

Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest

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Summary

1. Ecologists have long recognized that plant performance is affected by the density and composition of neighbouring individuals. With the advent of highly resolved species-level phylogenies, it has become possible to test whether such density-dependent neighbourhood interactions are also phylogenetically dependent. Most studies of density dependence have focused on a single life stage; however, the relative importance of different neighbourhood interactions may shift over the lifetime of an individual.

2. We examined effects of conspecific neighbour density, heterospecific neighbour density and average phylogenetic relatedness of heterospecific neighbours on the survival of seedlings, saplings, juveniles and adult trees of 29 focal tree species using long-term, spatially explicit forest dynamics data and a highly resolved DNA barcode phylogeny from the tropical forest of Barro Colorado Island (BCI), Panama.

3. Our results show a decline in the strength of conspecific negative density dependence across life stages: strong negative conspecific neighbour effects at early life stages gave way to weak positive conspecific neighbour effects for adult trees. In contrast, the effect of heterospecific neighbour density on survival showed no clear trend with life stage.

4. We found evidence of phylogenetic density dependence in the BCI forest, with a significant negative impact of neighbourhood relatedness on focal tree survival, but only for later life stages. In contrast to studies from other tropical forests, neighbourhood relatedness had a significant positive effect on seedling survival.

5. Furthermore, we found that focal species varied much more widely in their sensitivity to conspecific neighbour density than in their reactions to heterospecific neighbour density or phylogenetic relatedness.

6. *Synthesis.* Overall, our results demonstrate that both conspecific density dependence and phylogenetic density dependence influence tropical tree survival, but that their relative importance varies with life stage and among species. Our study highlights the need to incorporate multiple life stages and multiple species when assessing the factors contributing to individual survival and species coexistence for long-lived organisms.

Key-words: density dependence, determinants of plant community diversity and structure, Janzen–Connell hypothesis, neighbourhood analysis, phylogenetic relatedness, seedlings dynamics, species coexistence, tropical forest

Introduction

Neighbourhood interactions have long intrigued ecologists seeking to explain the maintenance of diversity in plant com-

munities (Harper 1977; Goldberg 1987; Stoll & Weiner 2000; Wright 2002). One prominent explanation for species coexistence that focuses on such neighbourhood interactions is the Janzen–Connell hypothesis (Janzen 1970; Connell 1971). This hypothesis assumes host-specific natural enemies, such as pathogens and herbivores, drive conspecific neighbour interac-

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tions in tropical tree communities. According to the hypothesis, an individual will have a low probability of recruitment and survival when located close to a conspecific tree or when surrounded by a high density of conspecific neighbours, thus leaving space for other species to recruit and slowing competitive exclusion. Community-level studies from both temperate and tropical forests have found strong evidence of conspecific negative density dependence (NDD) at neighbourhood scales (Harms *et al.* 2000; Hille Ris Lambers, Clark & Beckage 2002; Stoll & Newbery 2005; Queenborough *et al.* 2007; Carson *et al.* 2008; Comita & Hubbell 2009; Metz, Sousa & Valencia 2010; Zhu *et al.* 2010; Johnson *et al.* 2012).

In contrast, effects of heterospecific neighbour density on tree performance are generally weaker overall compared to effects of conspecific neighbours (Comita *et al.* 2010; Johnson *et al.* 2012). However, the grouping of neighbours into conspecifics vs. heterospecifics may be overly simplistic, as indicated by studies demonstrating that the identity of heterospecific neighbours can influence their effects (Uriarte *et al.* 2004). In particular, recent studies have found that neighbours belonging to species that are more closely phylogenetically related to the focal individual have a stronger impact on focal plant survival (Webb, Gilbert & Donoghue 2006; Metz, Sousa & Valencia 2010; Liu *et al.* 2012; Paine *et al.* 2012; Ness *et al.* 2013) in keeping with the idea that ecological interactions (e.g. competition, herbivory and pathogen transmission) are typically phylogenetically conserved (Novotny *et al.* 2002; Gilbert & Webb 2007; Bagchi, Press & Scholes 2010; Gómez, Verdú & Perfectti 2010; Liu *et al.* 2012; but see Cahill *et al.* 2008).

While community-wide studies have generally detected density-dependent patterns of mortality, not all species are equally impacted by their biotic neighbourhoods. Specifically, several recent studies have reported that the strength of conspecific neighbour effects varies widely among tree species (Comita & Hubbell 2009; Comita *et al.* 2010, 2014; Mangan, Herre & Bever 2010; Johnson *et al.* 2012; Lin *et al.* 2012). Furthermore, several of these studies (Comita *et al.* 2010; Johnson *et al.* 2012) have found that the strength of conspecific NDD (i.e. the effect on a per-neighbour basis) is correlated with species relative abundance, suggesting that a species' sensitivity to conspecific neighbours plays a role in determining whether the species is common or rare within the community. In contrast, effects of heterospecific neighbours appear to vary much less among species and to be unrelated to species relative abundance (Comita *et al.* 2010; Johnson *et al.* 2012). However, the degree to which tree species within a community are differentially impacted by the phylogenetic relatedness of their heterospecific neighbours is not known. If phylogenetic neighbourhood effects on survival vary widely among species, then the strength of phylogenetic density dependence may play a role in shaping the relative abundance and spatial distribution of species (and clades) within communities.

The relative importance of conspecific and heterospecific neighbour effects may shift over the lifetime of a tree (Hubbell *et al.* 2001; Peters 2003; Newbery & Stoll 2013; Piao *et al.* 2013). Conspecific NDD is often hypothesized to be

most evident at earlier life stages (e.g. seedling recruitment; Harms *et al.* 2000; Hille Ris Lambers, Clark & Beckage 2002) due to high initial densities resulting from limited seed dispersal (Nathan & Muller-Landau 2000), combined with higher susceptibility to natural enemies for juveniles compared to adult trees (Gilbert, Hubbell & Foster 1994). Strong conspecific NDD at early stages may thin conspecific neighbour densities to the point that conspecific interactions become negligible at later stages. At the same time, there may be an increase in the intensity of competition for light, water and soil nutrients as trees grow larger, leading to an increase in the impact of heterospecific neighbours. The relative importance of phylogenetic relatedness of neighbours may also show shifts across life stages. However, studies incorporating phylogenies into neighbourhood analysis have thus far been largely restricted to the seedling stage (but see Gonzalez *et al.* 2009; Uriarte *et al.* 2010).

Assessing neighbourhood effects across multiple life stages and for multiple species is a critical step in understanding how intra- and interspecific interactions structure ecological communities and maintain diversity, since it is the cumulative impact of such interactions across the lifetime of an individual that ultimately determines its fitness. Here, we examine conspecific, heterospecific and phylogenetic neighbourhood effects on survival from the seedling through adult tree stage for 29 focal tree species in the tropical moist forest of BCI, Panama. Using long-term, spatially explicit demographic data (Hubbell & Foster 1983; Condit 1998; Comita *et al.* 2007a, 2010), combined with a well-resolved community phylogeny (Kress *et al.* 2009), we addressed the following questions concerning neighbourhood effects on survival: (i) Does the relative importance of conspecific vs. heterospecific neighbourhood effects vary across life stages (i.e. seedling, sapling, juvenile and adult stages)? (ii) Is there evidence for phylogenetic density dependence in the BCI forest, and if so, are effects consistent across life stages? and (iii) How widely do species vary in their sensitivity to conspecific, heterospecific and phylogenetic neighbourhood effects?

Materials and methods

STUDY SITE AND DATA COLLECTION

This study was conducted in the 50-ha forest dynamics plot on BCI, Panama (9°9' N, 79°51' W). All trees and shrubs ≥ 1 cm dbh in the plot were mapped, identified to species and measured (diameter at 1.3 m, dbh) initially in 1980–1982, and again at 5-year intervals starting in 1985 (Hubbell & Foster 1983; Condit 1998). Starting in 2001, free-standing woody seedlings ≥ 20 cm tall and < 1 cm dbh were identified and measured every 1 to 2 years in 20 000 1-m² permanent plots located in the centre of each 5 × 5 m subquadrat of the 50-ha plot (Comita *et al.* 2007a, 2010). To date, > 350 000 individuals ≥ 1 cm dbh and > 160 000 seedlings have been measured in the BCI forest dynamics plot. In the present study, we used data from seven censuses of stems ≥ 1 cm dbh (1982–2010) and from two censuses of seedlings (2001–2006) to examine neighbourhood effects on survival across ~5-year census intervals. To calculate phylogenetic relatedness of neighbours, we used the species-level molecular community

phylogeny generated by Kress *et al.* (2009) based on a DNA barcode library of three markers (rbcL, matK and trnH-psbA). The phylogeny included 281 of the 325 tree and shrub species identified in the censuses described above.

FOCAL SPECIES AND LIFE-HISTORY STAGES

We assigned each individual in each census to one of four life-history stages [following the classification of Peters (2003)]: seedlings (≥ 20 cm tall – < 1 cm dbh), saplings (1–4.9 cm dbh), juveniles (5–9.9 cm dbh) and adults (≥ 10 cm dbh). We analysed survival in 29 focal tree species that met the following criteria: they were included in the BCI plot phylogeny, and they had at least 40 individuals in each of the above size classes in every census (Table S1 in Supporting Information).

DATA ANALYSIS

To examine neighbourhood effects on individual survival at multiple life-history stages, we used generalized linear mixed-effects models (GLMMs; Gelman & Pardoe 2006; Bolker *et al.* 2009) with binomial errors to model individual survival (lived/died) as a function of conspecific neighbour density, heterospecific neighbour density and phylogenetic relatedness of heterospecific neighbours to the focal tree. Conspecific and heterospecific neighbour densities were calculated by summing the basal area of conspecific neighbours and heterospecific neighbours ≥ 1 cm dbh within a given radius (5, 10, 15 or 20 m) of each focal individual, respectively. Seedlings may also be strongly influenced by other seedling neighbours or may be more strongly impacted by large trees than neighbouring saplings. Therefore, for seedlings, we also ran models in which neighbour densities were calculated as the number of conspecific and heterospecific seedling neighbours within the 1-m² plot where the focal seedling was located or as the basal area of conspecific and heterospecific neighbours ≥ 10 cm dbh within a given radius of the focal seedling.

To test for phylogenetic density dependence, the phylogenetic relatedness of heterospecific neighbours to the focal individual was calculated using the methods described in Metz, Sousa & Valencia (2010). Briefly, we calculated the mean observed phylogenetic distance between the focal individual and all other individuals within the given radius (or within the same seedling plot, for seedling neighbours) using summed branch lengths from the BCI plot phylogenetic tree of Kress *et al.* (2009). To correct for variation in species richness among neighbourhoods (Webb 2000; Kraft *et al.* 2007), we used a null model to randomly generate 10 000 local neighbourhood communities for a given species richness and then calculated the mean and standard deviation of expected phylogenetic distances among species for the neighbourhood of each focal individual. Species were drawn from the pool of all species in the phylogeny for neighbours ≥ 1 cm dbh and from the pool of species in the phylogeny that also occurred in the seedling census for seedling neighbours, weighted by their abundance in the respective census. We then calculated a standard effect size as follows:

$$NRI = \frac{-1 \times (\text{mean observed phylogenetic distance} - \text{mean expected phylogenetic distances})}{\text{standard deviation of expected phylogenetic distances}}$$

where NRI stands for Neighborhood Relatedness Index. Note that this index is identical to that used by Metz, Sousa & Valencia (2010), which differs slightly from the NRI of Webb *et al.* (2002) in that the

observed phylogenetic distance is the mean distance of all neighbours to the focal seedling and not the mean of all pairwise distances. Only species included in the phylogeny were included in calculations of heterospecific neighbour density and phylogenetic relatedness. Exclusion of species not in the phylogeny is not expected to have a major impact on our results since the 281 species included in the phylogeny make up ~94% of the individuals ≥ 1 cm dbh and >85% of the seedlings in the plot censuses.

For each of the four life stages, we ran a basic mixed-effects model of survival, which is as follows: $\ln(-\ln(1 - p_{ijk})) = \beta_{0j} + \beta_{1j} \times \text{size}_{ijk} + \beta_2 \times \text{CON}_{ijk} + \beta_3 \times \text{HET}_{ijk} + \beta_4 \times \text{NRI}_{ijk} + \beta_5 \times \text{INT}_k + \Phi_i$, where p_{ijk} is the predicted survival probability of each individual i of species j across census interval k as a function of initial size, census interval and neighbourhood variables (all fixed effects), along with random effects to account for variation among species and quadrat l (Φ_l). Specifically, neighbourhood variables included conspecific neighbour density (CON), heterospecific neighbour density (HET) and NRI, all calculated based on the neighbourhood composition and basal area at the start of the specific census interval (i.e. in census k for observations of survival from census k to census $k + 1$). Since the model included observations of survival from multiple censuses, census interval (INT) was included as a categorical fixed effect to take into account temporal variation in community-wide survival probabilities (e.g. due to drought events in some census intervals). Since initial size can significantly affect survival (Comita *et al.* 2009; Wang *et al.* 2012; Piao *et al.* 2013), we also included log-transformed size at the start of the specific census interval (dbh for saplings, juveniles and adults; height for seedlings) as a fixed effect in the model. To minimize model complexity, we did not include any interaction terms for the fixed effects in the basic model. For all life stages, we included species as a random effect in the model, since species' baseline survival rates can vary widely. We also included a random effect that allowed the effects of initial size to vary among species (i.e. varying slope), since species may show different relationships between size and survival. Because individuals located close to each other are likely to have similar probabilities of survival (i.e. spatial autocorrelation), we divided the plot into 20×20 m quadrats and assigned each individual ≥ 1 cm dbh to the quadrat number where it was located. For seedlings, quadrat was the 1×1 m seedling plot in which the individual was located. Quadrat was then included as a random effect in the model for each life stage. Values for all continuous independent variables were standardized prior to entering the model by subtracting the mean of the variable and dividing by one standard deviation. We ran the basic model for each life stage using four different neighbourhood radii: 5, 10, 15 and 20 m away from focal individuals (except when testing for effects of seedlings neighbour density, which was always calculated at the 1-m² scale). We compared models with different neighbourhood radii using AIC and BIC and found that while the best model varied with life stage (Table S2), all neighbourhood sizes gave qualitatively similar results (Fig. 1 and Fig. S1). We present results of the models with a 15 m neighbourhood radius in the main text (i.e. the best fit for juveniles and adult trees) and show results for models with other neighbourhood radii in Fig. S1.

Furthermore, to better understand changes in neighbourhood effects on individual survival with size, we also tested for a significant interaction between each neighbourhood variable and plant size (dbh, as a

continuous variable). We ran this model for all stems ≥ 1 cm dbh combined (as opposed to divided into size classes). Seedlings were not included in this particular analysis because seedling size was measured as height, rather than dbh.

To determine how much focal species vary in their responses to neighbourhood variables, we ran the same basic model as described above, but included random effects that allowed for variation among species in the effects of conspecific neighbour density (β_{2j}), heterospecific neighbour density (β_{3j}) and heterospecific neighbour relatedness (β_{4j}): $\ln(-\ln(1 - p_{ijk})) = \beta_{0j} + \beta_{1j} \times \text{size}_{ijk} + \beta_{2j} \times \text{CON}_{ijk} + \beta_{3j} \times \text{HET}_{ijk} + \beta_{4j} \times \text{NRI}_{ijk} + \beta_5 \times \text{INT}_k + \Phi_l$. To test whether there was significant variation among species for each neighbourhood variable individually, we compared the model with and without variation among species in that neighbourhood effect (e.g. the basic model vs. $\ln(-\ln(1 - p_{ijk})) = \beta_{0j} + \beta_{1j} \times \text{size}_{ijk} + \beta_{2j} \times \text{CON}_{ijk} + \beta_3 \times \text{HET}_{ijk} + \beta_4 \times \text{NRI}_{ijk} + \beta_5 \times \text{INT}_k + \Phi_l$, to test for variation among species in conspecific effects) for each life stage and each neighbourhood variables separately. We tested for a significant difference between those models using a likelihood ratio test (Bolker *et al.* 2009). Our census intervals are not all identically spaced, so we included a complementary log–log link and time offset of the log-transformed years in all models (Egli & Schmid 2001; Paine *et al.* 2012). All analyses were performed in the R 3.0.3 statistical software package (R Development Core Team 2014) with GLMMs run using the ‘lme4 1.1-7’ package for R (Bates, Maechler & Bolker 2012). The R code used to run the models is provided as Supporting Information (see Appendix S1).

Results

CONSPECIFIC AND HETEROSPECIFIC NEIGHBOUR EFFECTS ACROSS LIFE STAGES

Density of conspecific neighbours had a significant impact on survival at all life stages, but varied from strongly negatively at the seedlings stage to weakly positive for adult trees (Fig. 1a and Fig. S1a). Seedlings were negatively impacted by conspecific neighbours of all sizes, but were most strongly impacted by conspecific seedlings neighbours. There was an overall trend of decreasing strength of conspecific NDD with life stage (Fig. 1a and Fig. 2a). Moreover, when all individuals ≥ 1 cm dbh were analysed together, the interaction effect of conspecific neighbour density with dbh on survival was significantly positive, confirming that conspecific NDD becomes weaker with increasing tree size (Table 1). Interestingly, while conspecific NDD was always weakest for the adult stage compared to earlier stages, the effect of conspecific neighbour density on adult survival was significantly negative at the 5-m neighbourhood scale, but weakly positive at larger neighbourhood scales (Fig. S1a).

There was also large variation in heterospecific neighbour effects among life stages, but no clear directional trend (Fig. 1b and Fig. S1b). Seedling survival was significantly negatively impacted by the density of heterospecific neighbours ≥ 1 cm dbh, but not significantly affected by heterospecific seedling or adult tree (≥ 10 cm) neighbours (Fig. 1b).

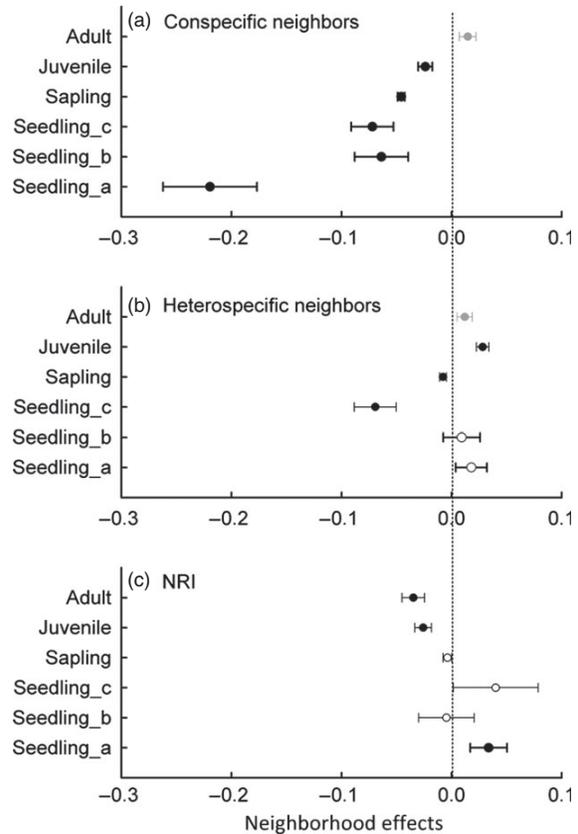


Fig. 1. Neighbourhood effects of (a) conspecific neighbours, (b) heterospecific neighbours and (c) neighbourhood phylogenetic relatedness (Neighbourhood Relatedness Index) on survival. Estimated coefficients (\pm SE) from generalized linear mixed-effects models are shown separately for four life stages for the basic model (see Materials and methods). For sapling, juvenile and adult stages, conspecific and heterospecific neighbour densities were calculated by summing the basal area of conspecific neighbours and heterospecific neighbours ≥ 1 cm dbh within 15 m of each focal individual, respectively. For the seedling stage, Seedling_a, Seedling_b and Seedling_c signify that conspecific and heterospecific neighbour densities were calculated using only seedling neighbours within the same 1-m² seedling plot, only adult trees ≥ 10 cm dbh within 15 m of the focal seedling and all individuals ≥ 1 cm dbh within 15 m of the focal seedling, respectively. Dotted lines are at zero, so that the left of the line indicates a negative effect of the neighbourhood variable on survival, while the right indicates a positive effect on survival. The black circles indicate significant effects ($P < 0.05$), grey circles signify marginally significant effects ($0.05 < P < 0.1$) and white circles mean no significance.

Saplings were also significantly negatively impacted by heterospecific neighbours ≥ 1 cm dbh, while juveniles were positively affected and adults were not significantly impacted (Fig. 1b). Where significant, effects of heterospecific neighbours on survival were weak compared to effects of conspecific neighbours (Fig. 2a,b). In the model testing for an interactive effect of size and neighbourhood variables on survival of individuals ≥ 1 cm dbh, the interaction of heterospecific neighbour density with dbh was significantly positive (Table 1), reflecting the fact that heterospecific effects were

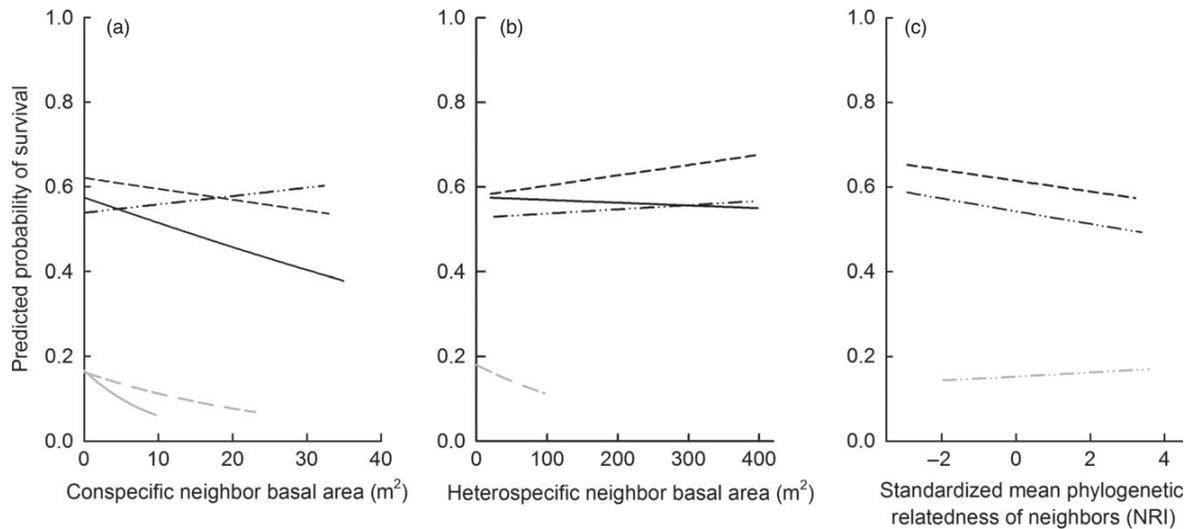


Fig. 2. Predicted effects of conspecific and heterospecific neighbour densities and phylogenetic relatedness on the probability of survival for individuals in the Barro Colorado Island forest. Only significant ($P < 0.05$) or marginally significant ($0.05 < P < 0.1$) neighbour effects are shown (Fig. 1). Lines show predictions based on model results (for the basic model; see Materials and methods), with all independent variables assigned to their mean values except the variable shown on the x-axis. Grey lines denote seedlings as focal individuals (grey dash-dotted lines = only seedling neighbours analysed; grey solid lines = only adult neighbours analysed; grey dashed lines = only neighbours ≥ 1 cm dbh analysed). Black lines are shown for saplings (solid lines), juveniles (dashed lines) and adults (dash-dotted lines).

negative at the sapling stage, but positive or insignificant at later stages (Fig. 1b).

PHYLOGENETIC DENSITY DEPENDENCE IN THE BCI FOREST

The phylogenetic relatedness of heterospecific neighbours had a significant impact on survival, but the direction and strength of the effect varied with life stages (Fig. 1c). Both juveniles and adults were significantly negatively affected by NRI, indicating that at these life stages, individuals surrounded by closely related heterospecific neighbours were less likely to survive compared to individuals whose neighbours were distantly related (Fig. 2c). In contrast, phylogenetic relatedness of seedling neighbours had a significant positive impact on seedling survival (Fig. 1c). Thus, seedlings surrounded by more closely related neighbours had a higher probability of survival. The pattern of increasing negative effect of heterospecific neighbour relatedness with size was confirmed by a significant negative interaction between dbh and NRI in the model testing for interactive effects of size and neighbourhood variables on survival of individuals ≥ 1 cm dbh (Table 1).

VARIATION AMONG SPECIES IN STRENGTH OF NEIGHBOURHOOD EFFECTS

At all life stages, the effect of conspecific neighbours varied more widely among focal species than effects of heterospecific neighbour density or phylogenetic relatedness (Fig. 3 and Fig. S2). We detected significant variation among species in conspecific neighbour effects at the sapling ($\chi^2 = 349.95$,

$P < 0.001$), but not juvenile and adult stages. For seedlings, there was significant variation among species in effects of conspecific adult tree ($\chi^2 = 33.12$, $P < 0.001$) and ≥ 1 cm dbh neighbours ($\chi^2 = 29.2$, $P < 0.001$) and marginally significant variation among species in the effect of conspecific seedling neighbours ($\chi^2 = 7.017$, $P = 0.07$). Significant variation among species in heterospecific neighbour effects was detected at the sapling ($\chi^2 = 174.8$, $P < 0.001$) and juvenile ($\chi^2 = 13.02$, $P < 0.01$) stages, and significant and marginally significant variation among species in effect of NRI was detected at the sapling ($\chi^2 = 40.79$, $P < 0.001$) and adult stages ($\chi^2 = 7.31$, $P = 0.06$), respectively. However, variation among species in effects of heterospecific neighbours and NRI was generally substantially smaller than variation in conspecific effects (Fig. 3 and Fig. S2).

Discussion

DO CONSPECIFIC AND HETEROSPECIFIC NEIGHBOUR EFFECTS VARY ACROSS LIFE STAGES?

It has long been assumed that NDD is strongest at earlier life stages, but to our knowledge, no previous study has analysed density dependence from the seedling through adult tree stage at a single site using the same methodology. Our results reveal a significant and strong impact of conspecific neighbour density on survival for our 29 focal species, consistent with previous studies of density dependence on Barro Colorado Island (Wills *et al.* 1997; Hubbell *et al.* 2001; Peters 2003; Volkov *et al.* 2009; Comita *et al.* 2010), as well as other sites (reviewed in Carson *et al.* 2008; Comita *et al.* 2014). Moreover, we found substantial differences among life

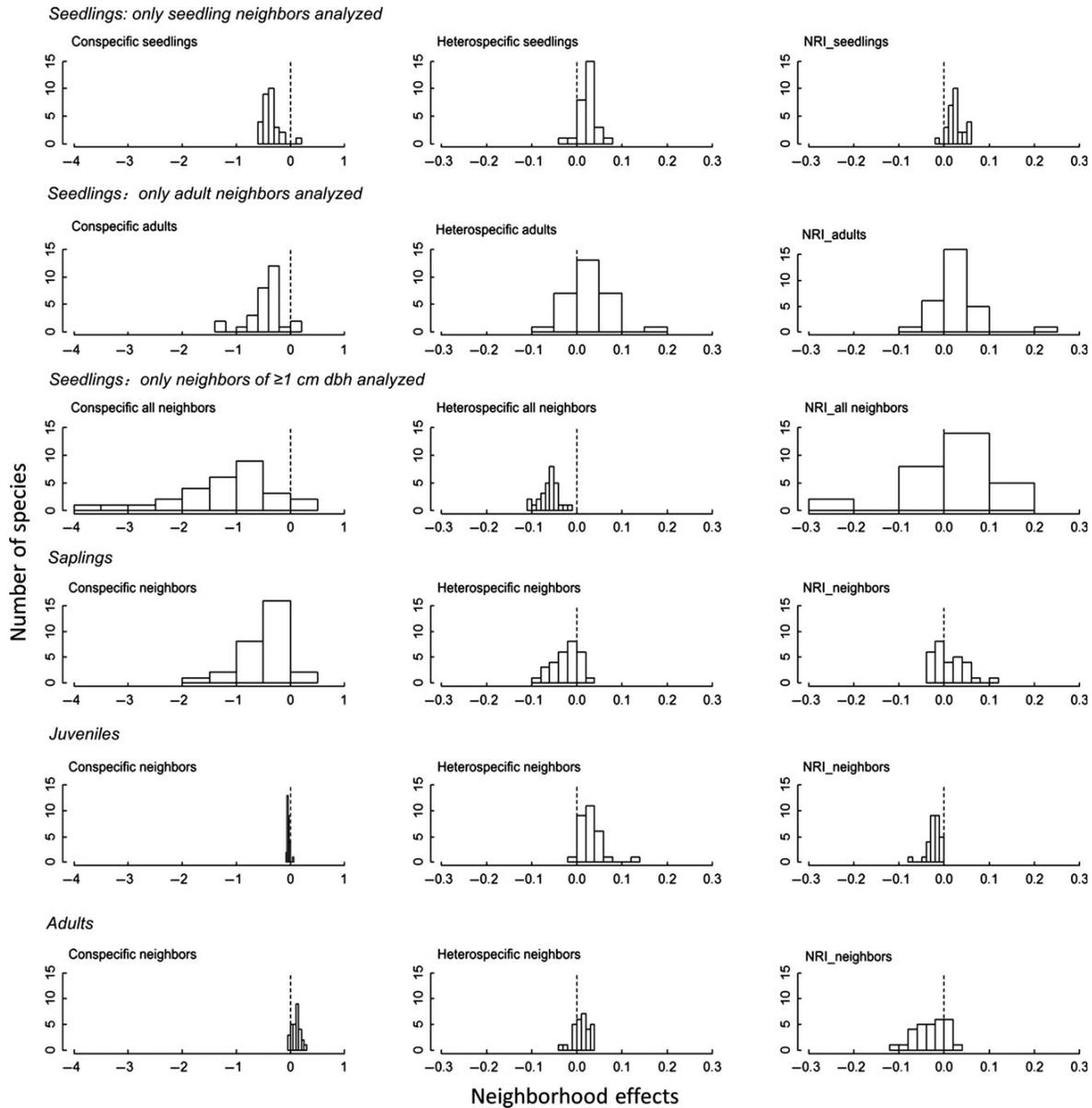


Fig. 3. Histograms showing estimates of conspecific neighbour density, heterospecific neighbour density and neighbourhood phylogenetic relatedness on survival for 29 common tree species in the Barro Colorado Island 50-ha forest dynamics plot, Panama. Note the difference in x-axis scale for conspecific neighbour effects (left column) compared to heterospecific neighbour and Neighborhood Relatedness Index (NRI) effects (centre and right columns, respectively). Results are from generalized linear mixed-effects models in which effects of all three neighbourhood variables were allowed to vary simultaneously among species. Results are shown for four different life stages: seedlings, saplings, juveniles and adults. For seedlings, three types of neighbours were analysed as follows: seedlings, adults and all neighbours ≥ 1 cm dbh. Dashed lines are at zero, so that bars to the left of the line indicate a negative effect of the neighbourhood variable on survival, while bars to the right indicate a positive effect on survival.

stages in conspecific neighbour effects, with a decrease in the strength of NDD from the seedling to sapling to juvenile to adult tree stage (Fig. 1). A positive interaction between size and conspecific neighbour effects verified that the negative effect of conspecific neighbours becomes weaker with increasing tree size (Table 1). Our results confirm that earlier life stages are more strongly impacted by conspecific neigh-

bours. This lends support to the idea that density-dependent survival at seedling and sapling stages, in particular, plays a significant role in fostering tree species coexistence and maintaining diversity in tropical forests.

The decreasing conspecific NDD with increasing plant size observed here likely reflects a shift in the relative importance of different biotic and abiotic interactions over the lifetime of

Table 1. Interactive effect of size (dbh) and neighbours on survival of 29 focal tree species in the Barro Colorado Island forest. Values are coefficients (and standard errors) estimated by a generalized linear mixed-effects model of neighbourhood effects on survival of individuals ≥ 1 cm dbh. CON, HET and NRI refer to conspecific neighbour density, heterospecific neighbour density and phylogenetic relatedness of heterospecific neighbours with 15 m of the focal individual, respectively

	Estimate	SE	z-Value	P value
(Intercept)	-0.181	0.066	-2.730	<0.0001
dbh	0.032	0.017	1.930	0.054
CON	-0.037	0.003	-13.280	<0.0001
HET	0.000	0.003	-0.170	0.866
NRI	-0.009	0.003	-2.560	0.010
dbh:CON	0.022	0.003	8.610	<0.0001
dbh:HET	0.016	0.002	7.740	<0.0001
dbh:NRI	-0.008	0.003	-2.710	0.007

a tree. In particular, natural enemy attack may have a larger impact at earlier compared to later stages due to ontogenetic shifts in plant defence and tolerance (Boege & Marquis 2005). In addition, strong conspecific NDD at early life stages acts to thin conspecific neighbour densities over time, such that large trees are surrounded by relatively few conspecifics. As a result, at later life stages, impacts of conspecific density may be negligible compared to other factors, such as interspecific competition and/or environmental conditions (Comita, Condit & Hubbell 2007b; Newbery & Stoll 2013).

Pathogens, in particular, have been shown to mediate negative conspecific effects on seedling survival in the BCI forest (Augsburger 1983; Gilbert, Hubbell & Foster 1994; Mangan, Herre & Bever 2010), as well as in other tropical and temperate forests (Packer & Clay 2000; Bell, Freckleton & Lewis 2006; Liu *et al.* 2012). In our study, seedling survival was most strongly impacted by the density of conspecific seedling neighbours and less so by larger conspecific neighbours. Previous studies have found that seedling–seedling competition is weak in tropical forests (Paine *et al.* 2008; Svenning, Fabro & Wright 2008). Therefore, the strong NDD at the seedling stage was likely driven predominantly by specialist natural enemies.

Conspecific neighbours had a significant negative impact on survival from the seedling through the sapling and juvenile stages, but adult tree survival tended to be positively correlated with conspecific density (except at the 5-m neighbourhood scale; Fig. 1 and Fig. S1). This positive relationship may reflect habitat preferences resulting from environmental filtering, that is trees survive well and occur at higher densities in the most suitable habitat for the species. Studies from tropical forests world-wide, including BCI, have found evidence for tree species associations with topographic or edaphic habitats (Clark, Clark & Read 1998; Webb & Peart 2000; Harms *et al.* 2001; Gunatilleke *et al.* 2006; John *et al.* 2007; Chuyong *et al.* 2011). John *et al.* (2007) reported that 40% of BCI tree species were significantly associated with soil nutrient values. In addition, of our 29 focal species, 19

exhibited significant associations with one or more topographic habitat types in the BCI 50-ha plot (Harms *et al.* 2001). Thus, it is likely that the positive relationship between adult survival and conspecific density reflects habitat preferences.

Previous studies have found both negative effects of heterospecific neighbours, likely resulting from interspecific competition for resources (Tilman 1987; Getzin *et al.* 2006; Wang *et al.* 2012), as well as positive effects, potentially due to a herd immunity effect in which specialized natural enemies have a harder time locating their host trees if the host trees are surrounded by non-susceptible neighbours (Wills & Green 1995; Peters 2003). In our study, both seedlings and saplings were negatively impacted by heterospecific neighbours ≥ 1 cm dbh, suggesting that interspecific competition for light and/or below-ground resources impacts survival at these stages. In contrast, juveniles were positively impacted by heterospecific neighbour density, consistent with the herd immunity hypothesis. However, a positive relationship between heterospecific neighbour density and juvenile survival could also result from habitat effects (Comita & Hubbell 2009): high recruitment and survival lead to high overall density in sites that are beneficial for all species (e.g. light gaps).

IS THERE EVIDENCE FOR PHYLOGENETIC DENSITY DEPENDENCE IN THE BCI FOREST?

Negative impacts of closely related neighbours could result from competition, if closely related species have similar resource requirements and occupy similar niches (e.g. Burns & Strauss 2011; but see Silvertown *et al.* 2006). Our results revealed that survival in the BCI forest was influenced by the phylogenetic relatedness of heterospecific neighbours. However, significant negative effects were only detected for later life stages, specifically juvenile and adult trees (i.e. individuals ≥ 5 cm dbh). These individuals had a reduced probability of survival when surrounded by closely related neighbours. Evidence from BCI suggests that closely related tree species are ecologically similar: Lebrija-Trejos *et al.* (2014) tested for phylogenetic signal in 19 functional traits related to resource capture, defence and stress tolerance and concluded that trait conservatism is widespread in the BCI flora.

Studies have also found a phylogenetic signal in the host range of natural enemies, with closely related species sharing more pathogens and insect herbivores (Novotny *et al.* 2002; Gilbert & Webb 2007; Liu *et al.* 2012). However, at the seedling stage, when individuals are thought to be most vulnerable to and impacted by natural enemy attack, we found a significantly positive relationship between heterospecific neighbour relatedness and survival. Our results are consistent with the study of Lebrija-Trejos *et al.* (2014), which found a positive relationship between first-year seedling survival and the proportion of closely related heterospecific neighbours in the BCI forest. Such positive relationships likely result from closely related species sharing similar habitat affinities in the BCI tree community. Evidence for such habitat filtering comes from a study of species in the genus *Psychotria* conducted on BCI.

Specifically, Sedio *et al.* (2012) found that both hydraulic traits and species' responses to water availability were phylogenetically conserved, leading to phylogenetic clustering of species within microhabitats. Thus, while many tree species on BCI differ in their habitat associations (Harms *et al.* 2001; John *et al.* 2007), closely related species may be more likely to be associated with the same habitats than distantly related species.

Phylogenetic niche conservatism may vary strongly across space. Although consistent with previous studies from BCI, our finding of positive phylogenetic density dependence at the seedling stage contrast with results from several recent studies that reported negative impacts of neighbourhood phylogenetic relatedness on seedling survival in other tropical forests (Bagchi, Press & Scholes 2010; Metz, Sousa & Valencia 2010; Paine *et al.* 2012). For example, in a study of 163 species in Yasuní National Park (Ecuador), Metz, Sousa & Valencia (2010) found seedling survival was higher when local neighbours were distantly related to the focal seedling. The conflicting results found for studies conducted at our site, BCI, and those conducted at other sites may reflect differences in phylogenetic niche conservatism at different sites. For example, Baldeck *et al.* (2013) found that congeneric species pairs showed significantly higher niche overlap than expected at BCI, but not at Yasuní, where the Metz, Sousa & Valencia (2010) study took place.

HOW MUCH DO SPECIES VARY IN THEIR SENSITIVITY TO CONSPECIFIC, HETEROSPECIFIC AND PHYLOGENETIC NEIGHBOURHOOD EFFECTS?

There is increasing recognition that plant species do not respond identically to changes in neighbour density (Comita *et al.* 2014). Our results provided further evidence of this: we found significant variation among our 29 focal species in their sensitivity to conspecific neighbours, heterospecific neighbours and neighbourhood phylogenetic relatedness for at least one life stage. However, the variation in strength of conspecific effects was generally substantially larger than for heterospecific or phylogenetic neighbourhood effects. A previous analysis of 180 tree species on BCI found that the strength of conspecific NDD at the seedling stage is correlated with species relative abundance in the BCI forest (Comita *et al.* 2010). Similar patterns have been reported for other tropical and temperate forests (Johnson *et al.* 2012; Lin *et al.* 2012). In order to have sufficient sample sizes for all life stages, our present study included only 29 common species. Therefore, variation among species in their sensitivity to neighbourhood variables was likely underestimated, because our study only included the most abundant species in the BCI forest dynamics plot. Nonetheless, our results clearly show that the strength of conspecific neighbour density effects vary much more widely among species than effects of heterospecific neighbour density or phylogenetic relatedness, and therefore likely play a larger role in shaping species relative abundances in the BCI community. In particular, wide variation among species in conspecific effects was observed for the

seedling and sapling stages, lending further support to the idea that non-random mortality at early life stages plays a critical role in structuring tropical tree communities.

Conclusions

Our study contributes to a growing body of literature on the impact of phylogenetic relatedness on neighbourhood interactions (Webb, Gilbert & Donoghue 2006; Bagchi, Press & Scholes 2010; Castillo *et al.* 2010; Metz, Sousa & Valencia 2010; Lebrija-Trejos *et al.* 2014). Our results reveal that strong negative conspecific density dependence at early life stages gives way to phylogenetic density dependence at later stages. The impact of conspecific neighbours on survival, as well as the variation among species in conspecific effects, appears to be substantially larger than for phylogenetic neighbourhood effects. However, even weak effects of phylogenetic relatedness on large tree survival could significantly affect the species composition and phylogenetic structure of tree communities, since large trees sustain populations through seed production. Finally, our study highlights the need to incorporate multiple life stages when assessing the factors contributing to species coexistence for long-lived organisms.

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Data accessibility

The Barro Colorado Forest Census Plot Data are archived and openly available for download from the Smithsonian Institution DSpace repository (<http://dx.doi.org/10.5479/data.bci.20130603>; Condit *et al.* 2012).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. R program code for generalized linear mixed models used in the analysis of neighborhood effects on survival.

Fig. S1. Neighborhood effects of conspecific neighbor density, heterospecific neighbor density, and neighborhood phylogenetic relatedness (NRI) of individual survival at scales of 5, 10, and 20 m.

Fig. S2. The variance of conspecific neighbor effects, heterospecific neighbor effects, and phylogenetic neighborhood effects among 29 focal species at each of four life stages.

Table S1. The 29 focal species used in the analysis of neighborhood effects on survival.

Table S2. AIC and BIC values for generalized linear models of focal individual survival of seedlings, saplings, juveniles and adults at four neighborhood scales (5, 10, 15, 20 m).