Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest

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Abstract
Density-dependent seedling mortality could increase with a species relative abundance, thereby promoting species coexistence. Differences among species in light-dependent mortality also could enhance coexistence via resource partitioning. These compatible ideas rarely have been considered simultaneously. We developed models of mortality as functions of irradiance and local conspecific density (LCD) for seedlings of 53 tropical woody species. Species varied in mortality responses to these factors, but mortality consistently increased with shading and LCD. Across species, density-dependent mortality on a per-neighbour basis was inversely related to species community abundance, but higher LCD in more common species resulted in a weak relationship between species abundance and density-dependent mortality scaled to species maximum LCD. Species mortality responses to shading and maximum LCD were strongly and positively correlated. Our results suggest that species differences in density-dependent mortality are more strongly related to physiologically based life-history traits than biotic feedbacks related to community abundance.

Keywords
Community compensatory trend, density dependence, irradiance, Janzen–Connell hypothesis, resource partitioning, seedling mortality, seedlings, shade tolerance, species coexistence, species richness, wet tropical forest.

INTRODUCTION
The processes that promote species coexistence are fundamental to plant community ecology but remain unresolved (Silvertown 2004). For species-rich wet tropical forest, there are at least two mutually compatible mechanisms that could enable species coexistence: negative density dependence (NDD) and resource-based niches. Both of these mechanisms could contribute to stable species coexistence (Chesson 2000). However, they rarely have been considered simultaneously (Augsburger & Kelly 1984).

Under NDD, natural enemies reduce seedling recruitment near conspecific trees and/or at high local conspecific seedling densities (LCD) (Janzen 1970; Connell et al. 1984). To enhance species diversity, NDD needs to be more severe in species that are more common in the community (Webb & Peart 1999), such that per-capita mortality increases with species abundance, a phenomenon that has been termed a community compensatory trend or CCT (Connell et al. 1984). Although not broadly recognized, there are two distinct mechanisms by which NDD could be more severe in common species (McCarthy-Neumann & Kobe 2008). First, less abundant species may escape detection by natural enemies (Feeny 1976) and thus have relatively low per-capita mortality induced by density-dependent enemies regardless of LCD; the greater apparentness of common species to natural enemies may promote higher density-dependent mortality.

Second, regardless of community abundance, all species could have a similar relationship between mortality and LCD, but the higher overall abundance of common species results in higher LCD and concomitantly higher mortality of individual seedlings, which also could result in a CCT (Connell et al. 1984; Webb & Peart 1999). The per-neighbour effect of conspecifics on seedling mortality may decrease with community abundance (Comita et al. 2010), which superficially appears to run counter to a CCT, but a CCT could still result if LCD increased with species community abundance (Richard K. Kobe and Benedicte Bachelor, unpublished data).

In testing for a CCT, it is thus critical to recognize that there are two components to NDD which may vary across species: the per-neighbour effect of conspecifics on seedling mortality (per-neighbour NDD) (e.g. Comita et al. 2010) and the maximum levels of LCD that a species attains (Richard K. Kobe and Benedicte Bachelor, unpublished data). Maximum LCD is expected to vary tremendously among species (see Results), due to variation in seed production per tree (which often is inversely related to seed mass), seed dispersal and abundance of reproductive adults (Clark et al. 1998). To account for these species differences, per-neighbour NDD can be scaled by maximum LCD. If effects of LCD on mortality of seedling $i$ of species $j$ is $(\text{per-neighbour NDD})_j \times \text{LCD}_{ij}$, then scaling (per-neighbour NDD) by maximum LCD, results in $[(\text{per-neighbour NDD})_j \times \text{maximum_LCD}_j] \times \text{LCD}_{ij}/\text{maximum_LCD}_j$. The first bracketed term is potential NDD or the maximum mortality attributable to density effects. Potential NDD characterizes the effects of LCD as a proportion of the species maximum LCD (second bracketed term) and expresses the effects of LCD on seedling mortality on the same scale for all species, enabling more straightforward species comparisons and a consistent basis upon which to evaluate a CCT (Richard K. Kobe and Benedicte Bachelor, unpublished data).

Species variation in density-dependent seedling mortality, regardless of community abundance, also could arise from differences in physiological, morphological and allocational traits. Slow-growing, shade tolerant, well-defended species (Coley & Barone 1996) may experience less severe density-dependent mortality from herbivory or disease than fast-growing, poorly defended species with short leaf lifespans (Kitajima & Poorter 2010). Among tropical tree species,
seedling shade tolerance is negatively correlated with disease susceptibility (Augsburger & Kelly 1984) and depression of growth and survivorship by soil microbial extracts (McCarthy-Neumann & Kobe 2008). If disease and soil pathogens are density dependent, then seedling susceptibility to shading and NDD should co-vary across species.

Resource-based niche theory predicts that if resources are heterogeneous and species differ in resource-dependent performance, different species will dominate at given levels or combinations of resource availability thus promoting species coexistence in a community (Denslowl 1980; Tilman 1982). Supporting evidence includes species differences in seedling growth and survivorship across broad (Kobe 1999) and subtle variation in irradiance (Montgomery & Chazdon 2002), trade-offs among species between high-light growth vs. low-light survivorship (Hubbell & Foster 1992; Kobe 1999) and trade-offs among species between high soil fertility vs. survival at low fertility (Russo et al. 2008).

We concurrently assessed effects of irradiance and conspecific seedling and mature tree densities on seedling mortality in 53 woody species (including canopy, subcanopy and understory trees and lianas, see Table S1) from a Costa Rican wet tropical forest through developing models of seedling mortality from field data. We also tested heterospecific seedling and tree density but effects were negligible. The major goals of this study were to assess if species variation in NDD was related to: (1) community abundance, which would be consistent with the regulation of tree populations through a CCT and (2) species shade tolerance, which would support that ensembles of species’ traits provide resistance to a wide range of stresses.

METHODS

Field site, sampling and measurements

The study was conducted at La Selva Biological Station, a wet tropical forest in the Atlantic lowlands of Costa Rica (10°26’ N, 84°00’ W). Mean annual rainfall is 4306 mm, with a mean monthly minimum of 100 mm (http://www.ots.ac.cr/meteoro/). A broad gradient in soil fertility runs from relatively rich entisols and inceptisols of alluvial soils. We identified potential transects from grid posts that could originate a 200-m transect with minimal interference (trails, indices of conspecific and heterospecific trees. Conspecific seedling density was characterized as the mean number of conspecific seedlings in a 1-m² quadrat that was experienced by the focal seedling over its lifetime. We also tested initial and maximum lifetime conspecific seedling density, but mean lifetime LCD typically provided better model fits.

For analyses of irradiance and conspecific seedling density, we included the 53 woody species with ≥ 20 seedlings across all transects. Because of small sample sizes, seedlings from all transects were combined; soil effects on mortality will be the focus of future work. For those 23 species that had ≥ 12 seedlings located within 20 m of a mapped conspecific tree, we also tested effects of conspecific tree neighbourhood (i.e. mapped trees of > 5 cm dbh).

Data analysis

We used survival analysis and maximum likelihood methods (see likelihood function in Kobe et al. 2002) to parameterize species-specific seedling mortality models as functions of canopy openness, conspecific and heterospecific seedling density, and neighbourhood indices of conspecific and heterospecific trees.

To parameterize the mortality models, we specified the hazard function (λ) as:

$$\lambda = \lambda_0 \exp \left( B_1 \text{light} + B_2 \text{density}_{\text{con}} + B_3 \text{density}_{\text{hetero}} + B_4 W_{\text{con}} + B_5 W_{\text{hetero}} \right),$$

where $A$ and $B_j$ are parameters estimated from the data, and $W_j$ is a neighbourhood index of trees > 5 cm dbh (see below). Each $B_j$ characterizes the sensitivity of mortality to changes in factor $j$. Note that $B_2$ (synonymous with $B_{\text{density}}$) is the per-neighbour effect of
conspecific seedling density and characterizes the influence on the hazard function of adding one conspecific seedling to the neighbour-

hood of the focal seedling. Probability of mortality over time interval \( t \) is the cumulative distribution function of an exponential random variable:

\[
\text{Probability of mortality}_t = 1 - \exp(-t \times \lambda).
\]  

We estimated joint 95% confidence intervals through inverting the likelihood ratio test. Uncertainty in parameter estimates was then propagated through the mortality models by calculating mortality from sets of parameters that jointly were contained within the 95% confidence space, thus accounting for covariance in error. Factors were significant when 95% confidence intervals for \( B_j \) did not encompass zero. We assessed relative empirical support for variants of eqn 1 by setting \( B_j \)'s equal to zero and comparing Akaike’s Information Criterion corrected (\( \text{AIC}_c \)) for small sample sizes. We report models with the greatest number of significant predictors that were within two \( \text{AIC} \) units of the minimum (Burnham & Anderson 2002).

**Neighbourhood indices**

We estimated con- and hetero-specific neighbourhood indices, which take into account abundance and sizes of mapped trees and their distances to focal seedlings, as predictors of seedling mortality. The maximum distance of a neighbourhood was truncated at 20 m, the extent of mapping. The general index was defined as:

\[
W = \sum_{i=1}^{\text{# adults}} (\text{dbh}(i) \times \exp(-\beta \times \text{dist}(i))),
\]

where \( \alpha \) and \( \beta \) are parameters estimated from the data and respectively, scale the contribution of diameter at breast height (dbh) and distance (dist) between the target seedling and tree to the index and thus seedling mortality. \( \alpha \) and \( \beta \) were estimated simultaneously with parameters of eqn 1. \( W \) increases with the number of trees in the vicinity, size(s) of neighbouring tree(s) and as distance(s) between tree(s) and the seedling decreases.

The index allows neighbourhood effects to be decomposed to contributions from proximity, numbers and sizes of neighbours through setting \( \alpha \) and/or \( \beta \) to zero (Tables S2 and S3). When \( \alpha = 0 \) and \( \beta = 0 \), \( W \) is the count of trees within a 20-m radius. We also tested a null index and three non-hierarchical indices: (1) eqn 3 with a neighbourhood radius (\( R \)) estimated from data (rather than 20 m), (2) count of conspecific trees within \( R \) and (3) distance to the nearest conspecific tree. We compared indices with \( \text{AIC}_c \) (Burnham & Anderson 2002).

**RESULTS**

**Seedling mortality increased with shading and local conspecific seedling and tree densities**

Seedling mortality increased with shading in 51% of species (27/53), conspecific seedling density in 47% (25/53) (Fig. 1), and the number of conspecific trees (\( W_{con} \)) within an estimated radius in 48% (11/23) of species. Seedlings of 16 species responded to both irradiance and conspecific seedling density and several other species responded to three factors or to other combinations of two factors (Table S1). The direction of significant effects was consistent across species (Table S4). Among species, mortality varied c. 8-fold with shading and seedling density (Fig. 1). Among species responding to conspecific seedling density, maximum observed seedling densities differed dramatically (Fig. 1), from 3 to 220 seedlings m\(^{-2} \).

The count of local conspecific trees (radius \( \leq 20 \)) was the best neighbourhood index to predict mortality (Tables S2 and S3) in 10 of the 11 species for which neighbourhood was supported. For the remaining species, *Calophyllum inophyllum*, count of conspecific neighbour trees was still strongly supported (\( \Delta \text{AIC} < 1 \)). Species differed in the neighbourhood size over which conspecific trees influenced seedling mortality, from a 9.2-m radius for *Protium costaricense* and *Casipora elliptica* to c. 17.7 m in *Hampea appendiculata* (Figure S2). Species neighbourhood radius was correlated with species mean tree diameter (\( r = 0.66, P = 0.03 \)), but not seedling or tree density (\( P > 0.10 \)).

Effects of heterospecific seedling and tree densities were not prevalent and when present were weak. Considered alone, heterospecific seedling density contributed to predicting mortality in 12 of 53 species but with weak empirical support relative to conspecific seedling density (\( \Delta \text{AIC} = 499.97 \)). After accounting for canopy openness, which often was negatively correlated with heterospecific tree density (Figure S3), the latter was positively correlated with seedling mortality for two species and negatively for two species. Lower variability in heterospecific vs. conspecific density could have made detection of heterospecific seedling and tree density effects less likely. Heterospecific effects were not considered further.

**Across species, seedling mortality response to conspecific density was negatively and weakly correlated with species abundance**

Seedling mortality sensitivity to local conspecific seedling density (\( B_{\text{density}} \) or per-neighbour NDD) was negatively correlated with overall conspecific seedling abundance in the community [Fig. 2a; \( r = -0.48, P = 0.02 \); \( r = -0.9 \) for log(seedling abundance)], but not with overall abundance of conspecific trees (\( r = -0.10, P = 0.67 \)). However, the relationship between \( B_{\text{density}} \) and overall seedling abundance reflected a similar relationship between \( B_{\text{density}} \) and maximum local conspecific seedling density (Fig. 2b). Indeed, species with greater seedling abundance in the community also had greater maximum LCD (Fig. 2c; \( r = 0.85, P < 0.001 \)) and could have concomitantly lower estimates of \( B_{\text{density}} \) (per-neighbour NDD) simply because LCD was on a finer scale for more common vs. less common species. For example, adding one seedling to the hazard function (eqn 1) of a common species with a maximum LCD of 220 has less effect than adding one seedling to the hazard function of a less common species with a maximum LCD of five (Fig. 1). Thus, the decrease in \( B_{\text{density}} \) with species abundance was likely an artefact of species’ different scales for LCD (Fig. 2).

To correct for species differences in maximum LCD (Fig. 1) and to avoid the artefactual relationship in Fig. 2a, we re-scaled local conspecific seedling density as a proportion of the species maximum LCD (see Introduction). This was accomplished by multiplying \( B_{\text{density}} \) (per-neighbour NDD) by species maximum LCD to estimate potential NDD (maximum mortality attributable to LCD). Potential NDD was negatively but weakly correlated with overall seedling abundance (Fig. 3a) and was not correlated with tree abundance (Fig. 3b).
Across species, potential NDD and shade tolerance were strongly correlated

Less shade tolerant species (\(B_{\text{light}}\) of higher magnitude) have rapid increases in mortality as irradiance decreases. Across species, seedling mortality response to shading was correlated with potential mortality response to conspecific seedling density (\(r = 0.70, P = 0.002\); Fig. 4). As above, we scaled \(B_{\text{density}}\) by maximum LCD to place species on the same scale for comparisons. In the absence of local conspecific seedlings, shading effects on mortality were similar among species; mean increases in mortality between 2 and 12% canopy openness ranged from 0.03 to 0.27. However, because of uncertainty in background mortality (\(\lambda\) parameter), propagated 95% support intervals were broadly overlapping. Nevertheless, under maximum LCD, there was greater variation among species in the mean effects of shading (from 0.19 to 0.98) because mortality sensitivities to shading and conspecific seedling density were correlated. Some species segregated per propagated 95% confidence intervals, but uncertainty in parameter estimates, especially in background mortality (\(\lambda\) parameter), yielded considerable overlap among most species (Figure S4).

**DISCUSSION**

Across species, seedling mortality responses to shading and conspecific seedling density were correlated; these results are consistent with a positive correlation between shade tolerance and resistance to soil pathogens (Augsburger & Kelly 1984; McCarthy-Neumann & Kobe 2008). Although juvenile density dependence may be pervasive (e.g. Harms et al. 2000), it may not necessarily constrain abundance of common species, as expected under a CCT (cf. Webb & Peart...
Rather, in the present study, density dependence manifested differently along a life-history axis, disproportionately increasing mortality of shade intolerant species (Fig. 4).

Seedling mortality generally increased with shading and conspecific seedling and tree density

Rarely have density-dependent mortality agents and irradiance been considered simultaneously (but see Augspurger & Kelly 1984; McCarthy-Neumann & Kobe 2008) or directly, even though substantial evidence supports the importance of each. In this study, the positive effects of light availability (e.g. Kobe 1999; Montgomery & Chazdon 2002) and negative effects of conspecific (seedling and larger tree) density (e.g. Webb & Peart 1999; Harms et al. 2000) on seedling survivorship are consistent with many previous studies that considered these factors singly. The effects of conspecific seedlings on seedling survivorship could be due to soil fungal pathogens (e.g. Mangan et al. 2010) or herbivores (Coley & Barone 1996), but resource competition among seedlings is typically weak and not a likely explanation (e.g. Wright 2002). The effects of conspecific trees also could have arisen from soil pathogens (McCarthy-Neumann & Kobe 2008), but we cannot rule out the possibility of stronger intraspecific than interspecific competition for soil resources (particularly tree effects on soil resources available to seedlings), or the alteration of soil nutrients or chemical properties by trees (McCarthy-Neumann & Kobe 2010).
Species that were more resistant to (conspecific) density-dependent mortality agents also were more shade tolerant

The correlation between shade tolerance (low sensitivity of mortality response to shading) and resistance to density-dependent mortality agents could arise from a set of traits, which themselves co-vary, that convey resistance to a wide range of stresses. More shade tolerant species tend to have tough leaves (Kitajima & Poorter 2010) that are well defended against herbivores (Coley & Barone 1996), have relatively high mass partitioning to carbohydrate storage, which could enable recovery from damage (Kobe 1997; Myers & Kitajima 2007), and higher tissue density and fibre content (Alvarez-Clare & Kitajima 2007), which could provide resistance to damping off (Augspurger & Kelly 1984) and other mortality agents.

Larger seed/initial seedling mass also could convey shade tolerance in the young seedlings examined herein. Because of seed mass – fecundity trade-offs, seed mass/initial seedling height could be related to maximum local conspecific seedling density, which in turn influenced potential NDD. However, this explanation was not supported. Due to lack of seed mass data for all species, we focused on initial seedling height, which is strongly correlated with seed mass ($r = 0.79, P < 0.001$) (Ellen K. Holste, Richard K. Kobe & Corine F. Vriesendorp, unpublished data). Across species, initial seedling height was not correlated with shade tolerance ($-B_{light}$) ($r = 0.23, P = 0.40$), survival at 1% openness (which includes background mortality; but no conspecifics) ($r = 0.31, P = 0.25$), maximum LCD ($r = -0.12, P = 0.66$), nor potential NDD ($r = 0.19, P = 0.5$), although the highest levels of LCD were attained by species with smaller seedlings. In a related growth study that included more species, initial seedling height and low-light survival (which depends on both $B_{light}$ and $A$, background mortality) were moderately correlated ($r = 0.44, P < 0.001$) (Ellen K. Holste, Richard K. Kobe & Corine F. Vriesendorp, unpublished data). These results suggest that foliar and whole plant traits (Kitajima & Poorter 2010), rather than seed reserve size, influenced species responses to both shade and density-dependent mortality agents, with a weak trend of higher survival overall for species with larger seedlings.

We found no support for an alternative explanation of species covariance in shade tolerance and density dependence, namely that shade intolerant species recruit into gaps in dense clumps, which confounds shade tolerance and density dependence as the gaps close. If this argument were valid, then irradiance (measured early in the study) should be positively associated with conspecific seedling
density, especially in shade intolerant species. However, we found a weak negative relationship instead \((r = -0.1, P < 0.001, \text{all species combined})\). Furthermore, on a species basis, irradiance and conspecific density were positively correlated in only three cases, but these included species with a full range of responses to irradiance \((0.04–0.36 \text{ for } B_{\text{density}})\) and not just shade intolerant species.

**No support for a CCT, but potential NDD decreased weakly with species community abundance**

Density-dependent mortality of seedlings could constrain abundance of common species through greater sensitivity of common species to density dependence or higher local densities of common species (see Introduction). Both of these mechanisms could result in a positive relationship between per-capita seedling mortality and community abundance (i.e. a CCT). However, our results do not support either mechanism. Common species were not more sensitive to density dependence (Fig. 3), which would be expected if common species had greater loads of natural enemies. The second mechanism assumes that all species, regardless of abundance, have a similar functional relationship between mortality and LCD and that common species have higher densities, which moves them up the mortality-density curve (Connell et al. 1984). Abundant species had higher local conspecific seedling density, but there was tremendous variation among species in mortality responses to conspecific density. Although we did not find evidence for a CCT, the strong effects of LCD on seedling mortality detected herein and its covariance with species shade tolerance, together with environmental variability in irradiance, could provide a stabilizing mechanism for species coexistence and may contribute to maintaining the relative abundances of species.

Our results also suggest that lower \(B_{\text{density}}\) (per-neighbour NDD or the sensitivity of a species’ mortality to the addition of one conspecific seedling) (e.g. Comita et al. 2010) in common species could arise as an artefact of the strong positive correlation between a species overall abundance and its maximum local seedling density (Fig. 2). More common species (herein measured as overall seedling abundance) had higher maximum local conspecific seedling densities and thus \(B_{\text{density}}\) applied to a finer scale for more common than less common species, resulting in a strongly negative relationship between species community abundance and per-neighbour NDD (Fig. 2). A similar artefact likely influenced the finding of Comita et al. (2010) that per-neighbour NDD decreased with species community abundance. In fact, rescaling per-neighbour NDD in Comita et al. (2010) to potential NDD results in an opposite trend of increasing density-dependent effects on seedling mortality with species community abundance (Richard K. Kobe and Benedicte Bachelot, unpublished data), consistent with a CCT (Connell et al. 1984). In contrast, herein we found that potential NDD decreased weakly with seedling community abundance (Fig. 3a), but this relationship was strongly influenced by two species with relatively low seedling abundance and high potential NDD.

**Caveats**

Although the present study may be unprecedented for temporal resolution in seedling dynamics, the total length of the study was c. 30 months. A longer term data set would encompass mast fruiting years for a greater number of species, which might reveal different relationships between community abundance and density dependence. To accurately estimate survival times, we included only seedlings germinating during the study. The survival of these young seedlings may differ from larger size classes due to ontogenetic effects and may partly explain the discrepancies between this study’s results with Comita et al. (2010), which excluded individuals < 20 cm height and found no relationship between (per-neighbour) NDD and shade tolerance. Shade tolerance and potential NDD may be more strongly correlated in young seedlings because shade-induced mortality has not filtered out shade intolerant species and restricted the range of species shade tolerances, which would be expected in the larger and older size classes examined by Comita et al. (2010). However, the most important difference between studies is that here density-dependent mortality was scaled to a proportionate basis to account for the tremendous species differences in LCD, while Comita et al. (2010) examined per-neighbour NDD and did not account for species covariance in LCD and community abundance.

Limited sample sizes for some species likely precluded detection of significant effects, as sample size was positively correlated with the number of significant factors \((r = 0.57, P < 0.001)\). Nevertheless, limited sample sizes enforce conservative results, which lend greater credence to the relationship between shade tolerance and density dependence but may have precluded detecting a stronger relationship between density dependence and species abundance. Because some species represented as seedlings were not present (or mapped in the case of lianas) as trees, overall abundance of seedlings was emphasized over trees as a metric of species abundance in the community; the relationship between NDD in seedlings and mature tree abundance would have provided a more direct assessment of how NDD could influence tree species coexistence. Individuals < 5 cm diameter that were outside the seedling transect were not mapped and thus we have not accounted for their potential influence (which we expect to be minimal, based on the low densities of individuals in this size class). We also have not yet tested for effects of neighbours of closely related species on density-dependent mortality. Finally, representation by 20 seedlings defined the least abundant species in the study; thus, very rare species were not encompassed.

**CONCLUSIONS**

Although density dependence was pervasive here and in other studies (Harms et al. 2000), it was not consistent with a CCT (Janzen 1970; Connell et al. 1984), where common species experience stronger NDD. There was tepid support for more intense NDD in rare species (Comita et al. 2010; Mangan et al. 2010), after correcting for species differences in LCD. In the absence of other compensating mechanisms (e.g. species differences in resource-based performance, dispersal), consistently stronger NDD in rare species would be expected to drive rare species to extinction over the long term, which is inconsistent with the high levels of tree species richness that are maintained in wet tropical forests (Richard K. Kobe and Benedicte Bachelot, unpublished data). Although seedling survival is the first bottleneck to community membership, the importance of seedling responses to irradiance and conspecific density to community dynamics has to be assessed in the context of other life-history stages and should be scaled over time and space (e.g. Pacala et al. 1996). Nevertheless, incorporating species-specific behaviour in models of wet tropical forest dynamics could be simplified if demographic responses to different factors are correlated across species. In particular, covariance in species resistance to density-dependent
mortality agents and shading suggest that a common set of physiological traits influence seedling responses to both shading and density-dependent mortality agents.

ACKNOWLEDGEMENTS

NSF (DEB 0075472, 0640904, 0743609) and the MSU Intramural Research Grant Program provided financial support. We thank Ademar Hurtado, Ralph García, Martin Cascante and Yehudi Hernández (field help), Orlando Vargas (taxonomy) and OTS (logistical support). The paper was improved through constructive comments from Brian Enquist, Scott Stark, Kaoru Kitajima, David Peart, two anonymous referees, Sarah McCarthy-Neumann, Tom Baribault, Ellen Holste, Beneditce Bachelot, Andrea Maguire, David Minor, and Megan Matonis.

REFERENCES


SUPPORTING INFORMATION

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

**Figure S1** Semi-variograms of residual variance in survival time.

**Figure S2** Neighbourhood radius by species.

**Figure S3** Correlation of canopy openness with number of heterospecific trees.

**Figure S4** Effects of shading on seedling mortality in the presence and absence of conspecific neighbours.

**Table S1** Species lifeform and AIC support for the seedling mortality models.

**Table S2** Formulations of the neighbourhood index.

**Table S3** AIC support for the neighbourhood indices.

**Table S4** Parameter estimates for the best-supported mortality models.

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Editor, Brian Enquist

Manuscript received 23 August 2010

First decision made 28 September 2010

Second decision made 4 January 2011

Third decision made 21 February 2011

Manuscript accepted 28 February 2011