

LETTER

Evolutionary history and distance dependence control survival of dipterocarp seedlings

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Abstract

One important hypothesis to explain tree-species coexistence in tropical forests suggests that increased attack by natural enemies near conspecific trees gives locally rare species a competitive advantage. Host ranges of natural enemies generally encompass several closely related plant taxa suggesting that seedlings should also do poorly around adults of closely related species. We investigated the effects of adult *Parashorea malaanonan* on seedling survival in a Bornean rain forest. Survival of *P. malaanonan* seedlings was highest at intermediate distances from parent trees while heterospecific seedlings were unaffected by distance. Leaf herbivores did not drive this relationship. Survival of seedlings was lowest for *P. malaanonan*, and increased with phylogenetic dissimilarity from this species, suggesting that survival of close relatives of common species is reduced. This study suggests that distance dependence contributes to species coexistence and highlights the need for further investigation into the role of shared plant enemies in community dynamics.

Keywords

Borneo, community compensatory trend, density dependence, Dipterocarpaceae, herbivory, host-range, Janzen–Connell hypothesis, phylodiversity, species coexistence, tropical rain forest.

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INTRODUCTION

Tropical forests have long provided a fertile testing ground for theories of species coexistence. The extraordinary diversity of these ecosystems challenges the contention from resource-based competition theory that the number of species coexisting at a single trophic level cannot exceed the number of limiting resources (MacArthur & Levins 1964; Tilman 1982). While plant growth is limited by 30 resources at most (Tilman 1982), almost 1200 tree species have been identified in a 52 ha plot in northern Borneo (Lee *et al.* 2004). This contradiction of theory by data has spurred tropical ecologists to seek mechanisms that prevent the most competitive species from excluding the rest from the community (Wright 2002; Leigh *et al.* 2004).

One theory that has gained much empirical support is the well-known Janzen–Connell hypothesis (Janzen 1970; Connell 1971). The Janzen–Connell hypothesis predicts that offspring located close to adult conspecifics (including their parents) will be attacked by natural enemies attracted to the adults (distance dependence) and high densities of conspecifics (density dependence). Offspring of other

species will not suffer this increased attack and hence will have a competitive advantage. The Janzen–Connell hypothesis has been supported by a large body of work (reviews in Hammond & Brown 1998; Wright 2002; Freckleton & Lewis 2006) and has been particularly influential in the tropical literature. However, several key questions remain unanswered (Freckleton & Lewis 2006).

While there is much evidence that locally abundant species suffer higher mortality in tropical forests (e.g. Webb & Peart 1999; Harms *et al.* 2000; Comita & Hubbell 2009), the agents responsible for this pattern are less well documented (but see Sullivan 2003; Bell *et al.* 2006). Insect herbivores have been invoked as drivers of distance and density-dependent mortality (see reviews in Coley & Barone 1996; Hammond & Brown 1998), but to date, evidence for this suggestion has only been obtained for a handful of species (e.g. Clark & Clark 1985; Blundell & Peart 1998; Sullivan 2003; Norghauer *et al.* 2006) and there is a particular dearth of data for palaeotropical forests (Bagchi 2006). Thus there is a need for studies that link distance- and density-dependent decreases in seedling survival and growth to increased attack by natural enemies.

While the Janzen–Connell hypothesis assumes natural enemies to be host specific, recent studies have challenged this assumption (Novotny *et al.* 2002; Gilbert & Webb 2007). Both insect herbivores and many fungal pathogens, on present evidence, attack multiple, closely related hosts. This leads to two interesting predictions. First, in order for distance and density dependence to contribute to species coexistence, conspecifics should be affected more than heterospecifics (Hille Ris Lambers *et al.* 2002). Second, because plant natural enemies have host ranges encompassing closely related species, we can extend the predictions of the Janzen–Connell hypothesis beyond just conspecifics. Seedlings of species that share natural enemies with a focal species will also suffer reduced survival close to adults of the focal species. The extent of this reduction will depend on the extent to which the species shares common pests with the focal species. Thus, given that the degree of shared pests declines with phylogenetic separation (Novotny *et al.* 2002; Weiblen *et al.* 2006; Gilbert & Webb 2007), we might predict that decreases in performance near adult trees, and for common species in general, will be greatest for conspecific seedlings and decline asymptotically with phylogenetic dissimilarity (Webb *et al.* 2002, 2006b).

Here, we assess the effects of proximity to adult *Parashorea malaanonan* Merr. (Dipterocarpaceae) and density of *P. malaanonan* seedlings on the performance (growth and survival) and leaf herbivory of conspecific seedlings. This is contrasted with the effects of *P. malaanonan* adults and seedlings on the performance of heterospecific seedlings, and these effects on heterospecifics are further examined in relation to the degree of phylogenetic relatedness of species to *P. malaanonan*. Throughout we use the term distance dependence to refer to the (usually negative) effects of distance from the closest *P. malaanonan* adult on performance and leaf condition. Density dependence is used to refer to (usually negative) effects of the density of conspecific seedlings on performance and leaf condition. It should be noted that while density effects are often discussed in the context of self-thinning, when direct competition between plants causes increased mortality, this is unlikely to happen at even the highest densities encountered in this study. Instead the effects we are testing for are almost certainly manifested indirectly, for example due to increased attack by pathogens or herbivores. Distance and density are generally highly correlated, because the highest seedling densities occur close to the parent trees, where most of the seeds fall. Distinguishing unequivocally between distance and density effects requires experimental manipulation. However, throughout, both distance and *P. malaanonan* seedling density are added to all the models, allowing for statistical control of the one when testing the effects of the other.

In this study, we test the following five hypotheses: (1) the survival and growth of conspecific seedlings will decrease with proximity to the nearest adult *P. malaanonan* more than heterospecific seedlings (distance dependence hypothesis); (2) increasing density of *P. malaanonan* seedlings will decrease the survival and growth of conspecific seedlings more than heterospecific seedlings (density dependence hypothesis); (3) leaf herbivory on *P. malaanonan* seedlings will decrease with distance to the nearest *P. malaanonan* adult (distance dependence hypothesis); (4) leaf herbivory on *P. malaanonan* seedlings will increase with conspecific seedling density (density dependence hypothesis); (5) The reduction in seedling performance close to adult *P. malaanonan* trees will be greatest for species closely related to *P. malaanonan*, declining for less related species (phylogenetic relatedness hypothesis).

MATERIALS AND METHODS

Study site

The research was conducted at the Danum Valley Field Centre (4°58' N, 118°48' E, 200 m a.s.l.), Sabah, Malaysia. The field centre is on the edge of the Danum Valley Conservation Area (DVCA), a 43 800 ha area of primary lowland evergreen dipterocarp forest, surrounded by a commercial logging concession of just under 1 million ha (Marsh & Greer 1992). The conservation area is a Class I (fully protected) forest reserve and has suffered little recorded human disturbance. It boasts a largely intact vertebrate fauna (Marsh & Greer 1992). On average, the field centre receives *c.* 2625 mm of rain every year (1985–2004) and no month receives < 100 mm of precipitation on average.

Study species

Parashorea malaanonan is one of the most common tree species in the DVCA (18.6 stems ha⁻¹; Stoll & Newbery 2005). Indeed, most of the forest within and around the DVCA is classified as *Parashorea malaanonan* (Class A) forest (Marsh & Greer 1992) and the Dipterocarpaceae is the dominant family in South-East Asian forests (Ashton 1988). It is a relatively fast growing species of dipterocarp, and its timber is classed as a White *Seraya* Light Hardwood. While, like most dipterocarps, *P. malaanonan* typically fruits as part of community-wide masting events (Ashton 1988), it also appears to fruit more regularly than other dipterocarp species in the area, and as a result seedlings of this species are relatively common (Bagchi 2006). The winged seeds are wind or gyration dispersed, with most seeds falling under the parent canopy, but some seeds disperse further (a mean density of 2.9 seeds m⁻² was recorded at 30 m, Bagchi

2006). Partly as a result, *P. malaanonan* populations are highly spatially aggregated, like most Dipterocarpaceae, and seedlings are for the most part clustered close to the parent tree (Ashton 1988). The seeds are recalcitrant, and seedlings can persist in the understorey for several years after germinating (Ashton 1988). Like all dipterocarps, *P. malaanonan* is dependent on ectomycorrhizal associations (Ashton 1988). Several herbivores have been recorded on *P. malaanonan* seedlings including orthoptera (Whitmore & Brown 1996), lepidopteran and coleopteran leaf rollers (Sawada & Mohamed 1999) and coleopteran stem and root borers (Bebber *et al.* 2002). Some of these herbivores have also been recorded on other dipterocarps and more distantly related species (Robinson *et al.* 2001) but no systematic characterization of *P. malaanonan* herbivores and their host range exists. *Parashorea malaanonan* was chosen for this study because it is such a characteristic species of the area, is a representative of the Dipterocarpaceae and seedling carpets are easy to locate.

Methodology

Seedling carpets of *P. malaanonan* were located by searching along the network of trails within 2 km of the field centre. Sites were considered suitable for the study if it was possible to set up 30 m transects away from the parent tree so that it was the closest adult *P. malaanonan* tree (diameter at breast height > 30 cm) along the entire length of the transect. Seven non-overlapping sites satisfied these criteria. The parent trees were located on the edge of clusters of *P. malaanonan*. Nine 2 m × 2 m plots were established at each site, including three plots each at 2, 15 and 30 m from the parent tree, respectively, corresponding to the areas of the seedling carpet directly under the parent tree, away from the crown of the parent tree and outside the area where most seeds were dispersed. At each distance, plots were located along a randomly chosen azimuth from the parent tree. All plots were located within the area where the parent tree was the closest adult *P. malaanonan*. All plots had greater than three *P. malaanonan* seedlings within them and avoided large trees and canopy gaps. We chose a cut-off limit of three seedlings in order to provide some within-plot replication. In practice this was not a strong restriction on plot location, and still allowed for a 15-fold range in *P. malaanonan* seedling density (0.7–11.0 seedlings m⁻²). At the end of the study canopy openness above each plot was estimated with a spherical densitometer in order to control for light availability in the analyses (Englund *et al.* 2000).

In April 2004, all tree stems in the plots were tagged with uniquely numbered aluminium labels. The heights of all seedlings < 1 m tall were measured. Where possible, plants were identified to species, and otherwise to the lowest

taxonomic level possible. Within each plot, multiple occurrences of the same unidentified morphospecies were recorded. The plots were re-measured in June 2005, and any recruits were also recorded.

In order to estimate leaf herbivory, a maximum of five *P. malaanonan* seedlings were selected from each plot at random. In November 2004, the top four leaves on each of these seedlings were marked with a unique number written on the underside of the leaves with a water-based permanent marker. The length, breadth and remaining area of the top four leaves of these selected seedlings were measured using a CI-202 portable leaf area meter (CID Inc., Camas, WA, USA). If the length or breadth of leaves had been reduced by damage, then the original dimensions were estimated with a ruler. The stem and branches of each seedling were marked immediately before the last node with a water-based permanent marker. These seedlings were re-measured in May 2005. All the leaves surviving from the last census, as well as any leaves produced during the interval, were measured. The number of marked leaves missing and the number of empty nodes above the last node at the previous measurement were recorded.

We calculated damage to leaves by subtracting leaf area at the end of the study, $A_i(t)$, from initial leaf area $A_i(0)$ (either leaf area at the beginning of the study or, in the case of leaves produced during the study, an estimate of original leaf area). We used a regression of leaf length and breadth against area to estimate the original area of damaged leaves. Data for this regression were collected on a 2 m wide transect leading away from the parent tree at each site. The length, breadth and area of the first 10 intact *P. malaanonan* leaves on this transect were measured. The intact area of each leaf produced between measurements was estimated using the regression equation and the measurements of leaf length and breadth. The proportion of leaf area lost to a seedling between measurements (D) was then estimated as

$$D = \frac{\sum_{i=1}^L A_i(0) - A_i(t)}{\sum_{i=1}^L A_i(0)}$$

where A_i is the measured area of leaf i and L is the number of leaves on the seedling at the second measurement.

Because damage to leaves often leads to their loss, often early in their development, estimates of leaf herbivory solely on the basis of damage to remaining leaves can underestimate herbivory (Lowman 1984). The loss of leaves was estimated by counting the number of empty nodes (N) formed between measurements. N includes both nodes formed since the last measurement and those leaves lost between measurements. The proportion of leaves lost during the study, M , was then estimated as

$$M = \frac{N}{N + L}$$

Phylogenetic analysis

Seedlings that could not be identified to family at the first census were removed from the data prior to analysis. The list of families, or genera in the case of the Dipterocarpaceae, was arrayed on a phylogenetic tree using PhyloMatic (Webb & Donoghue 2005). PhyloMatic attaches taxa in a sample to a master tree (version R20050610.new) which is based on a published phylogeny of the angiosperms (APG 2003). The ages of several nodes within the master tree were taken from Wikstrom *et al.* (2001), and the ages of the remaining nodes were estimated using a smoothing algorithm (BLADJ) within Phylocom (Webb *et al.* 2006a). BLADJ positions nodes of unknown age at the midpoint between the closest nodes of known age (Webb *et al.* 2006a). Branch lengths connecting *P. malaanonan* to all other taxa were then extracted and halved. This gives an estimate of the time since the lineage containing *P. malaanonan* split from those containing the other taxa in the study (henceforth divergence time).

Statistical analysis

Seedlings were divided into *P. malaanonan* and heterospecifics in order to test hypotheses 1 and 2. Two plots were affected by large tree falls and were excluded from the analysis. Survival was modelled with a generalized linear mixed-effects model (GLMM) using a logit link and assuming a binomial error distribution. Log final height was modelled using a linear mixed-effects model, assuming a normal error distribution. In addition to terms for distance, density and their interaction, we added canopy openness, density of heterospecific seedlings and log initial seedling height as covariates in the analyses of *P. malaanonan* performance (hypotheses 1 and 2). To test for nonlinear effects of distance we added a variable with a value of 1 at 15 m and 0 otherwise to the models. Intercept terms for each plot nested within site were added as normally distributed random effects in both models. A size-independent measure of survival was predicted from the fitted models after standardizing all the covariates (log initial height, canopy openness and heterospecific seedling density) to their respective mean values. Log final height was calculated similarly, but initial height was standardized to a value of 1 cm. This results in values equivalent to relative growth rate (RGR), but accounting for the dependence of growth rate on size in tree seedlings. To test hypotheses 3 and 4, we modelled leaf damage and loss as functions of the covariates. Leaf damage and loss were averaged by plot prior

to analysis. Because *P. malaanonan* density and distance from the focal adult trees co-varied, the significances of both terms were assessed after first controlling for the effect of the other in all models. In separate models to test hypothesis 5, taxonomic group was substituted by divergence time in the analyses of survival and final height. For each individual, the number of confamilials in the plot was included as a covariate in these analyses. Individuals from the same family are not independent replicates of divergence time, so family was modelled as a normally distributed random effect in addition to plot and site. All statistical analyses were performed in R for windows 2.9.0 (R Development Core Team 2008).

RESULTS

We tagged 1998 seedlings in the first census including 576 of *P. malaanonan*. Seedlings from 40 families were identified while 227 seedlings could not be identified to family.

Survival and growth

Survival of *P. malaanonan* seedlings was higher at the intermediate distance (15 m) than at either 2 or 30 m from the parent tree (hypothesis 1, Fig. 1). This pattern was not observed in heterospecific seedlings, and the strength of this pattern was confirmed by the significant interaction between the nonlinear term for distance and taxonomic group ($\chi^2_1 = 12.6$, $P = 0.0004$, hypothesis 1). Density of *P. malaanonan* seedlings was not significantly related to the survival of either conspecific or heterospecific seedlings (hypothesis 2). RGR was not significantly related to either distance or *P. malaanonan* seedling density for either *P. malaanonan* or all other seedlings (hypotheses 1 and 2; Fig. 2).

Leaf condition

Leaf damage of *P. malaanonan* seedlings increased with distance from adult conspecifics and decreased with conspecific seedling density (Fig. 3a). Because distance and *P. malaanonan* density were correlated, the statistical significance of both terms was assessed by putting them into the model last. Doing this supported the negative relationship between conspecific density and *P. malaanonan* leaf damage, the opposite trend from that expected under hypothesis 4 ($F_{1,50} = 4.78$, $P = 0.033$). The analysis suggested that the apparent increase in leaf damage at greater distances was driven by the parallel decrease in the density of *P. malaanonan* seedlings ($F_{1,50} = 2.19$, $P = 0.146$, hypothesis 3). Leaf loss of *P. malaanonan* seedlings was unaffected by either distance from the nearest conspecific adult or conspecific seedling density (Fig. 3b, hypotheses 3 and 4).

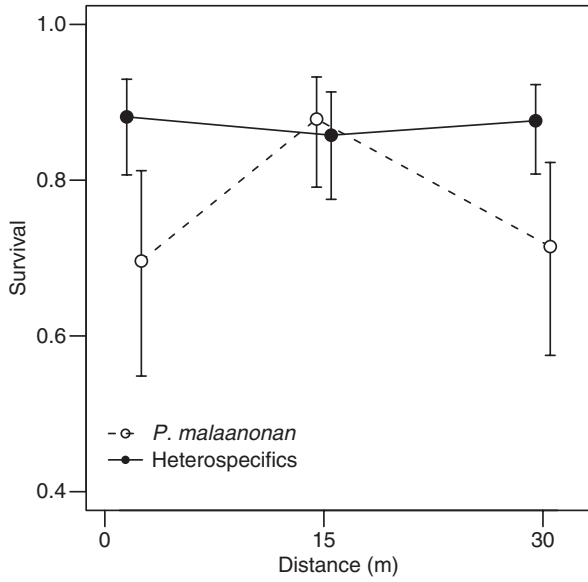


Figure 1 Seedling survival for *Parashorea malaanonan* and all other species as a function of distance from adult *P. malaanonan*. Survival is expressed as a prediction of the model fitted to the data. Covariates (log initial height, canopy openness and heterospecific seedling density) were set to their mean values for the prediction. Error bars represent the standard error of the mean after transforming to the proportion scale.

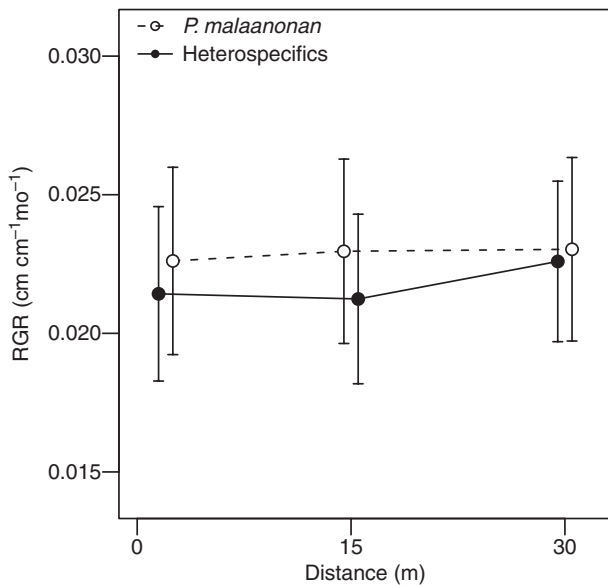


Figure 2 Relative growth rate (RGR) of height of *Parashorea malaanonan* seedlings and seedlings of all other species. RGR is calculated from the model fit to the data after setting initial height to 1 and canopy openness and heterospecific seedling density to their mean values. Error bars represent the standard error of the mean.

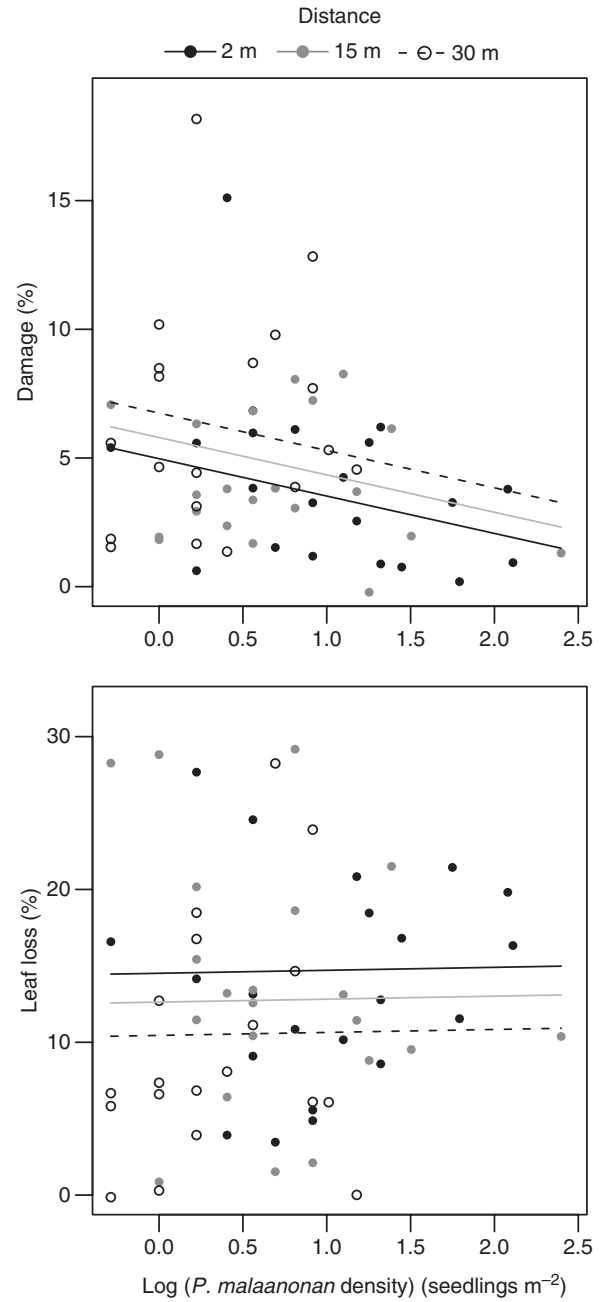


Figure 3 Effects of distance and conspecific density on percentage leaf damage (top panel) and percentage leaf loss (bottom panel) of *Parashorea malaanonan* seedlings. Points represent the mean observed percentages in the 61 plots set at three different distances from adult *P. malaanonan* trees. The lines represent the model predictions.

Phylogenetic effects

Seedling survival increased significantly with divergence time from *P. malaanonan*; seedlings from species distantly related to *P. malaanonan* had higher survival than those more

closely related (Fig. 4a, $\chi^2_1 = 10.9$, $P < 0.001$). This pattern was not dependent on the inclusion of *P. malaanonan* seedlings ($\chi^2_1 = 8.9$, $P = 0.003$ after excluding *P. malaanonan* seedlings). While there was some weak evidence that close relatives of *P. malaanonan* did better at 15 m (Fig. 4a) this pattern was not significant (interaction between the nonlinear contrast for distance and divergence time $\chi^2_1 = 1.80$, $P = 0.18$, hypothesis 5). Seedling growth was not significantly affected by divergence time ($F_{1,47} = 1.49$, $P = 0.23$, Fig 4b, hypothesis 5).

DISCUSSION

Evolutionary history affects seedling survival

One of the assumptions of the Janzen–Connell hypothesis is that herbivores and pathogens are specialized on their hosts (Janzen 1970; Connell 1971). However, it is becoming increasingly apparent that herbivores and pathogens are rarely monophagous and may attack several closely related hosts (Novotny *et al.* 2002; Weiblen *et al.* 2006; Gilbert & Webb 2007). If this pattern is general, the negative effects of neighbours should increase with their evolutionary relatedness and be strongest on conspecifics. Thus, we might expect the strength of the distance dependence observed in this study to decrease continuously with divergence time from *P. malaanonan* (hypothesis 5). In this study, we show that the effect of distance on survival was stronger for conspecific than heterospecific seedlings, as predicted (hypothesis 1). The interaction between divergence time and distance from *P. malaanonan* adults was weak, suggesting that the strength of distance dependence was not higher for close relatives of *P. malaanonan*. This may indicate that the host-ranges of herbivores and pathogens of *P. malaanonan* (at least those driving the observed distance dependence) do not encompass related species.

Instead of an interaction between distance and divergence time we uncovered a more general trend whereby overall survival, irrespective of distance from the focal tree, increased with phylogenetic dissimilarity from *P. malaanonan*. This is an important result as it suggests that phylogenetic density dependence is acting at a wider spatial scale, at the level of populations rather than just individual seed carpets. Given that the Dipterocarpaceae, and *P. malaanonan* in particular, dominates the canopy at Danum Valley, contributing 40% of the basal area (Newbery *et al.* 1992), we suggest that this reduction in survival is because herbivores and pathogens attacking dipterocarps will be abundant as their host plants are common. Furthermore, previous work in New Guinea suggests that large genera at the regional scale are attacked by more specialist herbivores than smaller genera (Novotny *et al.* 2002). If a similar pattern is observed in Borneo, it is possible that more natural enemies attack

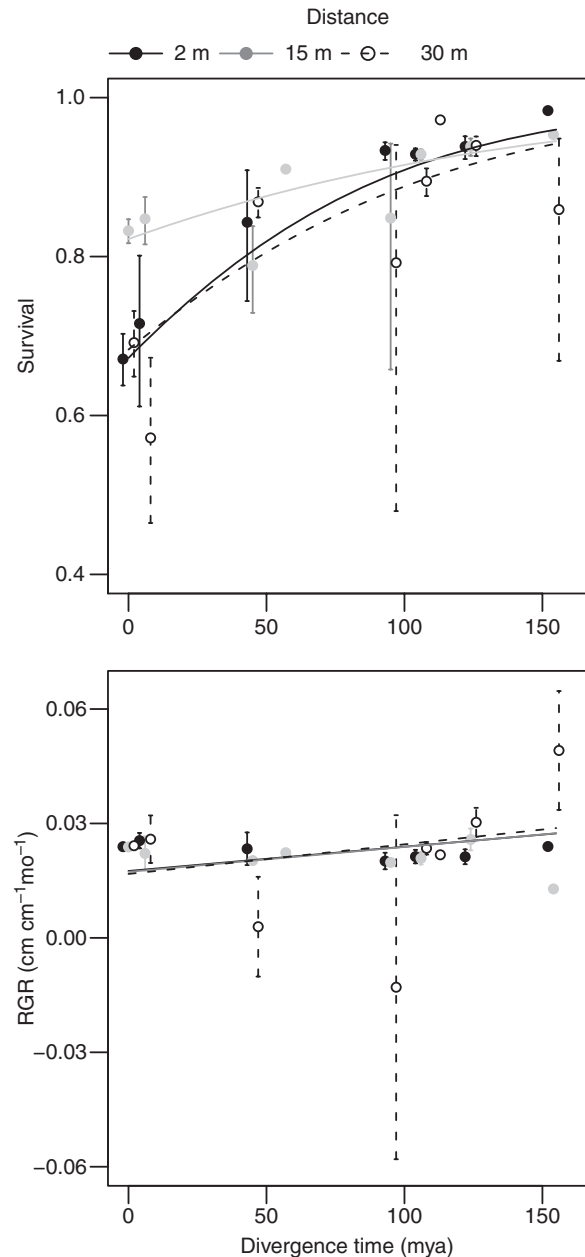


Figure 4 Relationship between phylogenetic relatedness of seedlings to *Parashorea malaanonan* (millions of years since divergence of lineages) and survival (top panel) and relative growth rate (RGR) of height (bottom panel). Points represent the mean observed proportion of seedlings surviving or mean RGR for each divergence time recorded at each of three different distances from adult *P. malaanonan* trees. Error bars are the standard errors of the means. Lines represent the model predictions. The data have been adjusted to statistically remove the effects of initial height on survival (initial height standardized to its mean observed value) and RGR (initial height standardized to 1). All other covariates (canopy openness and density of confamilials) were set to their mean values.

Dipterocarps than other families. As a consequence, not only dipterocarps but also species closely related to them experience increased mortality as seedlings. Trees of other families may also be subject to tight regulation, but we suggest that Dipterocarps and their close relatives may be subject to tighter control by specialist natural enemies. Our results agree with Webb *et al.* (2006b) where the average relatedness of seedlings in another Bornean rain forest declined over time. Taken together, these results suggest that evolutionary history is an important factor determining species interactions in plant communities.

It is possible that the extent to which seedlings are exposed to conspecifics (both adults and seedlings) may increase with phylogenetic similarity to *P. malaanonan*. Webb (2000) suggested that neighbouring trees in another Bornean forest were more closely related to each other than expected by chance. As a consequence, the extent to which seedlings are exposed to distance-dependent effects from their conspecific adults may decrease with divergence time from *P. malaanonan*. While our analyses control for the density of confamilial seedlings, we do not have data on adult densities at our sites and cannot rule out that this may be driving the observed phylogenetic trend. However, several families that are very common in the DVCA and common as seedlings in our plots (e.g. Annonaceae and Rubiaceae) are distantly related to *P. malaanonan* (Newbery *et al.* 1992; APG 2003). Seedlings from these families had high survival, which is inconsistent with the conclusion that the observed phylogenetic pattern is due to parallel species-specific distance-dependent effects. However, to unequivocally distinguish between these two possible mechanisms requires that the locations and identities of adults of other species are known.

Seedling survival is reduced by proximity to conspecific adults

In this paper, we demonstrate that proximity to *P. malaanonan* adults significantly decreased conspecific seedling survival while the negative impact on heterospecific survival was smaller (hypothesis 1). This second point is an important one; conspecifics must be affected more than heterospecifics for these processes to contribute to species coexistence (Hille Ris Lambers *et al.* 2002). Several studies have demonstrated distance dependence in tree seedling survival (Howe *et al.* 1985; Packer & Clay 2000; Hyatt *et al.* 2003), but very few tropical studies have considered the effects on heterospecifics (but see Queenborough *et al.* 2007; Comita & Hubbell 2009).

One surprising result was the nonlinearity in the relationship between distance and survival. Our initial expectation was that survival would increase smoothly with distance, but instead survival was greatest at an intermediate distance from the adult conspecifics. We would caution that

this nonlinear pattern is dependent on increased survival at one distance, 15 m, and relates to one species. However, if this result reflects a more general trend it highlights the importance of choosing the correct spatial scale when designing investigations into distance dependence. In fact, it could potentially explain some of the inconsistent results obtained by previous studies (Hyatt *et al.* 2003).

We suggest two possible ecological mechanisms that could account for peak survival occurring at intermediate distances. First, while specialist natural enemies might reduce survival close to adult conspecifics, the presence of an adult tree reflects the presence of suitable microhabitat for successful establishment (Janzen 1970). *Parashorea malaanonan* seedlings growing further away might experience less suitable conditions for establishment. The presence of a *P. malaanonan* tree does not necessarily reflect a suitable habitat for other species, which may be why heterospecific seedling survival and growth did not change between 15 and 30 m. A large body of research has demonstrated the importance of environmental conditions for seedling recruitment (Webb & Peart 2000; Palmiotto *et al.* 2004; Engelbrecht *et al.* 2007). Ectomycorrhizae are also important for the establishment of dipterocarp seedlings (Ashton 1988; Lee & Alexander 1996). Lee & Alexander (1996) found that high densities of adult conspecifics increased the extent of ectomycorrhizal colonization in seedlings of another dipterocarp species, *Shorea leprosula*. It is possible that in the work presented here the *P. malaanonan* seedlings at 30 m from adult conspecifics experienced lower ectomycorrhizal colonization, and this contributed to their reduced survival. In order to investigate the effects of distance on seedling performance it was necessary to establish our sites on the edge of *P. malaanonan* clusters, and thus areas beyond the canopy of the parent trees might reflect especially poor habitat for *P. malaanonan* and have lower densities of suitable mycorrhizal fungi. Interestingly, Stoll & Newbery (2005) found that the negative effects of conspecific neighbours extended to *c.* 19 m for *P. malaanonan* in analyses of permanent plot data from the DVCA. Seedlings at 15 m from adult conspecifics will be at the limit of the area experiencing negative effects, and thus any further displacement may not convey further advantage. Instead, seedlings located farther from parent trees are more likely to encounter unsuitable habitat, and hence do worse than seedlings at 15 m that are relatively free of specialist pests, but located in a more suitable habitat.

A second possible reason for the reduced survival at 30 m could be the reduction in density at that distance. Distance and density are often thought of as acting in synergy: survival is low at high density and close to parent trees, which is where the highest densities occur (Janzen 1970). However, in this study, we found that leaf herbivory increased as density decreased, and this appeared to be

driving an increase in herbivory with distance. It is possible that high densities of seedlings satiate leaf herbivores, especially if other factors like predation limit their populations. The finding that per plot herbivory was independent of conspecific density supports this hypothesis: the same amount of leaf damage was spread over more individuals at high density. Perhaps seedlings at *c.* 15 m from parent trees may suffer least from the combined damage of distance-dependent and positively density-dependent natural enemies. Predator satiation is often discussed in the literature with respect to seed predators (Janzen 1971). Perhaps leaf herbivores can be satiated in a similar way. Further data would be required to support such a pattern, but it raises an intriguing question and creates some uncertainty over the importance of leaf herbivores in causing density dependence.

CONCLUSIONS

The role of distance and density dependence in plant species coexistence is often emphasized in the literature (Wright 2002; Leigh *et al.* 2004; Freckleton & Lewis 2006). A key assumption in order for these processes to maintain species coexistence is that locally rare species will do better than their more common competitors. While many studies have demonstrated reductions in performance when a species is common, few studies have shown that rare species are not also affected. As a result it has been impossible to demonstrate an advantage to rare species. Here, we consider heterospecifics in our analyses and demonstrate that reductions in seedling survival close to adult trees were most pronounced for conspecifics. There is an emerging appreciation that pathogens and herbivores are rarely monophagous in their host ranges, and instead attack several, related species. We found little evidence that the negative effects of proximity to *P. malaanonan* adults extended to close relatives of *P. malaanonan*. However, we demonstrate that in a forest dominated by the Dipterocarpaceae, and *P. malaanonan* in particular, seedling survival declined with evolutionary relatedness to the dominant taxa. This pattern is consistent with our current understanding of host ranges of herbivores and pathogens. This is an exciting finding with important consequences for theories about plant species coexistence. Quite what those consequences might be is poorly understood and theoretical investigations and more data are sorely required.

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