

PHYLODIVERSITY-DEPENDENT SEEDLING MORTALITY, SIZE STRUCTURE, AND DISEASE IN A BORNEAN RAIN FOREST

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Abstract. Density-dependent models that partition neighbors into conspecifics and heterospecifics ignore the great variation in effect of heterospecifics on focal plants. Both evolutionary theory and empirical results suggest that the negative effect of other plants on a focal plant should be higher for closely related neighbors than for less related neighbors. Using community-wide seedling mortality data from a forest where density dependence has previously been found, we searched for significant phylogenetic neighborhood effects (the “phylodiversity” neighborhood) on seedling (<50 cm tall) survival at various spatial scales. Logistic regression models were used, with 19-mo survival of individual seedlings as the response.

We found a significant positive effect of nearest taxon phylodiversity on seedling survival at the 36-m² scale and the 4-m² scale, indicating that seedling survival is enhanced by being in a neighborhood where heterospecifics are not closely related. At all scales there was a strong negative effect of conspecific seedling density on focal survival, and at small scales there was also an effect of heterospecific density, indicating generalized competition. We place these results (for seedling dynamics over a relatively short period of time) in the context of changes in phylodiversity between different size classes of plants in the same forest, which integrate the effects of dynamics of all size classes over long time periods. At the 36-m² scale, there was an increase in nearest taxon phylodiversity (i.e., a decrease in phylogenetic clustering) from the seedlings (<50 cm tall) to the poles (1–5 cm diameter), consistent with the positive effect of local phylodiversity on seedling survival. In contrast, there was a marked decrease in average phylodiversity from seedlings to saplings at the same scale. The trees in the 1600 m² surrounding the seedling plots had much lower phylodiversity than either the seedlings or saplings.

Taken together, these results suggest that (1) over short time and spatial scales, local seedling phylodiversity has a positive effect on seedling survival, possibly via interaction with pathogens (which we discuss in detail), but (2) over longer time periods and larger spatial scales the effect of abiotic-related mortality results in habitat filtering for phylogenetically conserved traits.

Key words: Borneo; community phylogenetic structure; density dependence; phylodiversity; plant pathogen infection; seedlings.

INTRODUCTION

In both theoretical and empirical studies, intraspecific negative density dependence has been shown to be important for slowing competitive exclusion and maintaining diversity in rain forest trees (Wright 2002). Most analyses focus on the statistical effects of conspecific density on either focal-plant performance or species demographic parameters (Martinez-Ramos et al. 1988, Condit et al. 1994, Harms et al. 2000). In some cases, the effect of distance from focal plant to conspecifics has been used as a correlate of plant density (Hubbell 1980, Connell et al. 1984, Hubbell et al. 1990, Gilbert et al. 1994).

The strength of conspecific density (or interplant distance), relative to the effect of overall competitive pressure, can be measured by including the density (or distance) of heterospecifics as a separate factor in models (Connell et al. 1984, Uriarte et al. 2004). However, simply dividing species into conspecifics and heterospecifics obscures the great variation in effects of different species on any focal species (Pacala et al. 1996). One solution is to give separate “competition” parameters to each pairwise interaction (Canham et al. 2004, 2006). Unfortunately, a great deal of data is required to fit a model with so many free parameters. If the effect of one species on another was random with respect to the plants’ phenotypes, there would be no solution other than this multiparameter modeling. However, interspecific interactions are influenced by the anatomical and physiological similarity of the species involved, and gross similarity is not distributed at random among

Manuscript received 26 January 2005; revised 18 July 2005; accepted 21 July 2005; final version received 9 September 2005. Corresponding Editor: A. A. Agrawal. For reprints of this Special Issue, see footnote 1, p. S1.

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PLATE 1. The Air Putih River as it passes through granite hill forest at the Cabang Panti study area, Gunung Palung National Park, Indonesia. Photo Credit: C. Webb.

organisms; it is generally highest among taxa that share a recent ancestor (Felsenstein 1985, Harvey and Pagel 1991). In general, we expect greater negative interactions among individuals that are more phenotypically similar, be they competing for a similar vector of resources or negatively affecting each other via shared seed predators. Thus, we expect that closely related taxa should have a greater negative influence on each other than taxa that are more distantly related. Indeed, Uriarte and colleagues (2004) recently analyzed neighbor-dependent sapling growth at Barro Colorado Island and found that the negative effect of a neighbor on a target was greater when both plants were in the same taxonomic family. Adding a relatedness parameter to models of density dependence might therefore increase the predictive power of these models significantly, at the expense of just a few degrees of freedom.

The development of phylogenetic methods over the past few decades has exposed the nonequivalence of taxa assigned to the same traditional rank. For example, in a recent supertree study of the relationships among angiosperms (Wikström et al. 2001), the estimated minimum age of family clades varied over an order of magnitude (e.g., 108 Ma for the Aristolochiaceae, 9 Ma

for the Rhizophoraceae). Additionally, higher taxonomic groups defined using morphological (e.g., floral) characters might have little ecological coherence; either more- or less-inclusive clades than named-rank clades might be more ecologically meaningful classes. With the great progress made recently in resolving the phylogenetic relationships among organisms, we can now move beyond ranks (such as family and genus) to use phylogenetic distances (e.g., age) among taxa. In this paper, we include such a phylogenetic distance factor in the analysis of community seedling mortality in lowland rain forest at Gunung Palung in Indonesian Borneo (see Plate 1; Webb and Peart 2000). At this site, density-dependent seedling mortality has previously been found both in single species (Webb and Peart 1999, Blundell and Peart 2004) and as a community-wide compensatory trend (Webb and Peart 1999).

We take two approaches toward testing the contribution of the phylogenetic relatedness structure of neighbors (hereafter the neighborhood “phylodiversity”; cf. Faith 1992) to seedling dynamics. First, we examine its effect on the survival of seedlings in small quadrats in multifactorial models that also include the effect of conspecific density and heterospecific density. The

period chosen for the analysis is the same as that for which community-wide density dependence was found (Webb and Peart 1999). Second, we analyze changes in local phylogenetic structure with plant size class. Any influence of phylodiversity on seedling survival (a dynamic measure) should eventually leave an imprint on the phylogenetic structure of surviving plants (a static pattern). If, for example, mortality is higher in species that are sharing a neighborhood with closely related species than in species that are phylogenetically isolated from their neighbors, then this should be observed as an increase in phylodiversity (and a decrease in net relatedness) of plants of increasing size. Alternatively, if habitat filtering leads to strong phenotypic and phylogenetic attraction (Webb et al. 2002, Cavender-Bares et al. 2004), the plants in increasingly taller size classes should show decreased phylodiversity.

We thus ask the following questions: (1) Does adding a phylogenetic neighborhood (phylodiversity) term increase the fit of density-driven models of seedling mortality? (2) Does the influence of neighborhood phylodiversity vary with neighborhood scale? (3) Are changes in the (static) phylogenetic structure with increasing size classes consistent with phylodiversity-dependent seedling mortality?

Finally, we develop a mechanistic hypothesis for the mediation of these phylodiversity effects by pathogens, the most likely causal agents of density dependence in these forests.

METHODS

In 1993, Webb set up 28 36-m² seedling plots in lowland rain forest in the Gunung Palung National Park, West Kalimantan (Indonesian Borneo; site location: 1.2125° S, 110.1078° E; see Plate 1). The height of all woody plants was measured for plants taller than 5 cm and <1.0 cm dbh (diameter at breast height [1.3 m high]), and dbh was measured for plants 1.0–5.0 cm dbh. Each seedling plot was nested inside a 40 × 40 m tree plot in which all trees >10.0 cm dbh were measured and identified (see Webb and Peart [1999, 2000] for further details).

We constructed a single phylogeny that included all plant species occurring in any of the plots. We first ran the species list through the online tool Phylomatic (Chazdon et al. 2003, Webb and Donoghue 2005) to produce a tree topology based on the Angiosperm Phylogeny Group (APG) II backbone (APG 2003; P. F. Stevens, Angiosperm Phylogeny Website, version 6, *available online*),⁴ using the Phylomatic reference megatree R20040402. We then used the BLADJ algorithm of Phylocom (Webb et al. 2004, Moles et al. 2005) to constrain the internal nodes of the tree to the age estimates of Wikström et al. (2001). The algorithm then interpolates the other nodes of the tree for which

direct age estimates are not available. Because many of the genera in the plot have yet to be sampled in a phylogenetic study, many of the families were modeled in the final supertree as a polytomy, and all the genera were polytomies. This means that the significant phylogenetic results reported here are not dependent on, for example, phylogenetic conservatism in pathogen host use only among sibling species. Instead, they must reflect patterns of conservatism that extend at least to the root of genera nodes, and possibly beyond. It is likely that some ecologically relevant characters are even conserved at family nodes and above.

For the analysis of seedling dynamics, we used measures of survival of all individuals of all seedling species (5–50 cm tall) over a 27-month period from March 1994, in a subset of 12 of the plots ($n = 2296$ seedlings total). This subset included only plots with completed seedling identification as of November 1994, and was a sample of all 28 plots stratified by elevation and subhabitat. Individual plants were mapped to a 0.25-m² quadrat within the 36-m² seedling plot, allowing analysis in nested square neighborhoods of 0.25, 1, 4, and 36 m² (the design of the seedling plots included two 1-m walkways, which precluded using neighborhoods between 4 m² and 36 m²; see plot diagram in Webb and Peart [1999]). We first counted the total seedling number per quadrat (for each sized quadrat: 0.25, 1, 4, and 36 m²) at the beginning of the census period, and determined whether each individual was alive or dead at the end of 27 months. We also calculated the number of conspecific individuals and the relative phylodiversity of each species in the quadrat. Phylogenetic diversity (Faith 1992), or phylodiversity, is negatively related to the extent of phylogenetic clustering in a sample (Webb 2000, Webb et al. 2002, Cavender-Bares et al. 2004), and positively related to measures of phylogenetic distance among taxa in a sample. We measured relative phylodiversity in two ways, (1) using the mean phylogenetic distance (in units of millions of years) from the species of the focal individual to all other ($n - 1$) species in the quadrat, and (2) using the minimum phylogenetic distance to any heterospecific species in the quadrat (i.e., to the nearest taxon, or taxa, where several were equidistant). Both distances were then standardized by the mean expected phylogenetic distance, given the number of species in the quadrat, in order to correct for the effect of sample species richness; details of the same standardization for the indices of phylogenetic clustering, net relatedness index (NRI) and nearest taxon index (NTI), are given in Webb et al. (2002). We refer to the resulting metrics as relative average phylodiversity, APd', and relative nearest taxon phylodiversity, NTPd' (the prime indicates that the metric is relative to the identity of focal species; absolute APd and NTPd are used in analysis of size class; and "Pd" is used to differentiate from Faith's [1992] "PD," which is measured differently). Phylodiversity is oriented here

⁴ <http://www.mobot.org/MOBOT/research/APweb>

so that larger positive values of phylodiversity indicate communities whose species are less closely related.

We modeled survival of each seedling (categorical data: lived vs. died) using four separate logistic regressions: (1) survival as a function of the total number of seedlings in the same quadrat, (2) survival as a function of the number of conspecifics in the same quadrat and the number of heterospecifics in the same quadrat, (3) survival as a function of the number of conspecifics in the same quadrat, and (4) survival as a function of the number of conspecifics in the same quadrat, number of heterospecifics in the same quadrat, and relative phylodiversity of the community in the same quadrat. The total number of species in the quadrat was included in preliminary analyses, but was never a significant effect, and was dropped from final models.

For the static size class analysis, we used identity and height for all species alive in June 1996 in the full set of 28 seedling and tree plots. Based on plant size at that time, we assigned plants to four size classes: seedlings (0–50 cm tall), saplings (50 cm tall to 1 cm dbh), poles (1–5 cm dbh), and trees (>10 cm dbh). A total of 389 species were recorded as seedlings, 277 as saplings, 161 as poles, and 325 species as trees. We drew up a species list for each size class in each of the 28 plot locations, and this was passed through Phylocom (Webb et al. 2004) to calculate the net relatedness index and the nearest taxon index (Webb et al. 2002) of these species lists on the phylogeny of the whole pool of 548 species (see the Supplement). We recognize that not all taxa in the pool can occur in every size class (e.g., shrub and liana taxa will not be found in the tree plot samples), but we use a common phylogeny because measures of phylogenetic structure (NRI, NTI) are directly comparable only within a common pool phylogeny. We do not attempt to test whether the indices are different from zero (indicating either phylogenetic clustering or evenness; Webb 2000), because the null model of random sampling from the pool would be inappropriate. Because we are using estimates of absolute age between taxa, the effect of taxon sampling on phylogenetic distance is largely removed.

The indices NRI and NTI were multiplied by negative one to obtain measures of phylodiversity (average, APd, and nearest taxon, NTPd, respectively), directly comparable to those used in the analysis we have described of seedling mortality. Median values of phylodiversity for the 28 plots were compared across size classes. We conducted all analyses for both subprojects using the statistical language R (R Project 2004) and Phylocom (Webb et al. 2004).

RESULTS

Phylodiversity and seedling survival

A summary of the variation in numbers of individuals and species follows: for quadrats of 36, 4, 1, and 0.25 m², respectively, the number of individuals per quadrat

(mean ± SE) was 209 ± 22, 48.4 ± 4.4, 12.3 ± 0.63, and 3.66 ± 0.11; the number of species per quadrat was 48.0 ± 3.5, 18.8 ± 1.1, 7.46 ± 0.29, and 2.88 ± 0.072; the mean number of APG family clades per quadrat was 23.1 ± 1.1, 12.5 ± 0.52, 5.97 ± 0.19, and 2.70 ± 0.061; the mean number of individuals per species per quadrat was 4.36 ± 0.41, 2.56 ± 0.13, 1.65 ± 0.045, and 1.27 ± 0.018.

A total of 20 models were fit (Table 1), and, in all models in which it was present as a factor, the (logarithm of the) number of conspecific individuals was the most predictive factor for seedling survival. At quadrat sizes of ≤4 m², seedling survival was strongly negatively related to (the logarithm of) total seedling density. Heterospecific (log of) seedling density was negatively related to survival only at the smallest quadrat size (0.25 m²), at which scale the effect of total density was also strongest. Relative nearest taxon phylodiversity (NTPd') was positively associated with survival at the 36-m² and 4-m² scales. At both scales, the addition of the NTPd' phylodiversity term provided the best overall model fit, as measured by Akaike's Information Criterion (AIC). Relative average phylodiversity (APd') was negatively correlated with seedling survival at the largest (36-m²) scale.

Change in phylodiversity with increasing size class

From seedlings to poles, average phylodiversity (APd) decreased and nearest taxon phylodiversity (NTPd) increased, while phylodiversity declined from seedlings to trees for both measures (Fig. 1). The influence of the four size classes on phylodiversity was significant overall (Kruskal-Wallis rank-sum test; APd, $\chi^2 = 24.1$, $df = 3$, $P = 2.3 \times 10^{-5}$; NTPd, $\chi^2 = 34.7$, $df = 3$, $P = 1.4 \times 10^{-7}$), and the following pairwise comparisons were significant using Wilcoxon rank-sum tests: APd, seedling vs. sapling ($W = 209$, $P = 0.0023$), seedling vs. pole ($W = 257$, $P = 0.026$), seedling vs. tree ($W = 130$, $P = 6.5 \times 10^{-6}$), pole vs. tree ($W = 195$, $P = 0.0010$); NTPd, seedling vs. tree ($W = 207$, $P = 0.002$), sapling vs. tree ($W = 131$, $P = 7.2 \times 10^{-6}$), pole vs. tree ($W = 31$, $P = 9.2 \times 10^{-12}$). In a separate analysis, lists of seedling and sapling species were made for the 252 quadrats of 4 m²: both APd and NTPd decreased from seedlings to saplings (APd, $\chi^2 = 7.17$, $df = 1$, $P = 0.0073$; NTPd, $\chi^2 = 10.3$, $df = 1$, $P = 0.0012$).

DISCUSSION

Our analysis of community-dependent seedling survival suggests that at larger scales (4 m² and 36 m²) there is a significant beneficial effect of local phylodiversity (NTPd): that is, the chance that a seedling survives increases if surrounding plants are not closely related to it, even after the effects of conspecific and heterospecific density have been removed. There was no such effect at smaller scales. At the same scale of 36 m², we also observed an increase in phylodiversity from the seedling to the sapling to the pole size classes, when measured as

TABLE 1. Effect of local seedling density and phylodiversity on seedling survival, for four quadrat sizes. Five logistic models were fit for each of the four quadrat sizes: 0.25, 1, 4, and 36 m².

Quadrat size and model	AIC	df	Significance of factor				
			Log (total <i>N</i>)	Log (conspecific <i>N</i>)	Log (heterospecific <i>N</i>)	Phylodiversity (APd')	Phylodiversity (NTPd')
36 m ²							
Total density	3138	2295	NS				
Partitioned density	3114	2294		-0.11***	+0.28*		
Conspecifics only	3118	2295		-0.13***			
Complete (APd')	3103	2293		-0.15***	+0.25*	-0.25*	
Complete (NTPd')	3101	2293		-0.085**	+0.25*		+0.22**
4 m ²							
Total density	3129	2295	-0.21**				
Partitioned density	3114	2294		-0.17***	NS		
Conspecifics only	3112	2295		-0.18***			
Complete (APd')	3113	2293		-0.19***	NS	NS	
Complete (NTPd')	3111	2293		-0.14**	NS		+0.13**
1 m ²							
Total density	3123	2291	-0.20**				
Partitioned density	3109	2290		-0.23***	NS		
Conspecifics only	3107	2291		-0.24***			
Complete (APd')	3110	2289		-0.25***	NS	NS	
Complete (NTPd')	3110	2291		-0.21**	NS		NS
0.25 m ²							
Total density	2838	2093	-0.34**				
Partitioned density	2834	2092		-0.31***	-0.18*		
Conspecifics only	2838	2093		-0.33***			
Complete (APd')	2835	2827		-0.33***	-0.18*	NS	
Complete (NTPd')	2837	2091		-0.33**	-0.17*		NS

Notes: Survival is measured as a positive response, so a negative parameter estimate indicates a negative relationship of the factor with seedling survival. Phylodiversity increases with decreasing relatedness of the focal taxon to the other taxa in the sample. Akaike's Information Criterion (AIC) measures the complexity of the fitted model; a lower value indicates a better fit of the model to the data. Key to abbreviations: APd', relative average phylodiversity; NTPd', relative nearest taxon phylodiversity.

* $P = 0.05$, ** $P = 0.01$, *** $P = 0.001$.

nearest taxon phylodiversity, NTPd. These two results are consistent with each other: if survival is higher for seedlings that are more distantly related, then as the cohort ages the overall net relatedness should decrease, as closely related taxa are "weeded out." However, a contrasting pattern is observed in the measure of average phylodiversity: at the 36-m² scale, there is an apparent detrimental effect of APd on seedling survival, and a consistent decrease in APd phylodiversity is observed in the static data, from seedlings to saplings, and from seedlings to poles. We also observed that for both NTPd and APd measures, there was a large decrease in phylodiversity from seedlings to trees, i.e., tree species were far more clustered phylogenetically than were seedling species. Previous work showed trees in a plot to be more phylogenetically clumped than expected by chance (Webb 2000).

How can we reconcile these different results? When comparing different size classes for the same area, we must be aware that the different number of individuals in the different size classes, and thus the different expected number of species, could be leading to an artifactual change in metrics. While this remains a possibility, we feel it is not the cause of the patterns we observe, because the standardization of the indices uses the expected value of relatedness for a given n species (Webb et al. 2002),

which removes the main effect of sample species richness on phylogenetic relatedness. Additionally, there was no significant relationship of plot species richness with APd or NTPd within any size class (8 tests, $n = 28$ plots). However, thorough simulation studies to explore the behavior of these metrics are desirable and are underway (S. Kembel, *personal communication*; N. Kraft, *personal communication*).

Instead, we believe that the observed patterns result from the different aspects of phylogenetic structure captured by the two measures of phylodiversity. Imagine that the seeds arriving at a particular site are a random sample of all the plants in a forest, plants that occupy a number of habitats. Imagine also that some large clades of many taxa possess characters that will increase survival in this particular habitat, while other clades do not have these characters. Over time, there should be a net increase in average relatedness of the survivors at a site (i.e., a decrease in APd). However, if negative interactions are highest among taxa that are very closely related (sister species, or consectionals), there may simultaneously be a reduction over time in the phylogenetic distance to the most closely related surviving species (i.e., an increase in NTPd). All that is required for these two apparently opposite changes to occur simultaneously is that the characters for habitat filtering

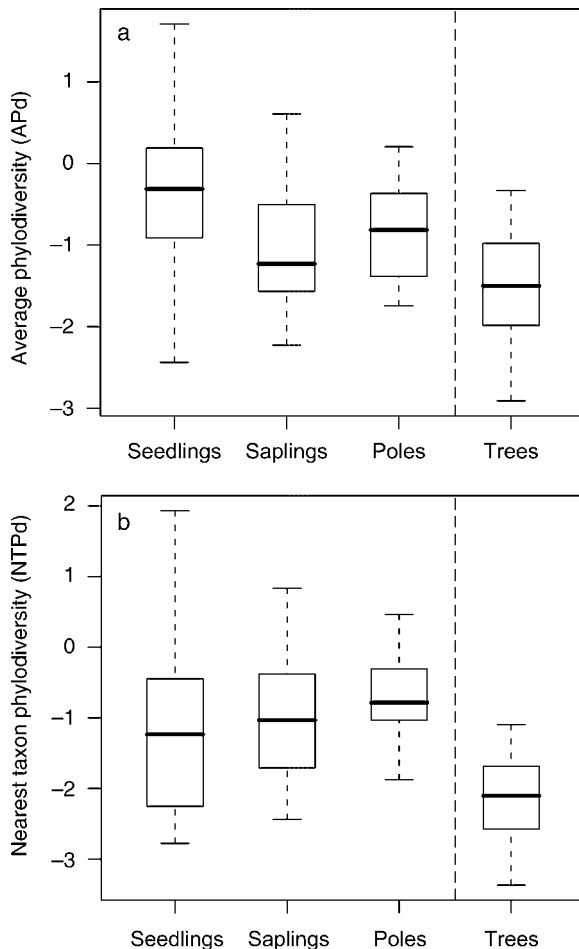


FIG. 1. Change in phylogenetic diversity with size class (seedlings, 0–50 cm tall; saplings, 50 cm tall to 1 cm dbh; poles, 1–5 cm dbh; trees, >10 cm dbh) for 28 plots (36 m² for seedlings to poles; 0.16 ha for trees, hence separation by dashed vertical line); box indicates median (heavy line) and quartiles, whiskers reach to points ≤ 1.5 times the interquartile range. Units of both APd and NTPd are one standard deviation of a random distribution of phylogenetic distance (Pd), zeroed to the distribution's mean. (a) Average phylogenetic diversity (APd = $-NRI$), which becomes more positive with decreasing mean relatedness among all pairs of taxa in the sample. (b) Nearest taxon phylogenetic diversity (NTPd = $-NTI$, which is the mean of the relatedness to the most closely related taxon to each taxon). Abbreviations are as follows: NRI, net relatedness index; NTI, nearest taxon index.

(Webb et al. 2002, Cavender-Bares et al. 2004) must be plesiomorphic to a clade, whereas negative interactions must occur among the most closely-related taxa within the clade. For instance, if disease cross-species susceptibility is highest in sister taxa, while drought tolerance important for long-term survival on ridges is shared among many taxa in a phylogenetic family, we should see a simultaneous increase in nearest taxon phylogenetic diversity (NTPd) and a decrease in “deeper,” average phylogenetic diversity (APd). If only taxa with a particular synapomorphy can survive in a particular place to

become trees, nearest taxon phylogenetic diversity (NTPd) must also eventually decrease, as the only survivors will belong to numerous “clumps” of related taxa. While this explanation surely oversimplifies the phylogenetic distribution of characters necessary for survival, we believe it helps explain the observed patterns. The large decrease of average and nearest taxon phylogenetic diversity in trees is expected because of both the larger spatial scale of the tree plots and the length of time over which processes have operated as seedlings grow to trees. During this time, the effects of habitat filtering have dominated change in both measures of phylogenetic diversity. We note that it is the combination of short-term dynamic data and static data reflecting long-term outcomes that provides these insights into community dynamics.

A framework for the influence of pathogens on phylogenetic diversity

As at other tropical rain forest sites (e.g., Augspurger 1984), available evidence points to pathogens being the primary cause of density-dependent mortality at Gunung Palung (Webb and Peart 1999). Pathogens have been shown to strongly influence plant community structure and diversity in a number of natural and agricultural plant systems (see review by Gilbert [2002]). To the extent that pathogens are more likely to cross-infect closely related hosts (Parker and Gilbert 2004), negative interactions between plant species should be strongest among very close relatives (Mack 1996). While the data presented in this paper are phenomenological, and do not point directly to pathogen influences, we use pathogens as an example in developing a framework that integrates the expected phylogenetic component of density dependence that we have outlined with a mechanistic, causal hypothesis. Invertebrate herbivores, with a species richness comparable to pathogens, might interact with plant phylogenetic diversity in a similar way (Weiblen et al. 2006).

Within a plant community, a plant pathogen species can have a single species of host plant (“monophagy”) or several (“polyphagy”). Monophagous pathogen–host dynamics have been well explored and tend to result in classic negative density-dependent effects in the plant (Burdon and Chilvers 1982). This will be the case either in a monoculture of the plant species or in a mixture with nonhost plant species. However, the population dynamics that result when pathogens can attack several plant species in a community are more complicated, and have been addressed mainly in the context of apparent competition (Price et al. 1988, Alexander and Holt 1998). Here, an increase in numbers of one plant species leads to an increase in pathogen inoculum, which could then affect other susceptible plant species in the community. In a tropical rain forest, the hundreds of plant species present are exposed to thousands of potential fungal pathogens, mostly unidentified (Arnold et al. 2000, Gilbert et al. 2002). Some of the pathogens are monophagous and some have many hosts (Lindblad

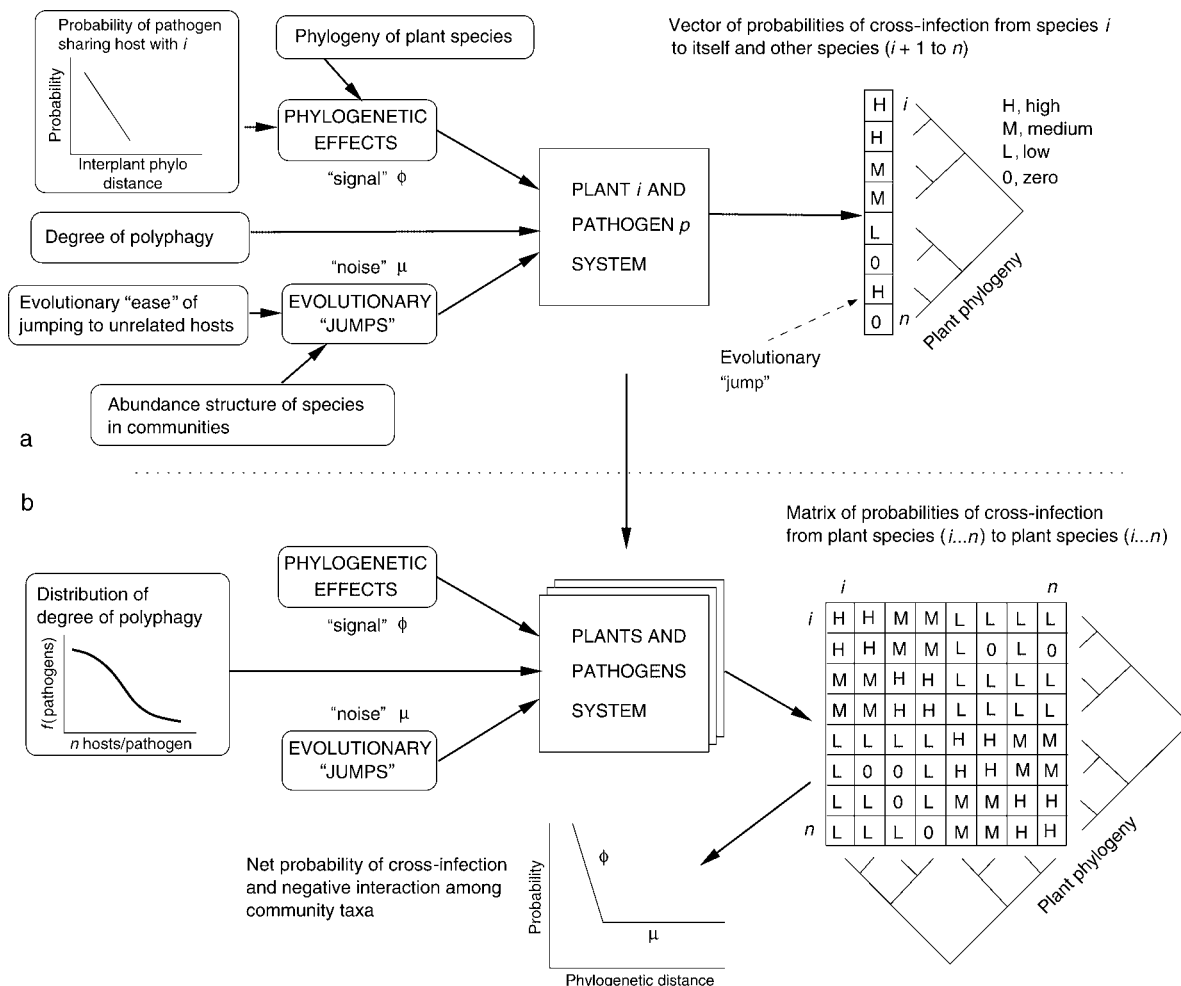


FIG. 2. Theoretical framework for the phylogenetic effects of pathogens. (a) Model of spread of single pathogen to other host plants ($i + 1$ to n) in the community. The output vector of probabilities of cross-infection is a function of the phylogenetic relatedness of other taxa to the host plant (i), the degree of polyphagy in the pathogen, and the "ease" of host switching to unrelated host plants. (b) Model of community-wide cross-infection by all pathogens. The output is a matrix of cross-infection probabilities, declining from a high rate (H) in closely related taxa to a low rate (L) in unrelated taxa. The mean baseline rate (μ) depends on the mean "ease" of pathogen host switching to unrelated taxa, both historically, and with contemporary rapid evolution in ecotypes. Note that the lower half of the matrix can differ from the upper half if the probability of infection from plant i to j is not equal to the probability from j to i .

2000, Woolhouse et al. 2001, Gilbert et al. 2002). Individual plant species might host dozens of species of fungal symbionts (Frohlich and Hyde 1999, Arnold et al. 2001), many with negative effects on the host (reviews in Gilbert 2002, 2005). Host susceptibility to pathogens will also be influenced in plastic ways by plant abundance, phenological state, season, nutrient availability, and other factors which stress a plant.

Analyzing and understanding this complicated network of interactions and effects might be greatly simplified by modeling pathogen host breadth as a phylogenetic function (Webb et al. 2002; cf. Weiblen et al. 2006). The barriers for a pathogen to infect a host plant are morphological and biochemical. Moreover, because both morphology and plant secondary chemistry are often conserved phylogenetically (Farrell and

Mitter 1993, Farrell 2001), a pathogen that can infect one species can most easily become adapted to phylogenetically closely related species. At the same time, while phylogenetic conservatism of morphology and biochemistry is pervasive in nature, so is parallel evolution, or homoplasy, of similar characters in unrelated lineages. Hence, pathogen adaptations to infection barriers might also be effective in phylogenetically unrelated plants, which partially explains why some pathogens can infect many unrelated plants in a community (Weste and Marks 1987, Eckenwalder and Heath 2001).

In general, the probability that a single pathogen can infect a particular set of hosts in a plant community should decline with increasing phylogenetic separation among the hosts, but with some host-sharing across some

apparently random plant species as well (Fig. 2a). Ecological association, through consistent community co-occurrence of unrelated but common species, might facilitate more distant host jumps. Considering the many pathogen species likely to be present, we expect variation in (1) the number of hosts that pathogens can attack, (2) the slope of their phylogenetically determined drop-off from closely related cohosts to less related nonhosts, and (3) the extent of nonphylogenetic host “jumps.” Combining the variation in all these pathogens, we expect that the net interspecific cross-infection probability will decline with increasing phylogenetic distance, down to a low baseline that represents the frequency of phylogenetically unrelated host “jumping” (Fig. 2b, matrix element L).

In this way, pathogens, which are already known to exert strong influences on plant survival in natural systems, might operate in a phylodiversity-dependent manner and might underlay the phylodiversity-dependent seedling survival observed at Gunung Palung. The most powerful way to confirm the phylogenetic-distance-dependent signal in pathogen interactions will be to experimentally cross-inoculate pathogens in replicated samples of both closely and distantly related taxa and to record the success in transmitting disease symptoms. The overall influence of pathogens might be confirmed with pathogen exclusion (i.e., fungicide) experiments.

Irrespective of their underlying mechanisms, phylodiversity-dependent dynamics have the potential to contribute to high overall species diversity, in a different way than other density-dependent phenomena. Single-species density dependence has the potential to cap the population size of species (Hubbell 1980) and, if present as a community compensatory trend across all species (Connell et al. 1984, Webb and Peart 1999, Wright 2002), will stabilize community composition and promote diversity by allowing rare immigrants to increase in number. Diversity-dependent dynamics, if found (Wills et al. 1997; but see critique in Wright [2002]), should increase overall survival in diverse sites and thus provide source or refuge populations that influence the metapopulation dynamics of species that would otherwise be poor competitors. None of these density and diversity dynamics reacts to or influences the specific identity of taxa: in theory, all taxa are considered to have equivalent influence or response. Phylodiversity-dependent dynamics, however, should operate differently, influencing the taxonomic (or rather phylogenetic) structure of the species composition of communities. The survival of species will be higher if they occur with unrelated taxa rather than with close relatives, and thus phylodiverse communities should be promoted, independently of their absolute species number, as found in this study. There has been much concern in the literature for the need to actively conserve sites and communities that have high phylogenetic diversity (e.g., Vane-Wright et al. 1991, Faith 1992, Moritz and Faith 1998). If phylodiversity-dependent dynamics operate in natural

systems, then the persistence and recovery of phylogenetic diversity might be assisted by nature itself.

ACKNOWLEDGMENTS

C. O. Webb thanks David Ackerly for informative discussions about phylogenetic structure and David Peart for many discussions on the nature of density dependence. Karen Garrett provided feedback in the development of the conceptual model. C. O. Webb was funded during analysis and writing by a grant from the National Science Foundation (DEB-0212873) and during the field work by a graduate fellowship (GER-9253849) and a Small Grants for Exploratory Research (SGER) grant to David Peart (DEB-9520889). We thank the various branches of the Indonesian government that permitted the fieldwork, and Darmawan and Suryadi, C. O. Webb's field assistants at Gunung Palung. The review comments of Mark Westoby and an anonymous reviewer are much appreciated.

LITERATURE CITED

- Alexander, H. M., and R. D. Holt. 1998. The interaction between plant competition and disease. *Perspectives in Plant Ecology Evolution and Systematics* **1**:206–220.
- APG [Angiosperm Phylogeny Group]. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* **141**:399–436.
- Arnold, A. E., Z. Maynard, and G. S. Gilbert. 2001. Fungal endophytes in dicotyledonous neotropical trees: patterns of abundance and diversity. *Mycological Research* **105**:1502–1507.
- Arnold, A. E., Z. Maynard, G. S. Gilbert, P. D. Coley, and T. A. Kursar. 2000. Are tropical fungal endophytes hyperdiverse? *Ecology Letters* **3**:267–274.
- Augsburger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. *Ecology* **65**:1705–1712.
- Blundell, A. G., and D. R. Peart. 2004. Density-dependent population dynamics of a dominant rain forest canopy tree. *Ecology* **85**:704–715.
- Burdon, J. J., and G. A. Chilvers. 1982. Host density as a factor in plant disease ecology. *Annual Review of Ecology and Systematics* **20**:143–166.
- Canham, C. D., P. T. LePage, and K. D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* **34**:778–787.
- Canham, C. D., M. J. Papaik, M. Uriarte, W. H. McWilliams, J. C. Jenkins, and M. J. Twery. 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. *Ecological Applications* **16**:540–554.
- Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* **163**:823–843.
- Chazdon, R. L., S. Careaga, C. O. Webb, and O. Vargas. 2003. Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecological Monographs* **73**:331–348.
- Condit, R., S. P. Hubbell, and R. B. Foster. 1994. Density dependence in two understory tree species in a Neotropical forest. *Ecology* **75**:671–680.
- Connell, J. H., J. G. Tracey, and L. J. Webb. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monographs* **54**:141–164.
- Eckenswalder, J. E., and M. C. Heath. 2001. The evolutionary significance of variation in infection behavior in two species of rust fungi on their hosts and related nonhost plant species. *Canadian Journal of Botany* **79**:570–577.

- Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**:1–10.
- Farrell, B. D. 2001. Evolutionary assembly of the milkweed fauna: cytochrome oxidase I and the age of *Tetraopes* beetles. *Molecular Phylogenetics and Evolution* **18**:467–478.
- Farrell, B. D., and C. Mitter. 1993. Phylogenetic determinants of insect/plant community diversity. Pages 253–266 in R. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**:1–15.
- Frohlich, J., and K. D. Hyde. 1999. Biodiversity of palm fungi in the tropics: are global fungal diversity estimates realistic? *Biodiversity and Conservation* **8**:977–1004.
- Gilbert, G. S. 2002. Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review of Phytopathology* **40**:13–43.
- Gilbert, G. S. 2005. Dimensions of plant disease in tropical forests. Pages 141–164 in D. Burslem, M. Pinard, and S. Hartley, editors. *Biotic interactions in the tropics: their role in the maintenance of species diversity*. Cambridge University Press, Cambridge, UK.
- Gilbert, G. S., A. Ferrer, and J. Carranza. 2002. Polypore fungal diversity and host density in a moist tropical forest. *Biodiversity and Conservation* **11**:947–957.
- Gilbert, G. S., S. P. Hubbell, and R. B. Foster. 1994. Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. *Oecologia* **98**:100–108.
- Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**:493–495.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.
- Hubbell, S. P. 1980. Seed predation and the coexistence of tree species in tropical forests. *Oikos* **35**:214–229.
- Hubbell, S. P., R. Condit, and R. B. Foster. 1990. Presence and absence of density dependence in a Neotropical tree community. *Philosophical Transactions of the Royal Society of London B* **330**:269–281.
- Lindblad, I. 2000. Host specificity of some wood-inhabiting fungi in a tropical forest. *Mycologia* **92**:399–405.
- Mack, R. N. 1996. Biotic barriers to plant naturalization. Pages 39–46 in V. Moran and J. H. Hoffman, editors. *Proceedings of the ninth international symposium on the biological control of weeds*. University of Capetown, Stellenbosch, South Africa.
- Martinez-Ramos, M., J. K. Sarukhan, and D. D. Pinero. 1988. The demography of tropical trees in the context of forest gap dynamics: the case of *Astrocaryum mexicanum* at Los Tuxtlas tropical rain forest. Pages 293–313 in D. Davy, M. J. Hutchings, and A. R. Watkinson, editors. *Plant population ecology*. Blackwell, Oxford, UK.
- Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, and M. Westoby. 2005. A brief history of seed size. *Science* **307**:576–580.
- Moritz, C., and D. P. Faith. 1998. Comparative phylogeography and the identification of genetically divergent areas for conservation. *Molecular Ecology* **7**:419–429.
- Pacala, S. W., C. D. Canham, J. Saponara, and J. A. Silander. and Kobe. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* **66**:1–43.
- Parker, I. M., and G. S. Gilbert. 2004. The evolutionary ecology of novel plant–pathogen interactions. *Annual Review of Ecology, Evolution, and Systematics* **35**:675–700.
- Price, P. W., M. Westoby, and B. Rice. 1988. Parasite-mediated competition: some predictions and tests. *American Naturalist* **131**:544–555.
- R Development Core Team. 2004. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004. A spatially explicit model of sapling growth in a tropical forest: Does the identity of neighbours matter? *Journal of Ecology* **92**:348–360.
- Vane-Wright, R. I., C. J. Humphries, and P. H. Williams. 1991. What to protect? Systematics and the agony of choice. *Biological Conservation* **55**:235–254.
- Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist* **156**:145–155.
- Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2004. Phylocom: software for the analysis of community phylogenetic structure and character evolution. Version 3.22. (<http://www.phylodiversity.net/phylocom>)
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33**:475–505.
- Webb, C. O., and M. J. Donoghue. 2005. Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* **5**:181–183.
- Webb, C. O., and D. R. Peart. 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* **80**:2006–2017.
- Webb, C. O., and D. R. Peart. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* **88**:464–478.
- Weiblen, G. D., C. O. Webb, V. Novotny, Y. Basset, and S. E. Miller. 2006. Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology* **87**:S62–S75.
- Weste, G., and G. C. Marks. 1987. The biology of *Phytophthora cinnamomi* in Australasian forests. *Annual Review of Phytopathology* **25**:207–229.
- Wikström, N., V. Savolainen, and M. W. Chase. 2001. Evolution of angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London B* **268**:2211–2220.
- Wills, C., R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a Neotropical forest. *Proceedings of the National Academy of Sciences (USA)* **94**:1252–1257.
- Woolhouse, M. E. J., L. H. Taylor, and D. T. Haydon. 2001. Population biology of multihost pathogens. *Science* **292**:1109–1112.
- Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**:1–14.

SUPPLEMENT

Supertree phylogeny files and taxonomic list (*Ecological Archives* E087-115-S1).