

REPORT

Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests

Halton A. Peters*

Department of Biological Sciences, Stanford University, Stanford, CA 94305, USA

*Correspondence: E-mail: hpeters@globalecology.stanford.edu

Abstract

Density-dependent mortality has long been posited as a possible mechanism for the regulation of tropical forest tree density. Despite numerous experimental and phenomenological investigations, the extent to which such mechanisms operate in tropical forests remains unresolved because the demographical signature of density dependence has rarely been found in extensive investigations of established trees. This study used an individual-based demographical approach to investigate the role of conspecific and heterospecific neighbourhood crowding on tree mortality in a Panamanian and a Malayan tropical forest. More than 80% of the species investigated at each site were found to exhibit density-dependent mortality. Furthermore, most of these species showed patterns of mortality consistent with the Janzen–Connell hypothesis and the rarely explored hypothesis of species herd protection. This study presents some of the first evidence of species herd protection operating in tree communities.

Keywords

Density-dependent mortality, genetic herd immunity, Janzen–Connell hypothesis, neighbourhood crowding, species herd protection, tropical forest dynamics.

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INTRODUCTION

Numerous mechanisms have been proposed to explain the maintenance of high species diversity. Tropical forests, among the world's most species-rich terrestrial ecosystems, are the focus of ongoing attempts to understand the importance of such mechanisms for community-level properties such as species richness and abundance. Beyond the obvious upper limits of population size imposed by the density-dependent self-thinning phenomenon that is widely observed and reasonably well-understood in tree plantations and other mono-dominant stands, it is still unclear whether trees in species-rich tropical sites are routinely regulated by the density and composition of their neighbours.

More than 30 years ago Janzen (1970) and Connell (1971) independently described how a density-dependent mechanism could lead to the high species diversity observed in tropical tree communities. According to the Janzen–Connell hypothesis, individuals are expected to experience lower recruitment success and survival near

their conspecific neighbours as a result of (1) pest propagation from adults to their nearby offspring; and (2) the enhanced proliferation of species-specific herbivores and pathogens among more densely packed hosts. In either instance, depressed densities of one tree species would leave space and resources critical for the establishment of other species with similar requirements but susceptible to different suites of enemies, and this was the basis for multi-species co-existence.

In the 30 years since density-dependence was posited as a potentially important mechanism for the maintenance of species diversity in tropical forests, both the prevalence of these effects and the scales at which they are relevant to species diversity have remained controversial. The experimental evidence provides numerous examples of individual seedling species that have been shown to have increased mortality when at high densities or in the proximity of conspecific adult neighbours (e.g. Augspurger 1983a,b, 1984; Clark & Clark 1984; Connell *et al.* 1984; Schupp 1988, 1992; Howe 1990; Hammond & Brown 1998; Webb

& Peart 1999; Packer & Clay 2000; Gilbert *et al.* 2001). Furthermore, a recent large-scale study of the seed to seedling transition in a tropical forest on Barro Colorado Island (BCI) in Panama found pervasive density-dependent recruitment at this early life history transition (Harms *et al.* 2000).

Still, critics have argued that density-dependent mortality was unlikely to be limiting populations of most tropical forest tree species because the demographical signature of density dependence that would be expected based upon the results of experiments with seeds and seedlings has been found among few species in established tree communities. Extensive analyses of density dependence in a fully-censused tree community in Panama have demonstrated evidence for density-dependent mortality in only 10% of the tree species present at this site (Hubbell *et al.* 1990; Condit *et al.* 1992a,b; Wills *et al.* 1997, but for a criticism of the findings on density-dependent recruitment see Wright 1999, 2002). Furthermore, in the absence of consistent overall indications of density-dependent mortality in forests of Panama and Peninsular Malaysia, a recent investigation concluded that mortality was largely random after trees reached 1 cm diameter at breast height (DBH) (Wills & Condit 1999).

These findings from fully-censused tree communities constitute the empirical underpinning for recent theoretical attempts to understand patterns of species richness and relative abundance in tropical forests that assume no density dependence, i.e. that tree communities consist of perfectly identical species with mortality probabilities that are independent of their densities (Hubbell 1997, 2001). Because of methodological limitations of several previous investigations, there is scant evidence supporting this assumption. The signature of density dependence has been underestimated in several previous studies because of the use of subplot-based analyses that divide large tree plots into many small subplots and ask how mortality in each of these subplots is related to its density (Hubbell *et al.* 1990; Condit *et al.* 1992b; Wills *et al.* 1997; Wills & Condit 1999). Trees that happen to be close to the edge of a subplot have little information about their real neighbourhoods included in the analyses, while extraneous information about other neighbourhoods is included. This effect was unintended by the original investigators. Previous studies have typically used square subplots ranging in length from 5 to 20 m, meaning that the proportion of trees near (i.e. less than 2 m from) the subplot edge ranges from 96 to 36%. Because most trees are near the edge of a subplot, even very strong density-dependent patterns can be difficult to detect. The present study uses analyses of individual focal trees, considers the influence of the neighbourhood centred at that tree, and then moves the neighbourhood from focal tree to focal tree, ameliorating the subplot edge problem that has severely

limited previous studies. Similar individual-based approaches have been successful at identifying density-dependent relationships between neighbourhood crowding and tropical tree survival (e.g. Condit *et al.* 1994; Hubbell *et al.* 2001), but they have not been applied widely enough to elucidate whether density dependence is a mortality mechanism influencing more than a few common species, or if observed community-level patterns of density dependence simply reflect the overwhelming influence of a few extremely prevalent species.

The ability of heterospecific neighbours to promote the maintenance of tree species co-occurrence by thwarting the transmission of biotic plant pests has rarely been considered. Recently it has been suggested that 'genetic herd-protection' (Wills & Green 1995) may operate at the species level to maintain diversity in tropical forests (Wills & Green 1995; Wills 1996a,b). This model (hereafter called the species herd protection hypothesis) is actually an extension of the Janzen–Connell hypothesis because it explicitly considers the implications of biotic interactions mediated by heterospecific neighbours. The incorporation of heterospecific effects into models of diversity maintenance is critical in species-rich tropical forests, where few of the near neighbours of an individual are likely to be conspecific, even among the most common or most highly aggregated species (Hubbell & Foster 1986; Kochummen *et al.* 1990). According to the species herd protection model, increased heterospecific crowding is expected to result in fewer encounters between a host and its species-specific pests and pathogens, even if the density of conspecific neighbours remains constant. This lower host-enemy encounter rate is predicted to increase host survival. While the presence of non-susceptible neighbours in a matrix of susceptible hosts might be expected to lead to increased survival and diversity, it has never been shown that enhanced protection from herbivores and pathogens could ever overcome the competition between heterospecific neighbours. The only other demographical investigation of this model did not find support for the species herd protection prediction: tree survival did not increase with the density of heterospecific neighbours (Wills *et al.* 1997).

In this study, I provide evidence that tree survival in two species-rich tropical forests, one in Southeast Asia, the other in Central America, is regulated by both pervasive conspecific and heterospecific density-dependent effects of neighbourhood crowding and biomass. Density dependence was found to be prevalent from the seedling and sapling stages through adulthood; and across a range of spatial scales. The relationships observed in this study provide support for the notion that the populations of most tree species in these tropical communities are maintained, in part, through interactions consistent with two models of density-dependent

regulation, the Janzen–Connell hypothesis and the species herd protection model.

METHODS

Study sites

This study made use of tree demographical data from two 50-ha (1.0 km × 0.5 km) lowland tropical forest research plots. One plot is in the Pasoh Forest Reserve (Manokaran *et al.* 1999), in the centre of the Malay peninsula, 140 km SE of Kuala Lumpur, and the other on BCI in the Panama Canal. The forest structure and dynamics of these sites have been contrasted in the course of other investigations (Condit *et al.* 1996, 1999, 2000a). Annual precipitation at Pasoh is *c.* 1800 mm with two distinct peaks in April/May and November/December, but with every month receiving more than 100 mm rainfall. BCI receives nearly 40% more rainfall than Pasoh, 2500 mm annually, but has a pronounced 4 month dry season from December to April during which mean monthly rainfall drops below 100 mm. The Pasoh forest canopy is evergreen, while at BCI about 6% of the canopy trees (comprising 10% of the forest crown area) are deciduous (Condit *et al.* 2000b). Pasoh forest has a higher density of small trees than BCI, with fewer very large (DBH ≥ 50 cm) trees (Condit *et al.* 1999). One consequence is that stand basal area is slightly greater at BCI (31.8 m² ha⁻¹) than Pasoh (30.3 m² ha⁻¹). Tree species richness in the Pasoh 50-ha plot (822 species) is 2.6 times that of BCI (314 species).

In both plots, all tree stems ≥1 cm DBH were tagged, mapped, measured, and identified (Pasoh: 1987, 1990, 1995; BCI: 1982, 1985, 1990, and 1995). Subsequent censuses have incorporated new recruits and recorded the mortality of individuals that were present in previous censuses. To ascertain whether density dependence exerts differential influence across the developmental stages of established trees, individuals of each species were assigned to one of three size classes: 1 cm ≤ DBH ≤ 5 cm, 5 cm < DBH ≤ 10 cm, and 10 cm < DBH. All analyses were performed separately on each size class for only those species that had at least 30 individuals in that particular size class. At Pasoh, 544 (66%) of the 822 species were included in this study (539, 255, and 213 in the smallest, medium, and largest size classes, respectively). At BCI 188 (60%) of 314 tree species were included (177, 94, and 97 in the smallest, medium, and largest size classes, respectively).

Analytical methods

Previous investigations of density-dependent tree dynamics in these plots have largely underestimated the influence of neighbourhood crowding on mortality because they utilized

a subplot-based approach in which the deaths of one census were regressed against the individuals present in the previous census. In addition to the statistical flaws associated with this method (Underwood 1997), this technique is extremely insensitive because the neighbourhood information is lost for those trees near the edge of the subplot. In previous studies of density dependence, most individuals were near the edge of the subplot throughout the range of subplot sizes that were considered. When a tree is near the edge of one of these subplots, information about nearby neighbourhood crowding just outside the subplot is lost, and replaced by information about neighbourhoods farther away from that tree. The subplot edge introduces errors into the analyses because it ignores the fact that as sessile organisms trees are expected to interact most strongly with their nearest neighbours. The subplot-based approach therefore tends to underestimate the influence of density dependence relative to stochastic processes, a prediction that helps to explain the findings of several studies that have used this approach (e.g. Connell *et al.* 1984; Hubbell *et al.* 1990; Condit *et al.* 1992b; Wills *et al.* 1997; Wills & Condit 1999).

In contrast, this study utilized an individual-based approach to determine the influence of neighbourhood numbers and basal area on tree survival. Numeric density is a measure of overall crowding, while tight correlations between DBH and height indicate that basal area can be used to approximate plant biomass (O'Brien *et al.* 1995). For each individual in the 50-ha plot, neighbourhoods with radii of 5, 10, 15, and 20 m from the focal tree were defined, and the stem and basal area density of conspecific and heterospecific neighbours was calculated. Survival of individual trees was approximated by the number of censuses in which the tree was known to have lived. Only trees present in the initial census (BCI: 1982; Pasoh: 1987) were used in these analyses, and individuals with neighbourhoods that exceeded the confines of the 50-ha plots were excluded from the analysis (but were included as neighbours of other trees). Analyses were also performed using only the first three censuses at BCI, but the results were virtually identical and therefore are not presented.

For each species, size class, and neighbourhood size, the importance of heterospecific and conspecific neighbours was determined by calculating standard partial regression coefficients from multiple regressions. The partial regression coefficient of a variable (e.g. conspecific density) reflects the relationship between that variable and the dependent variable (survival) that would be expected if all other variables in the regression model (e.g. heterospecific density) had been held constant experimentally (Sokal & Rohlf 1995). This technique allows for the influence of conspecific and heterospecific neighbours to be tested independently, and because all trees must be either conspecific or heterospecific, the analysis is not confounded by the total

density of neighbours. Transformations were performed using the Box–Cox procedure (Box & Cox 1964) to ensure *a priori* that the assumptions of the regression were not violated. Separate Box–Cox transformations were calculated for each species, size class, and neighbourhood radius. Significance tests were calculated from the Box–Cox transformed regression statistics. Because the denominator is positive in these analyses, the t -values always have the same sign as the standard partial regression coefficients.

In order to reduce the possibility of reaching spurious conclusions, the regression statistics calculated from the real Pasoh and BCI datasets were compared with a set of regression statistics calculated from artificially assembled forests in which the effects of neighbourhood crowding on tree survival had been removed. This was carried out by constructing 100 randomized data sets in which the location of all trees within each species and size class was retained while reassigning the survival fate of each tree to a randomly selected individual of the same species and size class (*sensu* Wills *et al.* 1997; Wills & Condit 1999). Regression statistics were then calculated for each of these randomized data sets. For each neighbourhood size and size class, the mean t -value of each species in the randomized datasets was

subtracted from the t -value calculated for that species from the real BCI and Pasoh data sets, yielding a distribution of t -value differences. The departure of these distribution means from zero indicated significant overall density-dependent relationships. Significant positive departures indicated a positive relationship between survival and neighbourhood numbers or biomass, while significant negative departures indicated the opposite relationship.

The results of this analysis were similar to those obtained using logistic regression on the binary response variable of survivorship between the initial and 1995 census interval at each plot. The novel analytical techniques presented here are preferable because they allow for the incorporation of more information about an individual's survival, a consideration that is becoming more important because of the increasing number of repeated demographic censuses becoming available at Pasoh, BCI, and other large, permanent tropical forest research plots.

RESULTS

The individual-based approach utilized in this study identified significant overall effects of neighbourhood

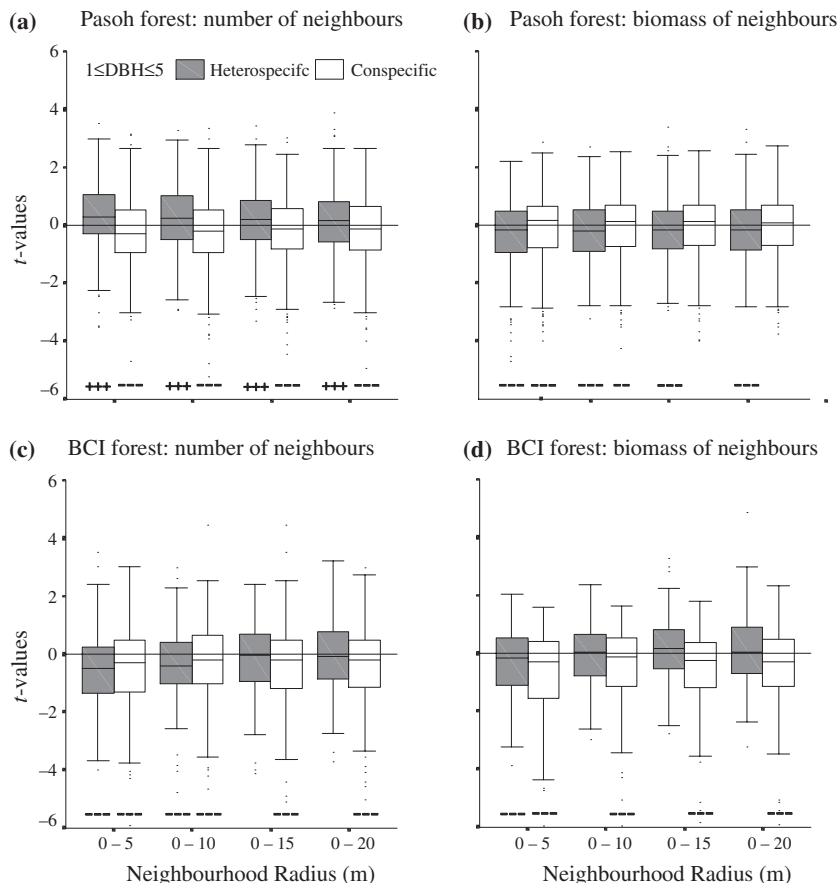


Figure 1 Box plots for the effects of heterospecific and conspecific numbers and basal area on survival among trees in the small ($1 \leq \text{DBH} \leq 5$ cm) size class at Pasoh and BCI. Each box shows the median and interquartile ranges of the distribution of t -values, with each t -value derived through independent analysis of a distinct species. Distributions with positive means that are significantly different from 0 are indicated by + ($P \leq 0.100$), ++ ($P \leq 0.050$), or +++ ($P \leq 0.005$), while negative means are indicated by - ($P \leq 0.100$), - ($P \leq 0.050$), or - ($P \leq 0.005$). Similar results were found in the medium ($5 < \text{DBH} \leq 10$ cm), and large ($10 \text{ cm} < \text{DBH}$) size classes at both sites. Negative t -values suggest a negative influence of neighbour numbers or basal area on survival. Positive t -values indicate just the opposite.

numbers and basal area on the survival of trees at both Pasoh and BCI (Fig. 1). Density dependence was prevalent even among trees larger than 10 cm DBH (Table 1). Furthermore, many of these effects were consistent with the Janzen–Connell and species herd protection models, suggesting that they would tend to maintain species diversity in tropical forests. Significant density-dependent relationships with survival were found in species with as few as 30 individuals in a size class.

Of the 544 species included in the study of Pasoh, 209 exhibited significant heterospecific or conspecific density-dependent effects of neighbourhood number on mortality at some neighbourhood radius. Marginally significant effects were found in an additional 100 species. At BCI, 113 of the 188 species included in this study displayed evidence of significant density-dependent mortality, while 21 additional species showed marginally significant effects. At Pasoh, 267 species exhibited significant heterospecific or conspecific density-dependent effects of neighbourhood basal area on survival at some neighbourhood radius, with 96 species demonstrating marginally significant effects. At BCI, mortality was found to be significantly density dependent in 95 of 188 species, with marginally significant density dependence evinced by an additional 25 species.

A comparison of the two sites reveals a number of interesting trends. First, although the Pasoh site has more than 2.6 times the species richness of BCI, the two sites had similar proportions of significant effects. At BCI, 154 (82%) of the 188 species tested in this study exhibited significant or marginally significant density-dependent survival, while at Pasoh 433 (80%) of the 544 species tested showed these effects. When all species present in the 50-ha plots are considered, 49 and 53% of them demonstrated significant or marginally significant density-dependent survival at BCI and Pasoh, respectively, despite the fact that many species present at these sites were too rare to be examined. Second, survival generally decreased with increased numbers or basal

area of neighbours at both sites. An important exception to this general trend was found at Pasoh, where the overall effect of the number of heterospecific neighbours was opposite to the effect of the number of conspecific neighbours (Fig. 1a). When the number of conspecific neighbours was held constant, having more heterospecific neighbours consistently resulted in increased survival for trees in the smallest and largest size classes at Pasoh. Finally, at Pasoh overall heterospecific relationships were consistently stronger in magnitude than conspecific relationships. At BCI, just the opposite was the case. Overall heterospecific relationships were generally smaller in magnitude than conspecific relationships.

At both sites, density-dependent mortality was most common for trees in the smallest size class, between 1 and 5 cm DBH, but this was largely because there are more small than large trees in these forests. As a proportion of the number of species examined in each size class, the prevalence of density-dependent mortality declines little across size classes (Table 1). Among the largest trees at Pasoh and BCI there were highly significant effects of neighbourhood numbers on survival, suggesting that density dependence influences the survival of even very large trees in these forests.

There was abundant phenomenological evidence for both the Janzen–Connell and species herd protection hypotheses at both sites. According to both hypotheses mortality is expected to increase with conspecific crowding. The herd protection hypothesis makes the additional prediction of decreasing mortality with increasing heterospecific crowding. Of the 323 species at Pasoh demonstrating significant or marginally significant relationships between conspecific crowding and mortality, 255 (79%) of these species exhibited patterns of mortality consistent with Janzen–Connell expectations at some size class or neighbourhood radius. Of these, 191 species also showed patterns of mortality that would be expected of individuals influenced

Table 1 At the Pasoh and BCI forests, the number of species examined in each size class, and the number of species exhibiting significant or marginally significant density-dependent mortality (The percentage of species examined that exhibit such effects follows in parenthesis.) for both the tree number and basal area analyses

Site	Size class	Crowding metric	No. species examined	No. species significant	
Pasoh	1 ≤ DBH ≤ 5	Tree number	539	232 (43)	
		Basal area	539	294 (55)	
	5 < DBH ≤ 10	Tree number	255	86 (34)	
		Basal area	255	108 (42)	
		10 < DBH	Tree number	213	84 (39)
			Basal area	213	97 (46)
BCI	1 ≤ DBH ≤ 5	Tree number	177	91 (51)	
		Basal area	177	95 (54)	
	5 < DBH ≤ 10	Tree number	94	32 (34)	
		Basal area	94	44 (47)	
		10 < DBH	Tree number	97	67 (69)
			Basal area	97	36 (37)

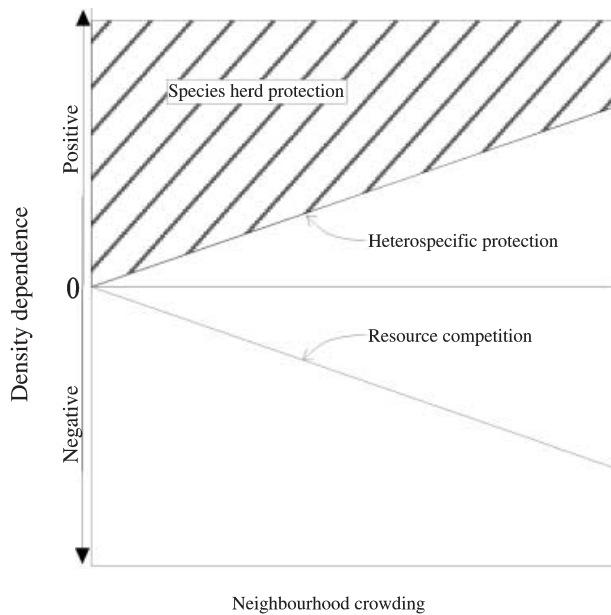


Figure 2 Only when the benefits of herd protection are greater than the disadvantages of resource competition, generalist pest propagation, or both will species herd protection be evident using the analysis presented in this study.

by species herd protection. At BCI, of the 118 species that displayed significant or marginally significant conspecific density-dependent mortality, 89 (75%) showed evidence of Janzen–Connell type density-dependent mortality, while 69 of these species demonstrated patterns of mortality consonant with the predictions of the species herd protection hypothesis. Given the constraints associated with detecting herd protection from tree demographic data (Fig. 2), it seems likely that this study underestimates the degree of species herd protection at these sites.

DISCUSSION

This study found widespread density-dependent mortality among well-established trees at Pasoh and BCI, two species-rich tropical forests. The overall patterns of survivorship found in these analyses are consistent with the Janzen–Connell hypothesis. Furthermore, this study provides some of the first evidence in support of the hypothesis that tree populations are regulated by species herd protection.

This study considered 544 and 188 species at Pasoh and BCI, respectively, far more than have ever been considered in previous investigations at either site. It is generally thought that density dependence must be prevalent to be an important regulator of species richness and abundance in tropical tree communities (Lieberman 1996; Chave *et al.* 2002). Over 80% of the species examined at each site

exhibited significant or marginally significant density-dependent mortality. Density dependence was detected among species with as few as 30 individuals in a size class – the minimum number of individuals tested in this study – demonstrating that both rare and common species can be regulated by these mechanisms.

These results represent a marked improvement in our understanding of the prevalence of density-dependent neighbourhood influences on mortality. In an 18 year study of the dynamics of an Australian tropical forest, Connell *et al.* (1984), using a subplot-based approach, found little or no evidence of conspecific density-dependent growth or mortality among seedlings, saplings, or adults. In a recent study on the 84 most common species at BCI, Wills *et al.* (1997) observed density-dependent relationships between subplot mortality and basal area among only 33 species. In a separate subplot-based study of 100 common species at Pasoh and BCI, Wills & Condit (1999) concluded, after finding few consistent relationships between mortality and neighbourhood crowding or basal area, that mortality was essentially random by the time trees reach 1 cm DBH. Both of these previous studies are inconsistent with the findings of the present study, indicating the effectiveness of the individual-based approach used here in detecting species-specific density-dependent relationships. In one of the few community-level studies employing an individual-based approach, Hubbell *et al.* (2001) found that when all trees were considered in one or a few groups, conspecific density and total tree density tended to increase tree mortality. The results presented here extend this finding. Previously observed patterns of community-wide density dependence seem unlikely to simply reflect the influence of a few hyper-abundant species. These patterns are apparently due to mechanisms that are very prevalent among tropical tree species and operate across a range of tree size classes and neighbourhood ranges.

It is surprising that density-dependent effects are as common at Pasoh as BCI. The effects of spacing and neighbour identity on the growth and survival of larger trees have been reasonably well studied in temperate forest plantations (e.g. Martin & Ek 1984; Richardson *et al.* 1999; Cao *et al.* 2000; Jobidon 2000) and mixed stands with low species richness (e.g. Budelsky & Schlesinger 1973; Wykoff 1990; Biging & Dobbertin 1992, 1995). Conspecific density dependence might be expected to be strongest among abundant species, reaching its limit in single species stands where self-thinning laws are applicable (Niklas *et al.* 2003). The 50-ha plot at Pasoh has more than 2.6 times the species richness of BCI, with many more rare species. The most common tree at BCI, for example, is five times as abundant as the most common species in the Pasoh plot. Nevertheless, density-dependence was as likely to regulate tree species populations at Pasoh as at BCI, a finding consistent with a

recent tropical-temperate forest comparison of density-dependence in the seed to seedling transition (Lambers *et al.* 2002).

Patterns of density-dependent mortality consistent with the Janzen–Connell hypothesis were widespread at both Pasoh and BCI. At each site there were strong, negative relationships between survival and both conspecific numbers and biomass. Of the species that demonstrated significant effects of conspecific crowding on mortality, greater than 75% showed patterns of mortality consistent with Janzen–Connell expectations. This study is among the first to show evidence in support of the species herd protection model operating in tropical forests. At both Pasoh and BCI, more than 75% of those species displaying Janzen–Connell type density dependence also exhibited patterns of mortality of the type that would be predicted by the species herd protection hypothesis, meaning that for a given density of conspecific neighbours, survival was enhanced by the addition of heterospecific neighbours. At Pasoh overall survival increased with increasing numbers of heterospecific neighbours among trees in the smallest size class (Fig. 1), an unexpected result unless the benefits associated with protection from pests and pathogens were generally greater than the costs associated with abiotic competition (Fig. 2). At BCI this unusual finding was not observed: survival declined with increasing heterospecific numbers or biomass.

It is not clear why species herd protection is evident at Pasoh but not BCI. The negative relationships between survival and basal area, both heterospecific and conspecific, are circumstantial indicators of density-dependent resource limitation at both sites (Chase *et al.* 2002). Regardless of neighbour identity, competition for scarce resources may be amplified as the biomass density of a region increases. Herd protection will only be evident in this type of analysis when the marginal benefit conferred by the presence of an additional heterospecific neighbour is greater than the detriment associated with increased resource competition and increased likelihood of encountering generalist plant pests and pathogens. Possible explanations for the different trends observed in the two forests include: more intense heterospecific competition, reduced abundance or virulence of plant pests and pathogens, and greater prevalence of generalist plant enemies at BCI. Because there may be instances in which the benefits of additional neighbours are positive but still smaller than the disadvantages resulting from augmented competition, this type of analysis seems likely to underestimate the prevalence of herd protection in the community (Fig. 2). No phylogenetic information has been incorporated into this study, an unfortunate limitation. Future studies of density dependence must strive to incorporate information on the specificity and abundance

of plant enemies, and must establish the influence of taxonomic affinities above the species level (e.g. Novotny *et al.* 2002) on density-dependent population regulation.

In order to address the possibility that the patterns reported here are simply localized, heterogeneous influences on mortality (e.g. treefall gaps, dispersal onto highly favourable or unfavourable sites), a number of the most common species at BCI were selected for further analyses. From each species a subset of trees with non-overlapping neighbourhoods was randomly selected, and all analyses used in this study were performed on these random subsets. This rarefaction was repeated 100 times for each species investigated. This analysis of a subset of species at BCI revealed that the patterns of mortality were very similar to those found when all individuals were included in the analysis, suggesting that the effects of neighbours were distinguishable from those of autocorrelated spatial heterogeneity.

Density dependence is expected to have its greatest impact in the earliest stages of plant establishment, when high susceptibility to herbivores, pathogens, and abiotic stressors results in low survivorship. Numerous studies of density dependence have found these effects to be present among individual seed and seedling species, but only recently have they been shown to be pervasive in an entire forest community (Harms *et al.* 2000). The results of the present study indicate that density-dependent mortality may be important even for very large trees at Pasoh and BCI. As a proportion of the number of species examined, density-dependent mortality was equally common in the largest and smallest size classes (Table 1). These results, together with those of Harms *et al.* (2000), indicate that density dependence is regulating tree populations at every developmental stage from seed to mature tree. There have been few detailed studies of density dependence among well-established trees (e.g. Condit *et al.* 1994; Gilbert *et al.* 1994), and little is known about the influence of density dependence on tree reproduction. Such studies are the critical next step in understanding trans-generational patterns of population regulation in forest tree communities.

The results of this study on two tropical forests, one Malaysian, the other Panamanian, suggest that the Janzen–Connell hypothesis, species herd protection, and other mechanisms of density-dependent mortality contribute to the regulation of tropical tree populations. Although the implications of this finding for tree species richness and abundance remain to be explored, they suggest that attempts to understand, manage, and conserve tropical forests must explicitly consider the influence of tree density and diversity on forest dynamics. Specifically, if the forests considered in this study are typical of other tropical forests sites, then one central assumption of the unified

neutral theory of biodiversity (Hubbell 1997, 2001), that density-dependent influences are neutral (i.e. symmetric), should be rejected. Both the density and identity of neighbours influence tree mortality, and the probability of survival varies among species. The incorporation of these effects into future models of population regulation may prove insightful.

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