# Seedling Density Dependence Promotes Coexistence of Bornean Rain Forest Trees

# SEEDLING DENSITY DEPENDENCE PROMOTES COEXISTENCE OF BORNEAN RAIN FOREST TREES

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*Abstract.* Density-dependent processes may occur at various spatial scales and may be generated by, and influence, various life stages in a population. When evaluating evidence for density dependence relevant to species coexistence, the nature of forest communities leads logically to a focus on particular scales and life stages. We assessed evidence for the dependence of seedling survival on the abundance of conspecific trees and seedlings over both wide (150-ha) and local (0.16-ha and 1-m$^2$) scales, in a species-rich Bornean rain forest. At the 150-ha scale, we identified a community-level compensatory trend in seedling survival (i.e., more abundant species had higher seedling mortality). There were parallel trends at the population level and on a local scale; seedling survival was inversely related to conspecific seedling density (in 1-m$^2$ quadrats) and tree basal area (in the surrounding 0.16 ha), for five out of 15 abundant species and for all species combined. As expected, seedlings of species with the highest adult abundance in 150 ha experienced the highest local densities of both conspecific seedlings and trees. Local density dependence in single-species analyses confirmed a dynamic interpretation of the community compensatory trend, i.e., that wide-scale seedling survival tends to decrease as a species' adult abundance increases. Taken together, our findings constitute strong evidence that density-dependent processes contribute to coexistence in this diverse rain forest community.

*Key words: Borneo; common vs. rare species; community-level coexistence; compensatory mortality; density dependence; pathogens; rain forest; seedling dynamics; spatial scale; tree species diversity.*

## Introduction

Elucidating mechanisms that promote coexistence is of special interest in tropical rain forests because of their extraordinary species richness. A fundamental question is whether there are ecological mechanisms that buffer the many rare species against local extinction, or limit the dominance of the more abundant species. Any such mechanisms are, by definition, density dependent. Our goal in this paper is to assess evidence for density-dependent dynamics that promote species persistence in a rain forest community.

High species richness does not necessarily imply that density-dependent mechanisms exist. Species-rich assemblages could, in theory, result from the random process of community drift, with rates of local extinction balanced by dispersal and speciation rates (MacArthur and Wilson 1967, Hubbell 1979, 1997), especially if there are processes that slow the rate of random species exclusion (Hutchinson 1961, Hurtt and Pacala 1995). However, models that predict long-term species persistence (sensu Connell and Sousa 1983), rather than eventual random-walk extinction, must contain density

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dependence, either explicitly (Janzen 1970, Connell 1971) or implicitly, e.g., due to resource limitation (Tilman 1982, 1988) or recruitment fluctuation (Chesson and Warner 1981).

Analyses of density dependence relevant to coexistence in rain forests must take account of the complexities associated with high tree species richness, spatial scaling, and the great range in individual sizes. We argue that the appropriate emphasis is on analyses that: (1) compare common and rare species in a multispecies statistical model, (2) treat as large a spatial scale as possible, and (3) use adult abundance as the independent variable. We further suggest that measures of response at the early life stages are likely to be most informative; in this study we focus on seedlings.

Inclusion of rare tree species is vital in analyses of density dependence, not only because most species are rare (Whitmore 1984, Richards 1996), but also because their populations are, by definition, closest to local extinction. Yet, even the very largest data sets available are limited. With a sample of ~240 000 trees, Wills et al. (1997) were able to test for density dependence in single-species analyses only for the most abundant 84 species out of 300. For each species analyzed, there must be adequate variation in density and adequate samples of individual response for statistical analysis. A demonstration that the abundant species experience negative density dependence does not imply that rare species' populations will be maintained. Hubbell

(1980) demonstrated that local density dependence in abundant species (via distance dependence) could explain only a small fraction of the observed forest species diversity.

A means of including rare species and comparing their responses directly with those of more common species was proposed by Connell et al. (1984). If species differ in abundance, but all share a similar density-dependent response to population abundance, a community-level "compensatory" trend (Connell 1978) will emerge: species' population growth rates will decline as a function of their abundances. Hereafter, we will refer to this as a community-level compensatory trend (CCT). We suggest that tests of population-level density dependence (which are also important for assessing scale effects) augment, but do not replace, community-level analyses.

Tests of density dependence require a measure of population abundance as the independent variable. Individual genets range from undispersed seeds to large canopy trees. Proximally, seed mortality could depend on seed density, and seedling mortality on seedling density. Alternatively, performance of a life stage may be influenced by density at another stage; e.g., seedlings may experience more herbivore damage when there are more conspecific canopy trees nearby (Janzen 1970, Shaw 1974). Thus, various life stages and spatial scales may be appropriate for identifying the agents responsible for density dependence (if any) and the mechanisms by which those agents act. However, we suggest that to evaluate the implications for coexistence, the scale of mechanisms is not primary. Indeed, density-dependent mechanisms can occur without promoting coexistence. Consider, for example, local aggregations of seedling progeny around widely scattered adults, with seedling survival being negatively density dependent on local seedling density. Such density dependence does not translate into density-dependent control on adult abundance or subsequent seed production, and thus may not act to promote coexistence of adults in the canopy. This hypothetical seedling density dependence could promote species coexistence, however, if seedling aggregations around different parents were to overlap, with seedling survival thereby becoming dependent on local adult density. Thus, although ecological interactions can lead to complex combinations of effects of size class and spatial scale (Schupp 1992), there are compelling reasons to focus mainly on adults for measures of population abundance. Further, it is appropriate to obtain these estimates of adult abundance on the largest practical spatial scale in the community of inference, i.e., approaching the scale on which we choose to record species as present in the community, and consider them rare or common.

In contrast to the measure of population abundance, which we have argued should logically be adult-based, there is no such logical restriction on measures of pop-

ulation response. Ideally, the entire life cycle would be included to assess population dynamics. More practically, for long-lived trees, we can focus first on stages that are most "dynamic," in terms of relatively high mortality, are plausibly subject to density-dependent effects, and are amenable to observation and experiment. Negative density-dependent responses at early life stages imply density dependence in the population unless counteracted by positive density dependence at later stages. In this study, we focus on seedlings.

Although a community-level (CCT) analysis is especially valuable, it also has limitations. The data for each species are summarized by a single point, representing the overall measures of population abundance and performance. The ecological significance of the CCT depends on a dynamical interpretation, i.e., that population performances will change if abundances change over time. Yet, the data used for the CCT do not include information on how population performance actually responds to variation in conspecific abundance. Additional population-level tests of density dependence, although limited to the more abundant species, can strengthen the dynamic interpretation of a CCT if they show that population parameters do respond to spatial variation in density (a surrogate for temporal variation). These analyses may also include spatial scales relevant to ecological mechanisms. In this study, we examine both community-level trends on the scale of our entire study area (150 ha) and single-species density dependence on local scales (0.16 ha and 1 m$^2$). In addition, by measuring the correlations between densities at different life stages (seedling and adult) and at different spatial scales, we evaluate the potential for mechanisms acting at one stage and scale to contribute to density dependence at other stages and scales.

Finally, density dependence may result from mechanisms responding to either the absolute density of a population or to its relative abundance (frequency), measured as a proportion. There is great spatial and temporal variation in the total abundance of seedlings on the forest floor (e.g., Fox 1972, Webb 1997). Hence, although density and relative abundance of a species will be correlated on any spatial scale, it is possible at the seedling stage to separate their effects statistically, to some extent. This distinction is less relevant for trees in a closed-canopy forest, because total stem density is less variable in space and time, in the absence of catastrophic disturbances.

These considerations lead to the following research questions, which we addressed for a diverse rain forest in Southeast Asia.

1) Among species, is seedling survival negatively correlated with conspecific adult abundance (at a scale of 150 ha); i.e., is there evidence for a CCT?

2) Is seedling survival negatively correlated with conspecific seedling density (at a scale of 150 ha)?
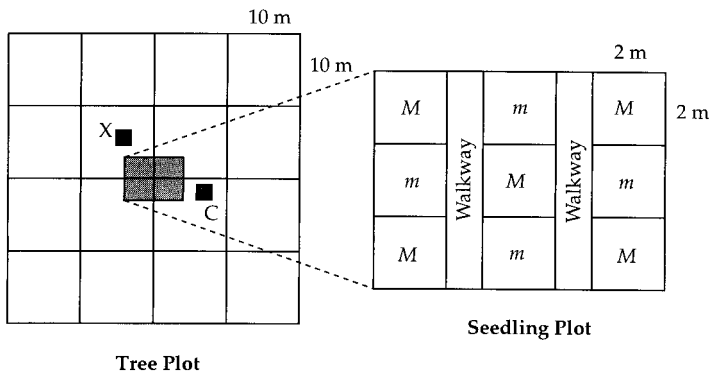
3) Are multispecies, wide-scale (150-ha) analyses of

FIG. 1.   Plot layout for sampling of trees and seedlings in rain forest at Gunung Palung, Indonesia, at each of 28 sampling locations. Each tree plot (0.16 ha) contained nine $2 \times 2$ m seedling plots, further divided into 36 $1 \times 1$ m plots. Abbreviations: $M$, major subplots (seedlings of all species individually monitored); $m$, minor subplots (only less common species individually monitored); $X$, a $2 \times 2$ m vertebrate exclosure; $C$, a similar, but unfenced, control plot. Walkways were not sampled.

density dependence consistent with single-species, local (0.16-ha, 1-m$^2$) scale analyses?

4) On a local scale (1 m$^2$), is seedling survival most influenced by conspecific seedling density, relative abundance, or total seedling density?

## MATERIALS AND METHODS

### Study site

Gunung Palung National Park (West Kalimantan, Indonesia; 1°15′ S, 110°10′ E) is a 90 000-ha protected area on the southwest coast of the island of Borneo (Laman 1995). Since its protection in 1937, the park has been undisturbed by humans, except for some non-mechanized logging of Bornean ironwood (*Eusideroxylon zwageri,* Lauraceae) and gaharu (*Aquilaria malaccensis,* Thymelaeaceae). The soils in the study area are granite-derived tropudults and dystropepts (Soil Survey Staff 1975, IDT and ODA 1987, Petersen 1991), with sandy-clay to sandy-clay-loam texture (Webb 1997).

We chose an area of hill forest (sensu Whitmore 1984) on the west slope of Gunung Palung (mountain), with a seedling layer consisting almost entirely of woody plants. Although relatively homogenous in physical substrate and elevation and lacking any major disturbances, the study area (~150 ha) included small-scale topographic heterogeneity, with broad- and narrow-topped ridges, steep slopes (up to ~40°), and narrow valleys with streams (C. O. Webb and D. R. Peart, *unpublished manuscript*).

Mean annual rainfall at the site over the three years of study was 4610 mm (August 1993–July 1996). There is usually a ''drier'' season from June to October each year, which in 1994 was severe (1994 calendar year rainfall: 3833 mm), and in 1995 was absent (1995 calendar year rainfall: 4966 mm). Seedling survival rates reported here are for 19 mo beginning after the 1994 drought.

### Overview of research design

Over the 150 ha, there were 28 stratified random sampling locations, each consisting of a 0.16-ha tree plot containing a central 36-m$^2$ seedling plot (Fig. 1).

Locations were stratified by local seedling density (in the central 36-m$^2$ area, evaluated prior to final plot selection), elevation, ridge system (north or south), and understory light level (gap vs. understory). Stratification provided a wide range of conditions over which to assess density-dependent effects. We measured the densities of all species of seedling (5–50 cm tall) in all 1008 m$^2$ of seedling plots (10 190 plants), and the densities and basal area of each tree species ($\geq 10$ cm dbh) in a total sample area of 4.48 ha (2862 trees).

Species-specific seedling survival was measured in a subset of 12 sampling locations, for 19 mo from November 1994. The 12 locations were those at lowest elevation, on both sides of the central stream. The relationships between seedling survival rate and both adult abundance and seedling density were examined using randomization procedures for the 149 tree species that occurred both as adults in the 28 tree samples and as monitored seedlings in the 12 seedling samples. We preferred overall basal area, rather than numbers of trees, as the primary measure of species' adult abundance, as in Connell et al. (1984). Because it includes the effect of tree size, basal area is more representative of biomass, canopy space occupied, and reproductive output than is density alone (basal area and density in our sample were significantly, linearly related).

We also tested whether the changes in species' relative abundances with increasing size were consistent with a CCT in seedling survival, by comparing abundances between successive size classes in species-specific, static (inventory) data. If there were a CCT in seedling dynamics, the higher mortality in seedlings of the more abundant species would tend to reduce their relative abundance in larger size classes, increasing community evenness (Martinez-Ramos and Soto-Castro 1993). Therefore, in all 28 plots, we measured densities of saplings (>50 cm tall, with dbh <1 cm), and poles (1–4.5 cm dbh), and tested whether the abundances of species common as seedlings were reduced more in the larger size classes than were the abundances of rarer species. We also compared an evenness index (Pielou's $J$; Pielou 1969) over size classes, controlling for the effects of sample size (Peet 1974, Nicholson et

al. 1988). Finally, we examined whether the inferences from dynamic measures of performance (i.e., density-dependent seedling survival) were quantitatively consistent with the static data on community structure, using a simple simulation model.

To assess local density dependence at the population level, we compared seedling survival with conspecific seedling density in 432 1-m² quadrats in the 12 locations in which we measured seedling dynamics. For tree–seedling interactions, we compared the same seedling performance data with conspecific adult basal area in the surrounding 0.16-ha tree plot. We sought evidence linking the agents of mortality to density-dependent effects, by recording probable cause of death, based on visible symptoms, where possible. We investigated the role of vertebrate herbivores separately, using vertebrate exclosure cages (80 cm tall chicken wire) and controls (each 2 × 2 m; Fig. 1).

### Seedling and tree inventory

In a pilot survey of total seedling density, we found a median density of 16 seedlings/m², with quartiles of 10 seedlings/m² and 20 seedlings/m². From the surveyed sites, we randomly located six sites for which a 4-m² sample had a total seedling density class of 0–10 seedlings/m², six with density 11–20 seedlings/m², and six with density ≥21 seedlings/m². We then systematically searched the study site (∼150 ha) for canopy gaps, and sited 10 seedling plots in the largest available canopy gaps in such a way that gap plots were also stratified by elevation and ridge system. We defined a gap to be a 5 × 5 m (or larger) column of empty space extending from the canopy down at least to 1 m height. The largest gaps were ∼100 m², with a maximum incident photosynthetically active radiation, measured at seedling quadrats in their center, of 10.2% of ambient light (using hemispherical photography; C. O. Webb and D. R. Peart, *unpublished manuscript*). Most gaps were formed by loss of portions of single crowns, confirming our experience that large, well-defined gaps are very uncommon in this forest. Hence, gaps in this study do not have the high light intensities characteristic of most rain forest gaps reported in the literature (e.g., Brokaw 1985, Brown and Whitmore 1992). The 12 seedling plots used to measure seedling survival had seedling densities and light environments similar to those of the larger sample (28 plots).

Each seedling plot was divided into nine subplots, each 4 m² (Fig. 1). We used a protocol that maximized samples of rare species, given practical constraints on sampling effort. The nine subplots at each location were divided into "major" and "minor" subplots. There were three major subplots, located along a diagonal, in plots of high total density. At low density, an additional two were located on the other diagonal (Fig. 1). All seedlings were identified to species and monitored in major subplots. In minor subplots, only species with ≤20 seedlings in the major subplots at

that location were identified and monitored individually. Total numbers of all seedlings were recorded in all subplots, so that densities and relative abundances could be calculated.

All subplots were inventoried for saplings and poles of all woody species, except the relatively infrequent shrubby palms (e.g., *Licuala* spp., *Iguanura* spp.) and seedlings of climbing palms (e.g., *Calamus* spp., *Korthalsia* spp.). There were no tree palms in the study area. Individual plants were not tagged (tags attract wild pigs), but were mapped; location, height, and species identity enabled reliable relocation.

The diameter and species identity of trees (≥10 cm dbh) were recorded in the 40 × 40 m (0.16-ha) tree plots, centered on the seedling plots.

### Species identification

For each tree, we collected fallen leaf specimens, and flower and fruit specimens when available. Vouchers were matched with named botanical specimens in the Herbarium Bogoriense and Harvard University Herbaria. In 4.48 ha, we found 325 morphotypes in 50 families, with Dipterocarpaceae being the most abundant family in terms of individual trees. We matched 90% of morphotypes to recognized species, and we will use the term "species" synonymously for "morphotype" (see Webb 1997 for a full species list). Seedlings were identified using field characters (Burger Hzn 1972, de Vogel 1980, Ng 1992, Webb and Curran 1996) and by matching with adults of the same species (Webb 1997). Analyses relating seedlings to adults included only those species matched between seedlings and adults with high confidence (90% of species that occurred as both seedlings and adults).

### Vertebrate exclosure experiment

A 2 × 2 m quadrat, surrounded by 80 cm tall chicken wire and supported by PVC stakes, was located randomly within 4 m of the edges of the central 36-m² seedling plot, at each of the 18 non-gap sampling locations. One 2 × 2 m control quadrat was similarly placed, marked only by stakes at its corners. Seedlings in the quadrats were mapped and measured for height in March 1995, and were monitored for mortality, growth, and recruitment over 24 mo. Only seedlings in the Dipterocarpaceae were identified to species.

### Analytical methods

The significance of the relationship between seedling survival and adult abundance could not be tested using standard methods, because survival rate variances were not homogeneous. This heteroscedasticity could not be removed by transformation. Instead, the observed slope of the regression was compared to a distribution of slopes generated by a Monte Carlo randomization (Manly 1997) that (1) assumed no relationship between seedling survival and adult basal area, and (2) recreated a similar variance distribution to that observed in the

original data, a necessary requirement for generating a distribution of unbiased slopes. Two alternate methods were used.

In the first method (A), observed basal area values ($\log_{10}$-transformed) were shuffled, i.e., randomly assigned to species. Species were then placed in five abundance classes, with equal numbers of species in each, based on the new basal area values. The measured survival rates were then linearly transformed so that the variance in survival rate of each new class was the same as in the corresponding class in the observed data, while preserving the class mean of the randomized data. Slopes of the simulated relationships were obtained by standard least squares fitting. This procedure was repeated 1000 times to generate the distribution of slopes under the expectation of no relationship between survival and log basal area. In method (B), a binomially distributed random number of survivors was generated for each species, based on the observed number of seedlings of each species at the start of the 19 mo, and a constant mean survival probability for all species (calculated as number of total survivors/total starting number of seedlings of all species), and regressed against the observed basal area for each species.

We used a randomization procedure similar to method (A) to compare how the relative abundances of common and rare species changed with increasing size (method C). We calculated, for all species, the ratio of the density of individuals in each size class to the density of the same species in larger size classes. Under the assumption that species' relative abundances are not changing rapidly in time, a pattern of lower ratios in common than in rare species is consistent with the action of density-dependent mortality. Therefore, we examined the relation between these species-specific, size class abundance ratios and conspecific basal area.

We tested the relationship, on the 150-ha scale, between seedling abundance ($N_t$) and seedling survival ($N_{t+1}/N_t$) using binomial randomization (as in method B). To deal with non-independence of the two variables, we first regressed $\log_{10}(N_{t+1} + 1)$ on $\log_{10}(N_t + 1)$ and compared the slope of the measured relationship with 1000 slopes generated under the expectation that survival rate was independent of abundance (method D). These slopes were calculated by generating a random number of survivors, $N_{t+1}^*$, from existing seedlings, $N_t$, of each species, using a binomial model with probability equal to the (arithmetic) mean of the observed species-specific survival rates. This method is similar to that used by Welden et al. (1991) to test for a negative relation between recruitment and species abundance. We included all relevant species (including those with single seedlings) in the randomization tests of multispecies trends. The tests produce expected survival probabilities that are not biased by small numbers of seedlings.

To analyze the effects of local conspecific seedling density (on a 1-$m^2$ scale) on seedling survival, we used a randomization procedure similar to that of method (D), but included only species with abundant seedlings (Method E). All randomizations were programmed in C, using IMSL statistical software libraries (Visual Numerics 1995).

Although more rigorous than standard methods when standard assumptions are violated, the randomizations did not allow for comparisons between the local effects of adults and seedlings on seedling survival. For this purpose, we used logistic regression (Menard 1995; using JMP software, SAS Institute 1995), in which the ordinal response (lived vs. died) of each seedling was related to local adult and seedling abundances. Including seedlings of all possible species (i.e., including where relevant, seedling species not recorded as trees), we modeled individual seedling survival as a function of (1) local adult basal area in the surrounding 0.16-ha plot, (2) conspecific seedling density in the same 1-$m^2$ quadrat, and (3) both adult basal area and seedling density. We also used logistic regression to test for the effect of relative abundance on seedling survival (frequency dependence). Individual seedling fate (lived vs. died) was regressed on the conspecific relative abundance experienced by seedlings in 1-$m^2$ quadrats.

## RESULTS

### Community-wide seedling dynamics

During the 19 mo over which species-specific seedling survival was measured, 373 out of 1603 seedlings died, among the 149 species included in the analysis. Mean survival over all seedling individuals was 0.76, whereas survival averaged across species was 0.83. Density per species ranged from 22.7 adults/ha to 0.22 adults/ha, and from 10 357 seedlings/ha to 9.9 seedlings/ha (Webb 1997). The hypothesized CCT was found (Fig. 2). Seedling survival was inversely related to tree species abundance, measured as basal area (method A: one-tailed $P = 0.002$, slope $= -0.064$, 95% CI: $-0.016$ to $-0.111$; method B: one-tailed $P = 0.013$). The relationship was also negative and significant using more orthodox, less appropriate statistics (Pearson correlation $r = -0.215$, $P = 0.0085$; linear regression, $F = 7.115$, $P = 0.0085$; logistic regression, maximum likelihood $\chi^2 = 7.752$, $P = 0.0054$; Spearman rank correlation, $\rho = -0.317$, $P < 0.0001$). The estimated slope of $-0.064$ represents a decrease in seedling survival of 6.4% per order of magnitude increase in adult basal area. Seedling survival was also negatively associated with adult tree density (method A: $P < 0.001$; method B: $P = 0.005$). Seedlings of the most abundant species (those with greatest basal area) were significantly taller than those of less abundant species (Fig. 3); the median heights of seedlings of high, medium, and low abundance were 23, 18, and 18 cm, respectively (goodness-of-fit comparison of distributions: $\chi^2 = 140.7$, $P < 0.0001$).

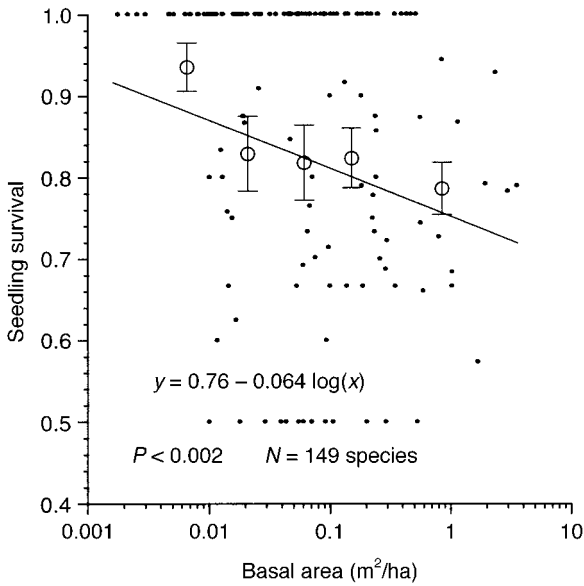Similar frequency-dependent trends were found

FIG. 2. Test of density dependence at the community level for rain forest seedlings at Gunung Palung, Indonesia. Raw data are represented by solid dots, $n = 149$ species (seven species with <40% survival are not shown). The significance of the slope of the regression of seedling survival on adult abundance (measured as basal area) was tested using Monte Carlo randomizations (95% CI for slope was $-0.017$ to $-0.111$). Open circles represent mean ($\pm 1$ SE) survival of equal-sized groups (29–30 species) in order of increasing mean basal area. Note log scale of x axis.

when mean seedling density over 150 ha was used as the measure of population abundance. Log seedling survival (in 171 species) over 19 mo declined significantly with log seedling density (method D: $P = 0.003$, slope $= -0.946$).

We have assumed that spurious trends were not in-troduced by random sampling of seedlings in space, rather than choosing random individuals, thus possibly undersampling seedlings of rare species that may occur at high densities near their parents. To check for this, we tested for a CCT using only those seedlings that must have been actively dispersed away from parents. We excluded all seedlings that had a conspecific adult (i.e., a tree larger than the estimated size of first re-production; C. O. Webb and D. R. Peart, *unpublished manuscript*) in the same sampling location. The rela-tionship of seedling survival to adult abundance (log basal area) remained negative and significant (method A: $P = 0.007$; method B: $P = 0.015$).

### Changes in relative abundance with increasing size

All size classes exhibited strong numerical domi-nance by a few species, and low relative abundance of many (Fig. 4). However, there was a general trend for the slope of the dominance–diversity curve to become less steep with increasing plant size. In other words, the relative abundances of the most common species decreased from seedlings, through saplings and poles, to trees. This trend was reflected in an increase in the community evenness index ($J$) with increasing size (Fig. 5).

Furthermore, the most common species tended to decline most in relative abundance as they grew through size classes. Among species, the ratios of the density in a size class to the density in a larger size class decreased significantly with increasing basal area in all cases, for saplings:seedlings (method C; mean ratio $= 0.68$, $P = 0.035$), poles:seedlings (mean ratio $= 0.33$, $P = 0.001$), and poles:saplings (mean ratio $= 0.58$, $P = 0.002$). There was no significant trend in the ratio of numbers of seedlings to numbers of adults (mean ratio $= 109$).

FIG. 3. Size class distribution of seedlings used in the analysis of community-level density dependence (Fig. 2). The 1603 seedlings were divided into three equal-sized groups consisting of the commonest, mid, and rarest species (as classed by adult abundance).
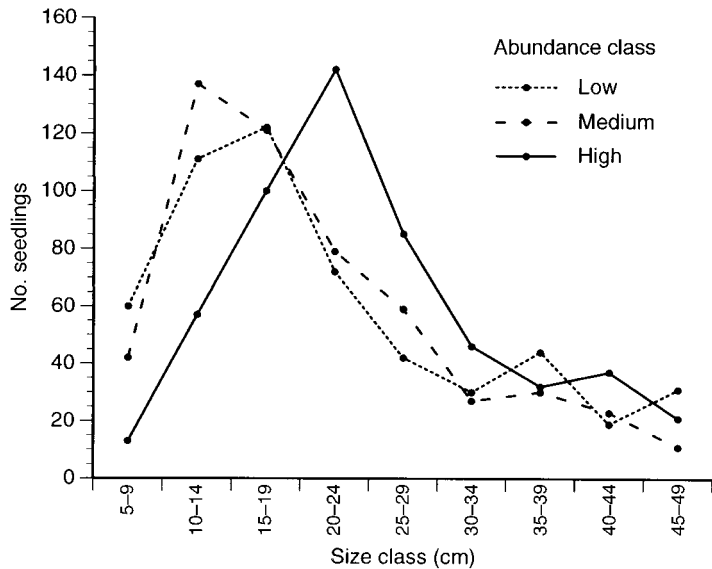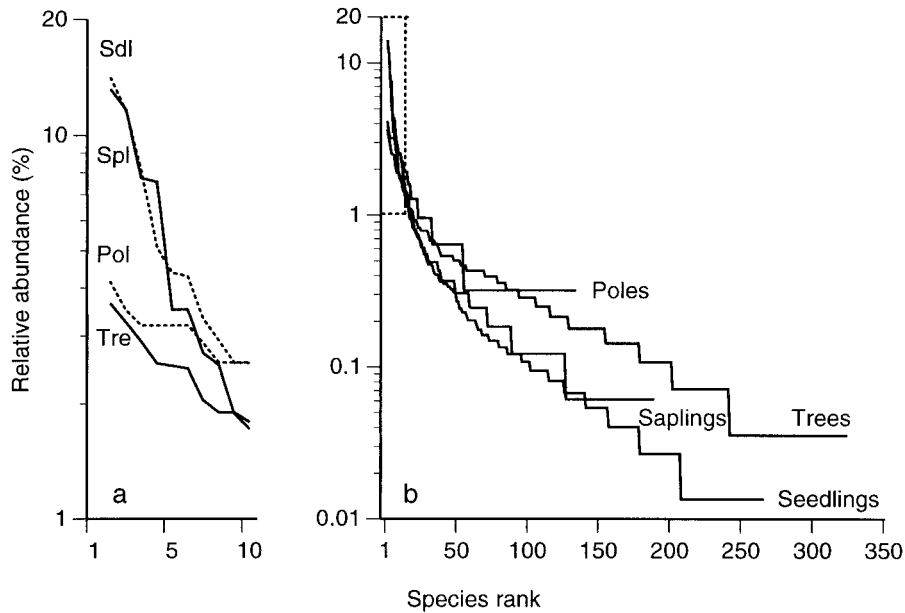
FIG. 4. Dominance–diversity curves for four size classes of tree species in rain forest at Gunung Palung, Indonesia, sampled over a 150-ha study area. Species are ranked in order of decreasing relative abundance. (a) The most abundant 10 species in each size class: Sdl, seedlings; Spl, saplings; Pol, poles; Tre, trees. (b) All species; note that the y-axis log scales have different ranges in panels (a) and (b). An area of 1008 m² was sampled for seedlings (5–50 cm tall), saplings (> 50 cm tall, < 1 cm dbh), and poles (1–4.5 cm dbh). Trees (≥10 cm dbh) were sampled in 4.48 ha.

To assess the potential for the community-level density dependence in seedling survival to cause the observed differences in species' abundances over size classes, we simulated changes in relative abundance for a hypothetical sample of seedlings, beginning with the same relative abundances of species that we measured over the entire study area. We included all 181 species for which we had estimates of both density and 19-mo seedling survival, and that occurred in our samples both as saplings and seedlings, thus avoiding the sample size bias in J (Nicholson et al. 1988, Peet 1974).

We applied the measured, species-specific annual rate of seedling survival to the proportions of individuals in each species, and iterated this simple, deterministic model over 25 yr. After 14 yr, the simulation produced a cohort with evenness (J) equal to that of the sapling species included in the model.

*Local density dependence*

There was a significant negative association between seedling survival and conspecific seedling density (in 1-m² quadrats) for four of the 15 common species that

FIG. 5. Changes in two measures of diversity, with increasing size class, for tree species in rain forest at Gunung Palung, Indonesia. Samples for evenness (Pielou's J; Pielou 1960) and species richness estimates were constrained to include the same number of individuals in each size class. The pole size class had the fewest total individuals in field samples (308 in 1008 m²); this number of individuals was randomly chosen 100 times from the remaining size classes to generate the data shown. Evenness values are means ± 1 SE (1 SE of poles = 0, as all measured poles were included). The SE values for numbers of species were too small to be visible on the figure.
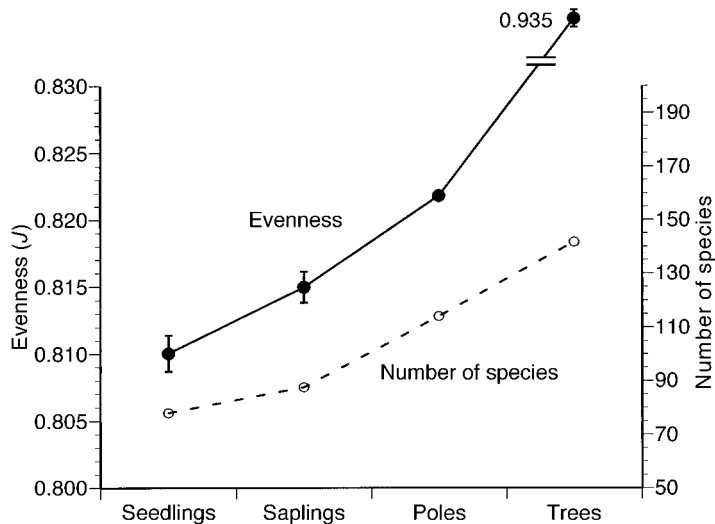
TABLE 1. Tests of density dependence in seedling survival for tree species in rain forest at Gunung Palung, Indonesia.

| Model of seedling survival vs.: | Model fit | | | | Parameter estimate | | |
|---|---|---|---|---|---|---|---|
| | df | No. seedlings | $\chi^2$ | Probability | Intercept | Slope | 1 SE of slope |
| a) Log conspecific seedling density (1-m² plots) | 1 | 1839 | 5.13 | 0.023 | 1.178 | −0.344 | 0.150 |
| b) Log conspecific tree basal area (0.16-ha plots) | 1 | 999 | 6.11 | 0.013 | 0.842 | −0.257 | 0.104 |
| c) Combined model | 2 | 999 | 9.39 | 0.009 | 1.023 | | |
| Consp. seedling density | 1 | | 3.30 | 0.069 | | −0.345 | 0.190 |
| Consp. tree basal area | 1 | | 3.54 | 0.060 | | −0.205 | 0.109 |
| d) Log conspecific seedling relative abundance (1-m² plots) | 1 | 1839 | 1.28 | 0.256 | | | |
| e) Total seedling density (all species in 1-m² plot) | 1 | 1839 | 1.23 | 0.266 | | | |

*Notes:* Logistic regressions of individual seedling survival were made against measures a–e. All species were combined in each analysis.

occurred in ≥20 quadrats (*Shorea parvifolia* King, *Diospyros* sp. "FLE," *Dipterocarpus stellatus* Vesque, *Baccaurea parviflora* (Muell. Arg.) Muell. Arg.; method E, $P < 0.05$). The coefficient of variation of seedling densities (1-m² scale) was significantly and negatively correlated with the $P$ value in the previous tests (Spearman rank, $\rho = -0.521$, $P = 0.046$). Thus, species with the greatest spatial variation in seedling density were the ones most likely to show significant density dependence.

In the logistic regressions that we will report here, each point represents the fate (survived or died) of an individual, matched with a measure of conspecific abundance. Note that these logistic, *individual*-based statistical models differ from our previous analyses, in which we used measures of survival over seedlings in a quadrat, and from the community-level analyses, in which each point represented the performance of a species matched to a measure of conspecific abundance.

When 214 species were combined in a single logistic model, seedling survival was significantly and negatively associated with the number of conspecific seedlings in the same 1-m² quadrat (Table 1a). There was no evidence for any effect of total seedling density (i.e., summed over species) on seedling survival (Table 1e). At the 1-m² scale, absolute seedling density influenced survival more than did seedling relative abundance. For only one out of 15 abundant species, *Dipterocarpus stellatus,* was seedling survival negatively affected by its relative abundance (logistic regression, $N = 32$ seedlings, $\chi^2 = 12.23$, $P = 0.0005$). Furthermore, when all species were combined in a single analysis, conspecific relative abundance had no significant effect on survival (Table 1d).

We detected a significant negative association between seedling mortality and conspecific adult basal area in the surrounding 0.16-ha plots for two out of 15 common species (*Calophyllum nodosum* Vesque and

*Diospyros* sp. "FLE"; logistic regression, $N = 69, 42$, $\chi^2 = 3.73, 6.83$, $P = 0.053, 0.009$, respectively). When all species were included in a single logistic regression, seedling survival declined significantly with 0.16-ha scale conspecific basal area (Table 1b). Finally, in a logistic regression including local abundances of both seedlings and adults, we found that seedling density (no./m²) and 0.16-ha basal area each had marginally significant effects on seedling survival (Table 1c).

Over the 19-mo monitoring period, cause of death was identified as follows: desiccation 33.3%, disease (caused by or associated with fungal necrosis) 4.7%, crushed by falling branch 2.6%, apex bitten off by vertebrates 1.7%, and seedlings missing without trace 55.6%. In the seedlings that were not missing, the probability of death by disease increased with increasing conspecific seedling density (1-m² scale; logistic model including all species, $N_{obs} = 206$, $\chi^2 = 6.99$, $P = 0.008$). The probability of death by disease increased even more strongly with (log) local adult basal area (logistic model including all species, $N_{obs} = 125$, $\chi^2 = 18.17$, $P < 0.001$).

*Vertebrate exclosures*

Vertebrate exclosures had no significant effect on seedling survival and growth over two years, but recruitment was significantly higher in the exclosures (all species combined; Fig. 6). The pooled growth rate of all seedlings in exclosures and controls was $1.55 \pm 0.089$ cm/yr (mean $\pm$ 1 SE). When individual seedling survival was regressed against conspecific density in a logistic model, including seedlings of all dipterocarp species, there was a significant negative effect of conspecific density in the control plots ($N_{obs} = 266$, $\chi^2 = 10.45$, $P = 0.0012$), but not in the exclosures ($N_{obs} = 271$, $\chi^2 = 2.87$, $P = 0.089$). This is weakly suggestive that density dependence may be stronger for seedlings exposed to vertebrate herbivores than for protected
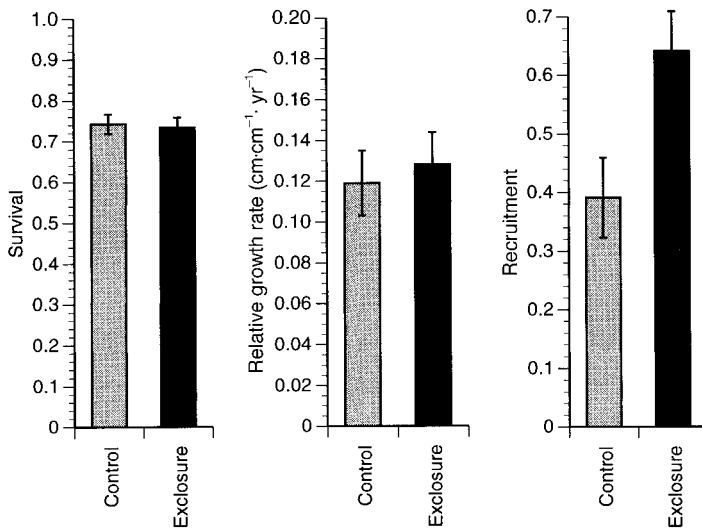
FIG. 6. Effects of exclosures on seedling dynamics in rain forest at Gunung Palung, Indonesia. Data (means ± 1 SE per quadrat) are from fenced 2 × 2 m quadrats ($n = 18$) compared to similar unexclosed controls ($n = 18$) over two years. There was no significant effect of exclosures (80 cm tall chicken wire) on seedling survival or growth (Survival: ANOVA, df = 1, ∞, $F = 0.053$, $P = 0.818$. Growth: ANOVA, df = 1, ∞, $F = 0.437$, $P = 0.513$), but recruitment was higher in exclosures (ANOVA, df = 1, ∞, $F = 6.67$, $P = 0.014$).

seedlings, despite the lack of an overall significant effect of caging on seedling survival.

### Correlations among stages and scales

As expected, overall adult abundance (150-ha scale) was significantly and positively correlated with total seedling abundance (150-ha scale; 238 species, $r^2 = 0.32$, $P < 0.0001$). Similarly, mean local (1-m²) seedling density was correlated with local tree abundance (157 species, $r^2 = 0.076$, $P = 0.0004$). The correlation between overall adult abundance (per 150 ha) and mean local seedling density was also positive and significant (157 species, $r^2 = 0.08$, $P = 0.0002$). The strengths of these correlations indicate the potential for mechanisms acting at one scale to generate relationships at larger or smaller scales.

### DISCUSSION

#### Community-level compensatory trends

More abundant species suffered higher seedling mortality than less abundant ones, a community compensatory trend (CCT; Fig. 2) that was significant whether species abundance was measured by adult basal area, adult tree density, or seedling density. Despite the scatter in seedling survival rates, the difference in mean survival between the most common species (72%) and the rarest species (92%) was substantial; compounded over 10 years, the cumulative survival rates would be 12% and 63%, respectively. Trends in relative abundance over size classes (statics), using the larger sample sizes from the plot inventories, were consistent with trends in seedling survival (dynamics). Further, community evenness ($J$) increased with increasing size (Fig. 5), consistent with the hypothesis that more abundant species suffer higher seedling mortality. The simulation of seedling survival confirmed that observed size-related trends in evenness are consistent with the action of density-dependent seedling survival.

Are there alternative explanations (i.e., other than compensatory density dependence) to explain the observed relationships? First, a spurious CCT could be found if the more common species tended to have smaller, younger seedlings, with correspondingly higher mortality (Harper 1977). The reverse, however, was true; common species had taller seedlings (Fig. 3). Independent evidence also indicates that common and rare species' populations were equally likely to have young seedlings; there was no relation between the proportion of individuals of a species fruiting in the previous (1994) mast-fruiting event, and conspecific adult basal area (C. O. Webb, *unpublished data*: $r^2 = 0.0043$, $P = 0.23$).

Second, intrinsic species differences in life histories, if correlated with species' abundances, could result in a significant CCT, even if there were, in fact, no compensatory density dependence. This would occur if common species had many small seedlings per capita adult, with high mortality, whereas rarer species had fewer, more robust seedlings per adult. However, we found no significant relationship between species' abundances and the ratio of seedlings per adult (a measure of per capita recruitment to the seedling class), so this important, alternative explanation is not supported. The observed trend in evenness with increasing size, however, is generally to be expected when there are species differences in survival rates, whether due to intrinsic species differences, density dependent dynamics, or both. As abundant seedlings of intrinsically more fecund species die more rapidly than the robust seedlings of less fecund species, an increase in evenness is to be expected. Evenness data alone, therefore, do not provide evidence for density dependence.

If seedling survival responds to changes in species' abundances in the pattern represented by the CCT, this "community-level density dependence" implies a brake on species that increase in abundance and, con-

versely, a tendency for rare species to be favored, thus enhancing persistence. Although it may appear that such a dynamical CCT would tend to equalize species' abundances, this is not necessarily so. Species differences in their (density-independent) population parameters, together with a dynamical CCT, will tend to stabilize species' abundances at different levels, as confirmed by simple simulations (see Chesson and Huntly 1989; C. O. Webb, *unpublished data*). At these different adult abundances, a CCT in seedling performance would be observed, but density dependence would not drive further changes in relative abundances. Unless species are effectively identical in their capacities for increase (as hypothesized by the random drift model), they are likely to have intrinsic tendencies to commonness or rarity. The observed distribution of relative abundances may possibly reflect the distribution of intrinsic population growth rates.

Connell et al. (1984), in the only other test involving seedling dynamics, found a CCT in Australian rain forest, but only for understory tree species, and only in recruitment, not in survival or growth. For sapling dynamics, Welden et al. (1991), in the second recensus of the Barro Colorado Island (BCI) 50-ha plot in Panama, found higher per capita sapling ($\geq$1 cm dbh) recruitment in rare species than in common species, consistent with a CCT. In contrast, He et al. (1997) found survival in plants $\geq$1 cm dbh to be significantly lower for rare than for common tree and shrub species in the Pasoh, Malaysia 50-ha plot, contradictory to a CCT. For static size class data, Hubbell and Foster (1986), in the first recensus at BCI, found a weak trend for the ratio of adults to saplings ($\geq$1 cm dbh) to be higher in rare than in common species (contradictory to a CCT). Connell et al. (1984) found, as we did, an increase in community evenness with increasing size class for all tree species, but did not test it statistically. In rain forest in Mexico, Martinez-Ramos and Soto-Castro (1993), also analyzing static patterns, found an increase in community evenness with increasing seedling size class. In summary, the evidence is limited and mixed, but several studies have found evidence to support a CCT, including both studies to date on seedling dynamics.

### Local, single-species density dependence: implications for the community

Our analyses of density dependence at the single-population level, and on smaller spatial scales, are consistent with, and support the dynamic interpretation of, the CCT. In those abundant species that showed evidence of density dependence, seedling survival always tended to be lower in areas of high conspecific abundance. Many authors have reported local seedling (or sapling) density dependence, generally testing seedling performance against seedling density (Howe and Primack 1975, Denslow 1980, Augspurger and Kelly 1984, Hubbell et al. 1990, Hubbell and Foster 1990, Condit et al. 1994; see reviews by Antonovics and Lev-

in 1980, Clark and Clark 1984, Connell et al. 1984), or seedling-to-tree distance (Janzen 1970, Augspurger 1992, Condit et al. 1992). Because of the significant positive correlations between densities at different scales and life stages, local-scale density dependence in seedling survival could contribute to the wide-scale density dependence that we found, which is most critical for coexistence of species in the canopy.

### Potential density-dependent mechanisms

Despite extensive fieldwork on seedlings, we could not assign specific causes to most seedling mortality events; although the data are suggestive, our assessment of mechanisms remains largely speculative. Total seedling density of all species (1-m$^2$ scale) did not influence seedling survival (Table 1e), suggesting that inter-seedling competition is not strong. Density-dependent effects on seedlings are more likely to be caused by herbivorous animals or pathogens, as suggested by Connell et al. (1984). Standing levels of insect-caused herbivory are relatively low in this forest (Blundell and Peart 1998), and insects are very seldom found on seedlings (C. O. Webb, *personal observation*).

Vertebrate herbivores (primarily deer: *Tragulus napu, Muntiacus muntjak muntjak, Cervus unicolor*; Blundell 1996) occur at the study site. Although vertebrates can have density-dependent effects on seedling survival (Coley and Barone 1996), we found only weak evidence for this. There was a stronger trend for density dependence (in dipterocarp seedlings) outside the exclosures than inside, but there was no overall effect of vertebrate exclusion on seedling survival and growth (all species combined; Fig. 6). Terborgh and Wright (1994) also found no effect of mammal exclusion on seedling survival at Barro Colorado Island or Cocha Cashu, Peru, and a similar significant positive effect on seedling recruitment, suggesting that mammalian herbivores may play a similar role in seed and seedling dynamics in neo- and paleotropical rain forest.

Pathogens are the most likely cause of the density dependence that we observed, because mortality associated with pathogen symptoms increased with density on both very local and larger spatial scales. We found that the proportion of deaths associated with pathogen symptoms increased with local conspecific seedling density, and more strongly with local conspecific adult basal area. Similar patterns of infection have been shown in other studies, in which the frequency of seedling infection decreased sharply with increasing distance from an infected adult (Zadocks and van den Bosch 1994), and in which the proportion of infected conspecific seedlings increased with local seedling density (Burdon and Chilvers 1982, Alexander 1992, Augspurger 1992). Our results suggest that adults could be the main source of pathogen inoculum (e.g., Gilbert et al. 1994), generating the observed CCT, over the 150-ha scale.

In summary, we present several consistent lines of

evidence for a community compensatory trend in seedling survival. These are based on dynamic data at the community and population levels, at the adult and seedling stages, on analyses on spatial scales ranging from 1 m² to the entire 150-ha study area, as well as supportive evidence from patterns in community structure. Our findings indicate that density-dependent seedling dynamics contribute to species coexistence in this diverse rain forest community.

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