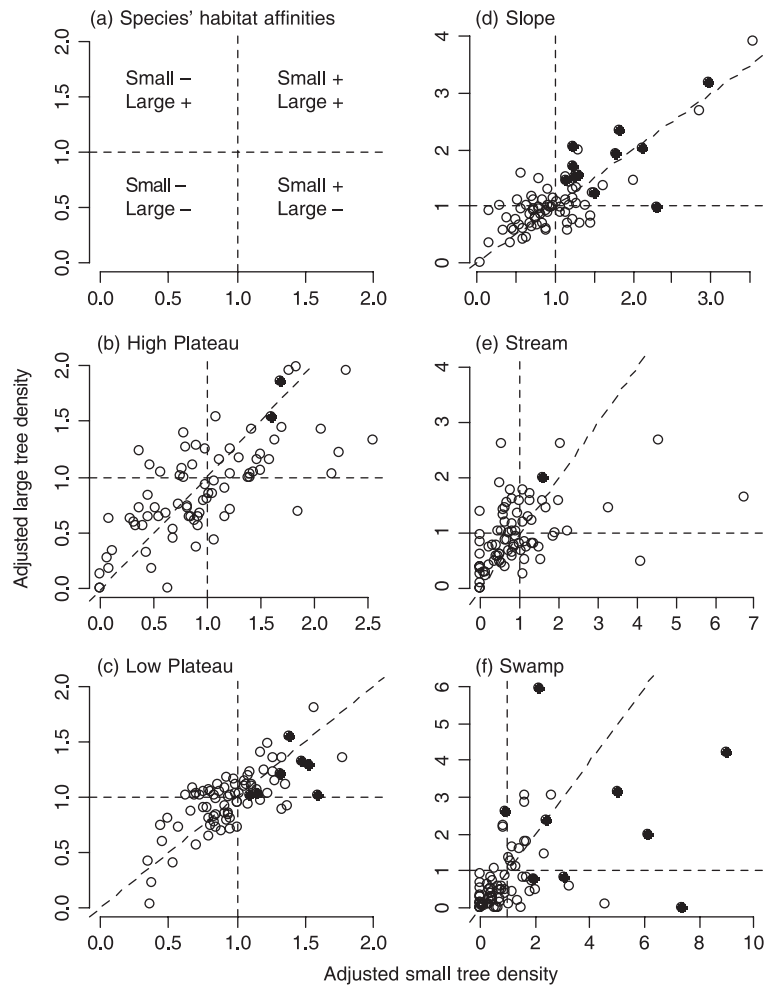
Fig. 3 Adjusted density of small and large trees of 80 species in the high plateau (b), low plateau (c), slope (d), streamside (e) and swamp (f) habitats of the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama. Adjusted density values > 1 indicate a positive affinity for the habitat, while values < 1 indicate a negative affinity (see Panel a). Species with identical adjusted densities at the small and large tree stages fall along the dashed 1:1 diagonal line. Black filled circles represent species that were significantly associated with the habitat at the small or large tree stage. For the swamp habitat (e), one species with extremely high adjusted density in that habitat (*Psychotria graciliflora*) was omitted from the plot for clarity.

dispersal kernels were available, the adjusted density of seeds in a species' associated habitat was significantly > 1 in eight (Table 2). This included all three species associated with the same habitat at the small and large tree stage for which seed dispersal information was available. Half of the species associated with a habitat only at the seedling stage also showed higher adjusted density of seeds in the species' associated habitat, despite the lack of association at the large tree stage.

For four out of the 12 species associated with a habitat at the large tree stage, small tree adjusted densities were significantly higher than adjusted densities of seeds in the associated habitat, suggesting that higher seedling establishment in preferred habitats contributes to habitat associations of these species (Table 2). However, four other species had significantly lower adjusted density of small trees than seeds, suggesting lower rates of seedling establishment in the preferred habitats of large trees. By comparison, in six out of the eight cases

where associations occurred at the small tree stage and seed dispersal could be simulated, the adjusted density of small trees was significantly higher than that of seeds in the associated habitat, and only one species had significantly lower adjusted density of small trees than seeds (Table 2).

Discussion

SMALL AND LARGE TREE HABITAT ASSOCIATIONS

For the 80 common species examined here, we detected 37 significant associations (among 30 species) with one of the five topographic habitat types at the small or large tree stage. Despite similar numbers of associations occurring at the two stages, associations were seldom consistent across stages. Species that were significantly associated with a habitat at one stage were usually not

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Table 2 Adjusted density of seeds and small trees for species significantly associated with one or more habitat type at the small or large tree stage in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama. Seed dispersal simulations were used to predict seed density into each habitat type. Species with adjusted seed density values significantly greater than one (in bold) had higher seed arrival in the favoured habitat relative to other habitats. Adjusted small tree density values significantly greater than adjusted seed density values (in bold) imply higher seedling establishment in the associated habitat type, while significantly lower values (italic) imply lower seedling establishment

Species	Habitat type	Seed adjusted density	Seed adjusted density 95% CI	Small tree adjusted density
Associated with habitat only at small tree stage				
Trichilia tuberculata	High	**1.19**	(1.03–1.36)	**1.61**
Coussarea curvigemmia	Low	**1.47**	(1.39–1.55)	1.38
Desmopsis panamensis	Low	0.95	(0.91–1)	**1.1**
Garcinia intermedia	Low	0.87	(0.8–0.94)	**1.15**
Tetragastris panamensis	Low	**1.27**	(1.21–1.34)	1.32
Tabebuia rosea	Slope	**1.72**	(1.42–2.03)	**2.31**
Faramea occidentalis	Swamp	0.67	(0.53–0.81)	**1.93**
Trichilia tuberculata	Swamp	1.25	(0.88–1.64)	**3.08**
Associated with same habitat at small and large tree stage				
Ouratea lucens	Low	**1.31**	(1.25–1.37)	**1.47**
Ocotea whitei	Slope	**2.83**	(2.58–3.11)	2.97
Unonopsis pittieri	Slope	**1.47**	(1.32–1.64)	**1.78**
Associated with habitat only at large tree stage				
Beilschmiedia pendula	Slope	1.19	(0.98–1.41)	1.22
Calophyllum longifolium	Slope	0.64	(0.53–0.74)	**1.24**
Cordia lasiocalyx	Slope	**1.57**	(1.43–1.72)	*1.14*
Guarea guidonia	Slope	**1.4**	(1.3–1.51)	*1.25*
Hirtella triandra	Slope	**1.55**	(1.44–1.67)	*1.3*
Xylopia macrantha	Slope	**2.46**	(2.13–2.81)	*1.83*
Brosimum alicastrum	Stream	1.02	(0.33–2.04)	1.6
Tabernaemontana arborea	Swamp	1.16	(0.44–2.11)	**2.38**
Tabebuia rosea	Swamp	**2.26**	(1.3–3.47)	2.12

associated with that habitat at the other stage. Similarly, in an analysis of seedling and adult tree habitat associations in a Bornean forest, Webb & Peart (2000) found only two out of 22 species associated with the same physiographic habitat type at both stages. In a separate study of habitat associations in Borneo, Paoli *et al.* (2006) found that only two out of 16 Dipterocarp species were significantly associated with the same habitat at both the juvenile and adult stages (defined as 1–10 cm d.b.h. and ≥ 10 cm d.b.h., respectively). Thus, it appears that few of the tropical tree species tested thus far show consistent associations with a single habitat type across multiple life stages, and that associations observed at later life stages are typically not the result of higher seedling establishment in the associated habitat relative to other habitats. Comparisons of adjusted densities at the small and large tree stages revealed that the differences in habitat associations typically resulted from small to moderate, habitat-mediated shifts in species distributions between the two life stages. However, a few species significantly associated with a habitat at one stage exhibited a negative affinity (i.e. adjusted density < 1) for that habitat at the other stage (Fig. 3).

For species that were associated with a given habitat at only the large tree stage, the lack of association at the small tree stage likely resulted from seed dispersal and seedling establishment outside of the favoured habitat (Webb & Peart 2000). However, as seed density is often higher in the preferred habitat of large trees, the lack of association at the small tree stage may also be the result of lower seedling establishment in the habitat. This is supported by the fact that for a third of the species associated with a habitat at the large tree stage, the adjusted density of small trees was significantly lower than that of seeds. In contrast, in cases where species were associated with a habitat at the small tree stage, our results support the idea that the association is a result of higher seedling establishment in the favoured habitat. For species associated with a habitat only at the small tree stage, the subsequent loss of association as small trees grow into the large tree stage would result from lower survival over time in the habitat with which small trees were associated. In some cases, species significantly associated with a habitat only at the small tree stage had higher predicted seed densities in the associated habitat, despite the lack of association at the large tree stage. This could result from high densities of reproductive adults in adjacent areas dispersing seeds into the habitat. Alternatively, these species may have a high density of reproductive adults or several highly fecund individuals present in the habitat, but not a higher overall density at the large tree stage, which includes all stems ≥ 1 cm d.b.h.

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Differences in species habitat associations between life stages suggest that sites that are initially beneficial for establishment and survival may not be suitable for continued survival at later stages, and vice versa. Such conflicts have been documented in a variety of environments and can arise for various reasons (Schupp 1995; Battaglia *et al.* 2000; Dovciak *et al.* 2003). For example, high seedling establishment rates in a habitat would result in a high density of small trees in that habitat. If negative density dependence in survival outweighs the benefits of the habitat, then survival would be reduced in the habitat with which small trees were associated and later life stages would therefore not be associated with that habitat (Webb & Peart 2000). Similarly, higher seed arrival in the preferred habitat of adult trees could result in low seedling establishment rates due to negative density dependence during germination and establishment. Studies from both temperate and tropical forests have shown that seed-to-seedling transition rates and survival of established seedlings are frequently density or distance dependent, resulting in shifts in species' distributions from one life stage to the next (Clark & Clark 1984; Wada & Ribbens 1997; Harms *et al.* 2000; Packer & Clay 2000; Lambers *et al.* 2002).

Alternatively, conflicts between species' habitat associations at different life stages may result from ontogenetic shifts in resource requirements rather than negative density dependence. Multiple studies have demonstrated shifts in tree species' light requirements from the seedling to adult stage (Clark & Clark 1992; Grubb 1996; Dalling *et al.* 2001; Lusk 2004; Poorter *et al.* 2005), as well as ontogenetic shifts in many physiological and morphological traits related to light capture (Kitajima & Fenner 2000). Similar size-dependent shifts in water use are known to occur in more arid systems (Donovan & Ehleringer 1992) and may underlie the conflicting small and large tree habitat associations observed here. We also cannot rule out the possibility that the observed differences in habitat association between the two stages are a result of shifts in rainfall patterns or other environmental variables during the lifetime of the trees in our study, such that the suitability of a habitat when small trees became established differed from the suitability of that habitat when large trees became established.

In addition to within-species differences in habitat associations, we also found differences in the number of species associated with each habitat at the two life stages (Fig. 2). Most notably, most associations at the large tree stage were with the wet, well-drained slope habitat, while only half as many species were associated with slopes at the small tree stage. Drought resistance has been shown to vary widely among tree species found on BCI (Engelbrecht & Kursar 2003) and correlates with species distributions on plateau vs. slope sites (Engelbrecht *et al.*, in press). Observed associations with slope habitats at the large tree stage are likely to result from lower survival of drought-sensitive species in drier habitats over time or during occasional severe

droughts such as those associated with El Niño events on BCI (Condit *et al.* 1995). At earlier life stages, however, differences in soil water availability may be less influential than other factors. Daws *et al.* (2005) reported elevated wet season mortality of new seedlings on slopes on BCI, potentially due to damage from water flow or to higher pathogen activity in the wetter environment. Thus, for at least some species, drier habitats may be safer for seedlings, which are highly vulnerable to physical damage and pathogen attack. This may explain the higher number of associations with the drier plateau habitats at the small tree stage. However, this pattern is largely the result of fewer associations with the low plateau at the large tree stage, where the more conservative *P*-value of 0.0005 was used as the cut-off for statistical significance due to the large number of expected false positives. Similar numbers of associations with low plateau would be found at the small and large tree stages if a cut-off of $P = 0.01$ was used for both stages (see Appendix S1). Seven additional species were associated with the low plateau habitat at the large tree stage at values of $P < 0.01$. Only two of these seven species were significantly associated with the low plateau at the small tree stage ($P < 0.01$), while the other five showed no significant associations at the small tree stage. Thus, while a larger number of species would be considered significantly associated with the low plateau at the large tree stage had we used a cut-off of $P < 0.01$, the overall pattern of species exhibiting inconsistent associations at the two life stages would not change.

ROLE OF SEED DISPERSAL

Simulations of seed rain across the landscape revealed that two-thirds of species associated with a habitat at the large tree stage are predicted to have higher seed densities in the associated habitat relative to other habitat types. This indicates that limited dispersal acts to reinforce species' associations with preferred habitats and may maintain associations formed as a result of historical climatic conditions or rare events, such as severe droughts. We also found some evidence of higher seedling establishment rates in the associated habitat compared with other habitats (as indicated by significantly higher adjusted density of small trees than seeds in the associated habitat); however, this was the case for only a third of species associated with a habitat at the large tree stage, and an equal number of species appeared to have lower rates of seedling establishment in the habitat that large trees of the species were associated with. This suggests that most species habitat associations do not begin to form during early life stages. Seed addition or seedling transplantation experiments are needed to fully assess whether seedling establishment and survival are higher or lower outside of the associated habitats.

Approximately one-third of the species associated with a habitat at the large tree stage did not have higher

seed densities in their preferred habitats, indicating that their seeds are often dispersed outside of the habitat. For these species, associations are likely to result from a contraction of the species' distributions over time due to higher survival in the preferred habitats. This is more likely to occur when species are associated with smaller habitats. The streamside and swamp habitats in our study were substantially smaller than the other three habitat types, which would explain why large differences in adjusted densities between the small and large tree stages occurred most frequently in these two habitats.

Conclusions

Our analyses of species' habitat associations suggest that species' ecological habitat preferences can differ between developmental stages, as most species were not associated with the same habitat type at different life stages. These results also suggest that habitat associations of adult trees are not the result of regeneration niche differences, as such associations are rarely evident at earlier life stages. Rather than focus on regeneration niche differences, theories of coexistence should be expanded to consider the importance of niche shifts during development.

The topographic habitat types defined here are known to vary in soil moisture availability and drainage; however, we cannot rule out the possibility that observed species' associations with those habitats result from historical events, biotic interactions, such as pathogen or herbivore pressure (e.g. Fine *et al.* 2004), or variation in other abiotic variables, such as nutrient availability (e.g. Newbery & Proctor 1984). Observations of species' performance in different habitats coupled with experiments manipulating seed and seedling distributions would provide further understanding of processes driving the observed patterns of habitat associations. The results presented here emphasize the need for such future studies to include multiple life stages when examining species' habitat preferences.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Adjusted densities of small and large trees of 80 species in five habitat types in the Barro Colorado Island 50-ha Forest Dynamics Plot, Panama.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01229.x

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