



## Research

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# Demographic consequences of heterogeneity in conspecific density dependence among mast-fruiting tropical trees

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The role of conspecific density dependence (CDD) in the maintenance of species richness is a central focus of tropical forest ecology. However, tests of CDD often ignore the integrated effects of CDD over multiple life stages and their long-term impacts on population demography. We combined a 10-year time series of seed production, seedling recruitment and sapling and tree demography of three dominant Southeast Asian tree species that adopt a mast-fruiting phenology. We used these data to construct individual-based models that examine the effects of CDD on population growth rates ( $\lambda$ ) across life-history stages. Recruitment was driven by positive CDD for all species, supporting the predator satiation hypothesis, while negative CDD affected seedling and sapling growth of two species, significantly reducing  $\lambda$ . This negative CDD on juvenile growth overshadowed the positive CDD of recruitment, suggesting the cumulative effects of CDD during seedling and sapling development has greater importance than the positive CDD during infrequent masting events. Overall, CDD varied among positive, neutral and negative effects across life-history stages for all species, suggesting that assessments of CDD on transitions between just two stages (e.g. seeds seedlings or juveniles mature trees) probably misrepresent the importance of CDD on population growth and stability.

## 1. Introduction

Negative density-dependent mechanisms that promote increased mortality of spatially aggregated and locally abundant species are widely considered to contribute to maintenance of high plant diversity in tropical forests [1,2], although the importance of these mechanisms remains debated [3]. Furthermore, positive density-dependent processes (facilitation or predator satiation) may also function in tropical tree communities such as those dominated by ectomycorrhizal plant species [4,5] or those reliant on mast fruiting for regeneration [6–9]. Despite the role of density-dependent mechanisms for structuring communities, empirical evidence directly relating density dependence (positive or negative) of vital

rates to population demography remains limited in tropical forests [10]. Testing the effects of conspecific density on vital rates, and in turn population growth rates, is important for understanding whether density dependence contributes to long-term population stability and species persistence in tropical forests globally.

Negative density-dependent mechanisms may promote coexistence at both local and landscape scales in tropical forests [11–14]. However, the contrary finding that high seed or seedling density may improve fitness [4,15] contradicts typical Janzen–Connell mechanisms acting via host-specialist herbivores or fungal pathogens [16,17]. Tropical forest trees reliant on mast fruiting to satiate large generalist seed consumers [18] are likely to demonstrate positive density dependence at early seed and seedling stages [8,19]. Seedlings of ectomycorrhizal trees may also benefit from positive plant–soil feedbacks when growing in close proximity to mature conspecifics that increases access to mutualist fungi and below-ground facilitation by established fungal networks [4,5].

In tropical forests, reports of negative plant–soil feedbacks consistent with Janzen–Connell mechanisms are common, but the study sites for this research are concentrated in neotropical forests that are characterized by a dominance of arbuscular mycorrhizal trees and an absence of mast fruiting [16,17]. Recent work in Asian tropical and subtropical forests dominated by mast-fruiting ectomycorrhizal trees has found evidence of weak negative density dependence effects of soil communities on seedling mortality [20] and weak distance-dependent relationships from mature trees on seedling herbivory [11]. Positive plant–soil feedbacks for ectomycorrhizal species would reinforce positive density-dependent effects of predator satiation, if access to established networks of ectomycorrhizal fungi improves growth and survival of seedlings and saplings in areas with high conspecific density [5,21].

Although previous research has supported the importance of density-dependent mechanisms on plant germination, recruitment, growth or survival, few studies have integrated these responses across life stages to understand their emergent effects on population growth rate (see example, Silva Matos *et al.* [10]). Making this connection is important, because an empirical demonstration of density dependence is not sufficient for understanding its significance for population demography [22]. This linkage requires integrating responses to conspecific density on vital rates and over long timescales using population models [10]. Including density-dependent effects on different vital rates separately and in concert may disentangle the magnitude and direction of density-dependent effects on population demography across vital rates and life stages. For example, in a mast-fruiting species, high conspecific density may enhance per capita probability of seedling recruitment due to predator satiation but there may then be a transition to negative density regulation of seedling growth or survival due to competition [8]. If density dependence switches from positive to negative across life stages, then the cost of mast-fruiting production may be higher than if estimated solely at the recruitment stage. Furthermore, density-dependent effects on early vital rates may not impact long-term population demography, especially for long-lived organisms.

We established a plot network around mature individuals of Dipterocarpaceae trees (dipterocarps) in Borneo to investigate seedling recruitment, growth and survival. We then monitored vital rates on these seedling populations for up to 10 years, which included multiple mast-fruiting events. To

estimate vital rates across all life stages of our species, we combined this detailed assessment of regeneration dynamics with estimates of growth and survival derived from a mapped forest dynamics plot. We further developed individual-based models (IBMs) from the vital rate functions to isolate the effects of conspecific neighbour density across life stages and to understand the cumulative consequences of conspecific density on population growth rates. We posited that mast fruiting would promote positive density-dependent recruitment leading to increased population growth rates in the IBM but that those positive impacts could transition to neutral or negative density dependence at later stages of development. To that end, we predicted that the effects of density dependence (either positive or negative) on growth or survival would lead to larger cumulative impacts on population growth rates than effects arising from density dependence in recruitment. This prediction is justified by the additive effects of growth and mortality on populations over multiple years, compared to the infrequent and stochastic effects of recruitment in mast-fruiting species.

## 2. Material and methods

### (a) Study sites

The detailed assessment of seed fall and recruitment took place in the Malua Forest Reserve (Malua), an area that was first logged more than three decades ago (N 05°05'20" E 117°38'32"; 102 MASL). This forest is located approximately 22 km north of Danum Valley Field Centre in Sabah, Malaysia. Mean annual rainfall (SE) recorded in Danum Valley from 1986 to 2018 was 2900 (90) mm. The primary forest in this area is dominated by dipterocarps, but these species have been the main target of the logging industry [23].

### (b) Experimental design

We chose three dipterocarp species (*Dryobalanops lanceolata*, *Parashorea malaanonan* and *Shorea parvifolia*) for the study. We selected these species because they were available in Malua Forest Reserve and are common in the nearby primary forest at Danum Valley. These species are all moderately shade tolerant as seedlings but vary in terms of growth rate, tolerance to resource limitations and fruit size (electronic supplementary material, table S1) [24] with *D. lanceolata* on the larger end (2.6 g; SEM: 0.34), *S. parvifolia* on the smaller end (0.5 g; SEM: 0.02) and *P. malaanonan* in the middle (1.9 g; SEM: 0.19) of dipterocarp fruit sizes. We located three reproductively mature trees (i.e. greater than or equal to 50 cm diameter at breast height) of each species based on the following criteria: (i) absence of stem and crown damage; (ii) isolated by greater than 100 m from a fruiting conspecific during the 2010 flowering and greater than 15 m from mature, flowering heterospecific dipterocarps and (iii) greater than 20 m from abandoned logging roads and skid trails. We placed nine plots of 2 × 2 m around each mature tree, located along three transects radiating from the stem at 0°, 120° and 240° N to prevent directional biases in seed fall from factors such as wind and slope. Along each transect, plots were centred at 2 m (directly under the crown), 6 m (crown edge) and 18 m (outside the crown) from the stem. There was a total of 81 plots (3 species × 3 mature trees per species × 9 plots per tree = 81 plots). These plots allowed us to assess the role of conspecific density dependence (CDD) on seed, seedling and sapling dynamics.

In addition to the detailed seedling data, we used the two censuses from the Forest Global Earth Observatory plot (Forest-GEO; 50 ha area of primary forest [25]), located in the Danum Valley Conservation Area (approximately 20 km from the seedling census plots), to estimate growth and survival of trees.

These data were collected following standard protocols [25], which include mapping, identifying and measuring the diameter at breast height of all stems greater than 10 mm. The first census began in 2010 and finished in 2016, and the second census began in 2018 and finished in 2019. In total, the first census included 250 trees of *D. lanceolata* (mean diameter = 74.1 mm, range: 10–1297 mm), 1940 trees of *P. malaanonan* (mean diameter = 124.8 mm, range: 10–1459 mm) and 823 trees of *S. parvifolia* (mean diameter = 184.3 mm, range: 10–1640 mm).

### (c) Masting events

A regional masting event (across Borneo with more than 75% of mature trees flowering; [26]) began in late July 2010 with seed fall finishing in early September 2010. All the dipterocarps in our study produce single-seeded fruits; therefore, we refer to these structures as seeds throughout the rest of the paper. A second masting event began in Malua in early August 2014 with seed fall finishing in early September 2014. A third regional scale masting event began in early August 2019 with seed fall finishing in early September 2019 (electronic supplementary material, table S2). To provide additional data on dipterocarp fecundity, we supplemented this seed production data with seed surveys carried out in 2001 and 2002 at Sepilok Forest Reserve in north-eastern Sabah [7,27]. Further details on the masting events and the electronic supplementary material, data from Sepilok are provided in the electronic supplementary material.

### (d) Seedling measurements

At each post-masting census, we tagged all individuals and recorded whether they were alive or dead (e.g. seeds with dead radicle or those not germinated after four months). Censuses continued approximately every three to six months after the September 2010 census until December 2020 (greater than 10 years after the initial census; 30 censuses in total). Beginning at the fourth census (eight months after the initial post-masting census), we measured height and diameter at base for all seedlings at every census. At the 16th census (six months after the second masting event) and 29th census (nine months after the third masting event), we began height and diameter at base measurements for all the new seedlings from the second and third masting events, respectively. However, intermediate seedling count censuses occurred at three and seven months after the first masting, three months after the second masting and five months after the third masting to check initial seedling survival in the first months and accuracy of our initial counts. In addition, at each masting, event seeds of all three species were collected from other mature trees and germinated. Viability was quite high during 2010 and 2014, with more than 90% germination rates, while they were slightly lower during 2019 (70% seed viability), probably due to the drier conditions during seed maturation that year. These estimates were based on hundreds of seeds for each species during each event.

### (e) Timing of mast flowering

We compiled data on mast flowering years from the literature and field observations to build a transition matrix that estimated the probability of mast flowering and non-mast flowering years. The data spanned a period from 1950 to 2019 and consist of documented records of mast flowering years in northeastern Borneo [6,7,19,28–31]. To estimate the transition matrix, we also included a post-flowering category that immediately followed every flowering year (i.e. there was 100% chance to go from flowering to post-flowering). This category prevented two consecutive general flowering years, which are uncommon. The resulting transition matrix resulted in a 24% chance of transitioning from non-flowering to flowering and a 76% chance of remaining non-flowering. The mean interval between flowering events was approximately 6

years based on 10 000 simulations. The transition probability matrix was estimated using the `markovchainFit` function in the `markovchain` package [32] in R (v. 4.0.3; <http://r-project.org>).

### (f) Analysis overview

We calculated vital rates for reproduction, growth and survival based on diameter using well-established regression methods based on the seedling and ForestGEO datasets combined. Four censuses were dropped from the seedling data to make intervals between censuses approximately six months (mean interval length = 173 days with a standard deviation of 42 days). The low quantities of heterospecific seeds on plots around the mature trees selected for sampling (electronic supplementary material, table S2) prevented the estimation of vital rates for heterospecific individuals. Therefore, the analysis focused solely on *Dryobalanops lanceolata*, *Parashorea malaanonan* and *Shorea parvifolia* individuals (i.e. conspecifics of the focal mature trees). The ANOVA tables, Wald statistics and variance components for all models are in the supporting information (electronic supplementary material, tables S3–S5).

### (g) Analysis of reproduction and flowering

Seed quantity around each tree during each masting event was fitted to a linear model with distance and direction from the mother tree as fixed independent variables (electronic supplementary material, table S3 and figure S1). We analysed natural-log of seed production as a function of tree diameter (a continuous variable and natural log-transformed) and a random term for tree individuals using a linear mixed model with a Gaussian distribution (see electronic supplementary material, table S4). Tree size did not affect seed production significantly for any of the three species. Based on these results and previous research, we assumed trees above 300 mm diameter could flower [27,33,34], although sensitivity analysis on flowering probability was carried out (see below). Models were fitted using the `asreml-R` package (ASReml 4, VSN International, UK) in R (v. 4.0.3; <http://r-project.org>).

### (h) Analysis of recruitment

Recruitment was defined as the probability of a seed becoming a seedling. All seeds either germinated or died within four months of seed fall, and mortality of germinants stabilized around six months after seed fall (based on regular seedling counts during the first masting event). Seedlings were considered recruited after approximately six–eight months, but the timing of the first measurement of seedling size varied with mast year from six months after 2014 to 10 months after 2010. We calculated the mean size and standard deviation for each species of recruited seedlings pooled for all three masting events.

We supplemented the recruitment data with 467 plots of 1 × 1 m, distributed in and around Danum Valley during the 2019 masting event (see details in electronic supplementary material). The plots were sampled for total seed counts at the end of the peak of seed fall (September 2019) and seedlings were counted and tagged five months later (February 2020). Of these 467 plots, 12 plots had *D. lanceolata* seeds, 42 plots had *P. malaanonan* seeds and 72 plots had *S. parvifolia* seeds. The probability of recruitment (total recruits divided by total seeds per plot) for each species was analysed as a function of density with a binomial distribution and logit link function (see electronic supplementary material, table S5 for Wald statistics). Electronic supplementary material, figure S2 shows the raw data plotted with a loess curve to show the data trend. Models were fitted with the `asreml-R` package in R.

### (i) Analysis of growth and survival

For the combined seedling and adult tree datasets, we modelled log diameter at time  $t + 1$  (Gaussian distribution with identity



link) and survival at time  $t + 1$  (binomial distribution with logit link) as a linear function of the diameter ( $z$ , natural-log of diameter in mm) from the previous census (equation (2.1)). Diameters were all standardized to diameter at the base of the stem using locally derived allometric equations [35]. We parameterized growth and survival using the optim function in R with the Nelder-Mead simplex.

$$V(z) = \beta_0 + \beta_z z, \quad (2.1)$$

Whereby  $V(z)$  is the vital rate (growth or survival) as a function of diameter of the previous census ( $z$ ) and a size effect ( $\beta_z$ ) with an intercept ( $\beta_0$ ). A neighbour interaction term was used to assess the effect of conspecific neighbours on focal individuals as a function of neighbour size relative to focal size (equation (2.2)).

$$\alpha(z, x) = \sum_{i=1}^n \frac{x_i}{z}, \quad (2.2)$$

whereby  $x$  is the diameter of the neighbours (standardized by the distance from the focal tree) from  $i$  to  $n$  individuals and  $z$  is the diameter of the focal individual. The conspecific neighbour effect at each census was the sum of the interaction term for all the conspecific neighbours from the previous census within each  $2 \times 2$  m plot in the detailed seedling census and a circular neighbourhood of 15 m radius around individuals for the ForestGEO plot. The 15 m neighbourhood of the saplings and trees was based on previous research assessing the spatial effect size of neighbouring trees [36]. The neighbourhood interaction term (equation (2.2)) was included as an exponential index in (equation (2.1)) to assess the effect of neighbour size and density on growth or survival of the focal individual (equation (2.3)).

$$V(z) = (\beta_0 + \beta_z z) \exp^{\beta_N \alpha(z, x)}. \quad (2.3)$$

The parameter  $\beta_N$  determines the magnitude and direction of the conspecific neighbour effect on the vital rate. Therefore, the model combines the effect of neighbour size and density whereby values of the exponential term below one decrease (negative density dependence) and values above one increase (positive density dependence) on growth or survival. We accounted for unequal sample intervals by standardizing the growth to 182.625 days (six months). This standardization was achieved by dividing the change in size between intervals by the number of six-month intervals between censuses then adding this average growth to the size at timepoint  $t$ . The model of diameter at  $t + 1$  also estimated variance as a function of size ( $\sigma_z^2$ ) to account for heteroscedastic size data due to combining the detailed seedling (recruitment after fruiting plots) and tree (ForestGEO) datasets (equation (2.4)).

$$\sigma^2 = \ln(\sigma_0^2) + \ln(\sigma_z^2 z). \quad (2.4)$$

Variance is a function of diameter ( $z$ ) on the natural-log scale with an intercept ( $\sigma_0^2$ ). Electronic supplementary material, tables S6 and S7 provide all parameter estimates for growth and survival equations.

## (j) Building dynamic models

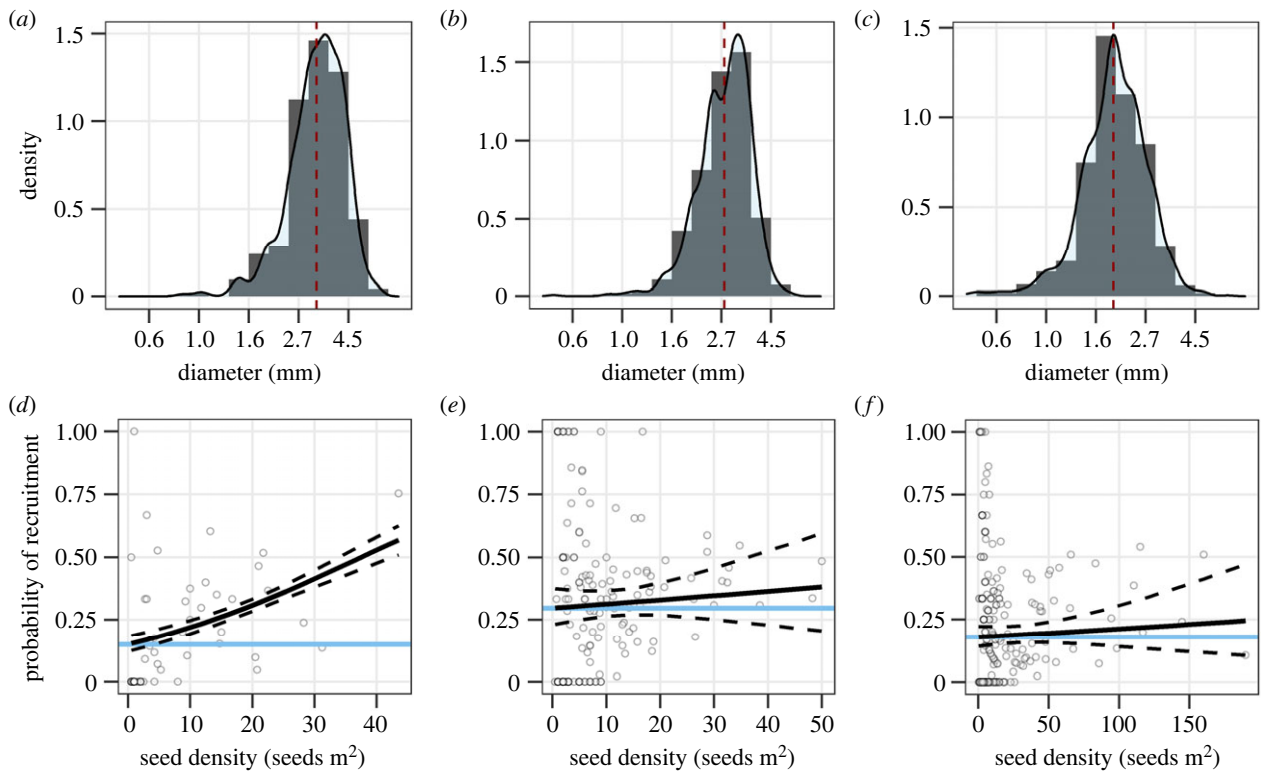
We built an IBM from the vital rate parameters estimated above for each species and simulated 250 years with flowering and non-flowering years randomly assigned based on the transition matrix. We initiated the simulation by randomly sampling 5000 seedlings based on the mean and standard deviation of measured recruitment size followed by a 100-year burn-in period, which was chosen as the minimum time required for the simulated population to develop a structure that included a range of size classes and trees of flowering size. At each time step, we used the survival parameters to assess the survival of

each individual and the growth parameters to determine the change in size of individuals. Based on the estimated probability of survival, individuals were assigned a 0 for dead or 1 for alive using the rbinom function in R. The mean and standard deviation (calculated with the estimated variance parameters) from these vital rates were used to assign a random size at the next period using the rnorm function in R. The average value of the neighbourhood interaction term for each size was estimated with a linear log-log relationship between size and the estimated interaction value from the data. This model was then used to calculate an interaction value of each individual based on their size using the predict and simulate functions in R. For scenarios with no neighbourhood density for all or some of the vital rates, the neighbourhood interaction term was set to zero making the vital rate the intercept for recruitment or (equation (2.1) for growth and survival (the R code for the IBM is presented in electronic supplementary material).

During general flowering years, trees above the minimum flowering diameter (300 mm) were assumed to be able to flower [33,34]. The percentage of individuals flowering is variable among masting years, but commonly, in general mass flowering events in Borneo large numbers of individuals per species flower. We used similar proportions from Sun *et al.* [34] as a basis for defining the probability of flowering such that on average 50% of trees greater than 300 mm flowered during a masting year. The probability of flowering was set to increase with size such that 300–400 mm were given a 25% probability, 400–500 mm were given a 50% probability and greater than 500 mm were assigned a 75% probability of flowering (i.e. not all trees flower or produce seeds during every masting event; Maycock *et al.* [7]). We then assigned each of these mature trees a flowering or no flowering value using the rbinom function (flowers = 1 and no flowers = 0). To determine the sensitivity of our conclusions to uncertainty over flowering probabilities in this system, we tested three alternative patterns of flowering probability with size (20, 40 and 60% probability for trees of 300 mm diameter, increasing by 10% with every 100 mm diameter increment).

Because fecundity did not significantly change with tree size, the number of seeds produced for each tree was randomly assigned using the rnorm function based on the average and standard deviation of seed production per species, and each seedling was assigned a random recruitment size using the rnorm function and the average and standard deviation of recruitment size. A mean probability of recruitment was calculated from the vital rate function (in scenarios with no density effects this value was the intercept for every individual within a species), and the rbinom function was used to randomly assign them a 0 for failed to recruit or 1 for recruited.

We compared five scenarios to test the effect of conspecific neighbourhood density on different vital rates (recruitment, growth and survival) and in turn population growth rate. Scenario 1: a model with no density effects on any vital rate ('null'). Scenario 2: density impacts on growth with no density effects on survival or recruitment ('growth'). Scenario 3: density impacts on survival with no density effects on growth or recruitment ('survival'). Scenario 4: density impacts on recruitment with no density effects on growth or survival ('recruitment'). Scenario 5: density impacts on all vital rates ('all'). The population growth rate ( $\lambda$ ) was calculated for each scenario as the average change in population size (log-transformed) between each time-step for 250 years after the 100-year burn in period. We also calculated a form of elasticity whereby the change in population growth rate of each scenario was relativized against the null scenario divided by the standardized effect size of density ( $\beta$  of density minus the mean  $\beta$  of density for each species in each scenario and divided by the standard deviation). The vital rate parameters were estimated on 1000 bootstraps of the data, and 95% confidence intervals of the population growth rates



**Figure 1.** Recruitment size distribution and probability. The histogram of size overlaid by the distribution (black line) and mean recruitment size (red dashed line) for (a) *Dryobalanops lanceolata*, (b) *Parashorea malaanonan* and (c) *Shorea parvifolia*. Size data is log-scale transformed, but the x-axis labels are on the normal scale for interpretation. The probability of recruitment (black line with dashed line of 95% CI) as a function of total seed density for (d) *Dryobalanops lanceolata*, (e) *Parashorea malaanonan* and (f) *Shorea parvifolia*. Points represent recruitment of plots from 2010, 2014 and 2019, and the horizontal blue line represents intercept (baseline with no neighbours). (Online version in colour.)

were calculated from these 1000 bootstrap estimates using the `mean_cl_normal` function in the `Hmisc` package.

### 3. Results

#### (a) Seed production

During a single masting event, *D. lanceolata* trees produced 1277 seeds on average (95% CI: 751–2173), *P. malaanonan* produced 10135 seeds on average (95% CI: 7519–13661) and *S. parvifolia* produced 8064 seeds on average (95% CI: 5282–12310). None of the species showed a significant relationship between tree size and total seeds produced (electronic supplementary material, table S4 and figure S3).

#### (b) Recruitment

Mean diameter at recruitment (figure 1a–c) was largest for *D. lanceolata* (mean = 3.3 mm, s.d.: 1.3) followed by *P. malaanonan* (mean = 2.7 mm, s.d.: 1.3) and *S. parvifolia* (mean = 2.0 mm, s.d.: 1.4). Recruitment probability increased with conspecific density for all species (figure 1d–f; electronic supplementary material, table S5), but these models only explain a small amount of variation (McFadden's  $R^2$  was 0.2, 0.02 and 0.02 for *D. lanceolata*, *P. malaanonan* and *S. parvifolia*, respectively), as environmental variation is ignored. All three species had improved recruitment probability with greater conspecific density (*D. lanceolata* slope with density = 0.05, 95% CI: 0.01–0.08; *P. malaanonan*: slope with density = 0.008, 95% CI: –0.01–0.03, and *S. parvifolia*: slope with density = 0.002, 95% CI: –0.004–0.008), although the relationship was only significant for *D. lanceolata*. Therefore,

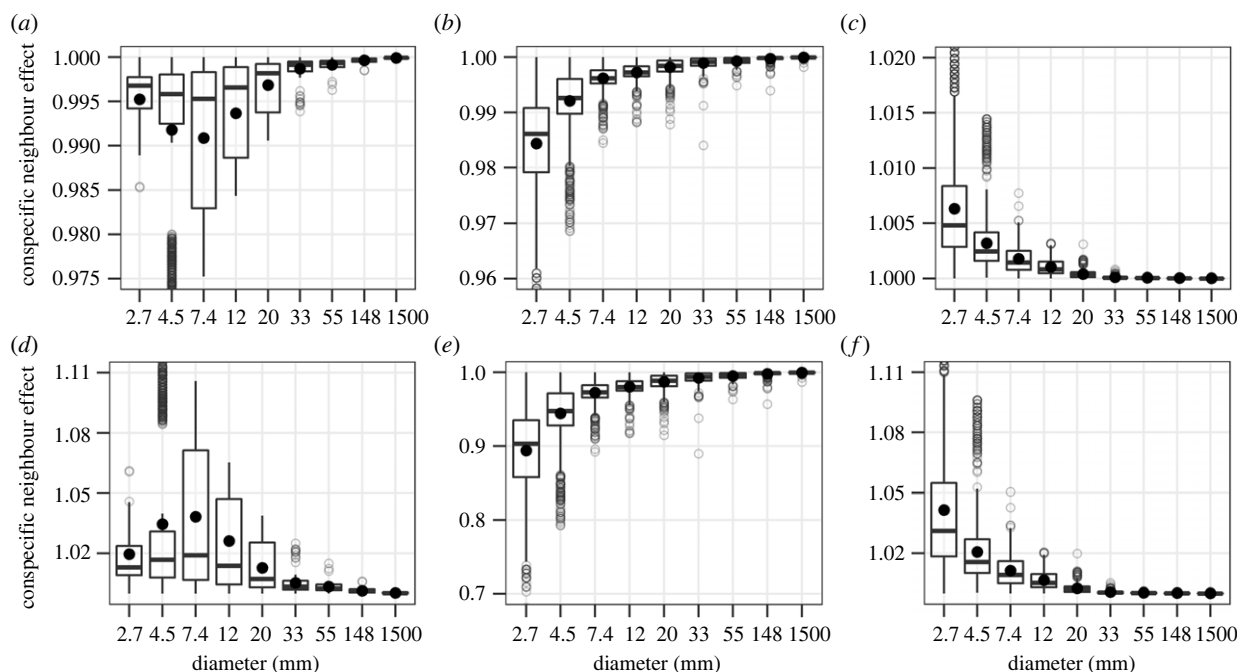
increasing from 1 to 50 seeds per  $m^2$  resulted in a 48.3% increase in probability of recruitment for *D. lanceolata*, an 8.3% increase in probability of recruitment for *P. malaanonan* and an 1.6% increase in probability of recruitment for *S. parvifolia*.

#### (c) Growth

Increasing conspecific neighbourhood density decreased growth significantly for *D. lanceolata* ( $R^2 = 0.92$ ) and *P. malaanonan* ( $R^2 = 0.98$ ) while *S. parvifolia* ( $R^2 = 0.94$ ) was not affected significantly by conspecific density (electronic supplementary material, table S6 and figure S4). This resulted in minor conspecific neighbour effects on seedling growth, with an average maximum reduction of approximately 0.9% on the size at  $t+1$  for *D. lanceolata* (densities greater than 60) and 1.5% on the size at  $t+1$  for *P. malaanonan* (densities greater than 40) and conversely, an increase of approximately 0.6% on the size at  $t+1$  for *S. parvifolia* (densities greater than 100) relative to an individual with no neighbours (figure 2a–c). The effect of conspecific neighbours reached an asymptote of one for individuals between 50 and 150 mm diameter for *D. lanceolata*, between 33 and 55 mm for *P. malaanonan* and between 20 and 33 mm for *S. parvifolia*.

#### (d) Survival

The overall effect of conspecific density ( $\beta_N$ ) on survival for *D. lanceolata* (McFadden's  $R^2 = 0.03$ ) and *S. parvifolia* (McFadden's  $R^2 = 0.02$ ) was not significantly different from zero, indicating density-independent survival (electronic supplementary material, table S7 and figure S5). The  $\beta_N$  parameter was significant and negative for *P. malaanonan*



**Figure 2.** Conspecific neighbour effects on growth and survival. (a–c) Box and whisker plots of the conspecific neighbour effect on growth (i.e. percentage increase or decrease on growth) as a function of focal tree size (binned with the x-axis labels depicting the maximum size of the bin). (d–f) Box and whisker plots of the conspecific neighbour effect on survival as a function of focal tree size. Some data points are removed for readability. Models were fitted on the log scale for diameter, but x-axis labels are on the untransformed scale for ease of interpretation. Black points are means and black bars are medians.

(McFadden's  $R^2 = 0.03$ ; electronic supplementary material, table S7), indicating negative density-dependent survival. The resulting conspecific neighbour effects on tree survival was an average maximum decrease of 3.8% in the probability of survival per six months for *D. lanceolata* (densities > 60), an average maximum decrease of 10.6% in the probability of survival per six months for *P. malaanonan* (densities > 40) and an average maximum increase of 4.2% in the probability of survival per six months for *S. parvifolia* (densities > 100) relative to an individual with no neighbours (figure 2d–f). The effect of conspecific neighbours reached its asymptote for *S. parvifolia* around 30 mm diameter while the effect of conspecific neighbours was evident at diameters greater than 55 mm for *D. lanceolata* and greater than 30 mm for *P. malaanonan* (figure 2d–f).

### (e) Population demographics

The IBMs produced population growth rates ( $\lambda$ ) consistently greater than one for all three species (figure 3; electronic supplementary material, figure S6), except for the scenarios including CDD on growth and all three vital rates for *D. lanceolata*. *Dryobalanops lanceolata* showed effects of conspecific density on  $\lambda$  that were either negative (growth scenario) or positive (survival and recruitment scenarios). These effects were additive as the scenario incorporating conspecific density effects on all vital rates led to an intermediate  $\lambda$ , although values in this case were still significantly lower than in the null scenario with all conspecific density effects excluded. The inclusion of density effects on tree growth and survival for *P. malaanonan* decreased  $\lambda$  relative to the null scenario, while  $\lambda$  showed an increase when a density effect on recruitment was included (figure 3). The positive effect of density on recruitment was overshadowed by growth and survival, which led to the greatest decrease in  $\lambda$  for *P. malaanonan* with density effects on all three vital rates. *Shorea parvifolia* showed consistent positive effects of conspecific density on  $\lambda$  for all vital rates except

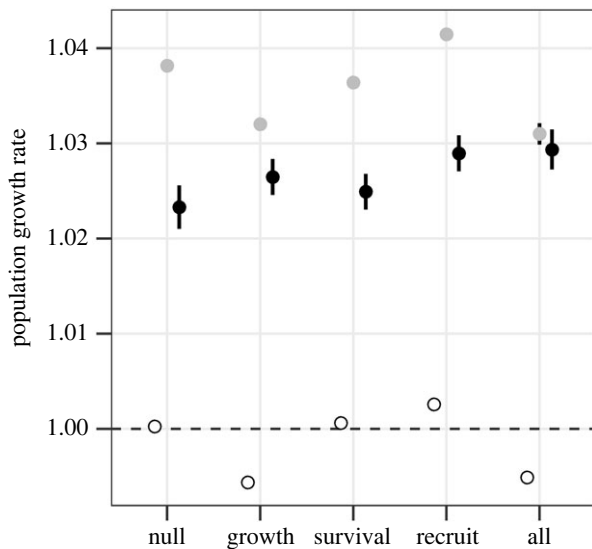
survival, which was neutral. The combined effects of conspecific density on all vital rates of *S. parvifolia* led to significantly higher values of  $\lambda$  relative to all other scenarios except that including effects on recruitment alone (figure 3) suggesting the importance of density on recruitment. Our pseudo-elasticity analysis showed that the effect of conspecific density on population growth rates was equal across vital rates for *D. lanceolata* and *P. malaanonan*, but the conspecific density effect on recruitment had a stronger impact on the population growth rate of *S. parvifolia* than the impact of either growth or survival (electronic supplementary material, figure S7).

Within each species, the final population size varied among scenarios (electronic supplementary material, figure S8), but the population size class structure among replicate simulations was similar across scenarios (electronic supplementary material, figure S9). The sensitivity analyses of flowering probability on population growth rates showed that increasing the probability of flowering for 300 mm trees increased the population growth rates. The response was linear and consistent whether density was excluded in the scenario (Null) or included (All) and for all three species (electronic supplementary material, figure S10).

## 4. Discussion

Our analysis of multiple long-term datasets on recruitment, growth and survival indicates that negative CDD was relatively uncommon across vital rates relative to neutral and positive conspecific density effects. However, negative density dependence had a disproportionately strong impact on population growth rates when these processes were built into IBMs that accounted for the cumulative effects of CDD across life stages. All species showed a positive conspecific density-dependent signal for recruitment, which supports hypotheses linking recruitment success to predator satiation [9] and positive





**Figure 3.** Population growth rate for each scenario. Population growth rates were estimated from the IBMs for each species (*D. lanceolata* = white, *P. malaanonan* = grey and *S. parvifolia* = black) where neighbourhood density is included for growth, survival, recruitment, all vital rates or a null with no conspecific neighbour effects. The dashed line is a  $\lambda$  of one. The 95% confidence intervals were estimated from 1000 bootstraps of each scenario. *D. lanceolata* and *P. malaanonan* had low variation, so 95% CIs are obscured by the data points.

plant–soil feedbacks [4] for ectomycorrhizal trees in Southeast Asian tropical forests. Only three of the nine vital rate  $\times$  species combinations provide evidence of the negative density dependence required for regulation of population growth rate by Janzen–Connell mechanisms [37,38]. However, for two of the three species, negative CDD dominated over the positive and neutral processes and resulted in an overall reduced population growth rate, relative to the null model, in the scenario with conspecific density effects on all vital rates.

### (a) Patterns of population growth rate

The combined effects of CDD on population growth rates showed that recruitment, survival and growth contributed additively. This led to two distinct patterns of response across species: (i) negative effects overwhelmed positive effects, reducing population growth rates (*D. lanceolata* and *P. malaanonan*) and (ii) neutral and positive effects caused incremental increases, enhancing population growth rates (*S. parvifolia*). The first outcome supports our expectation that positive CDD at early life stages is overshadowed by negative CDD at later life stages. Interestingly, the consistent evidence for neutral and positive CDD on vital rates (six of nine rate  $\times$  species combinations) did not translate into strong positive effects on  $\lambda$ , suggesting that negative CDD, although less common, is highly influential in population dynamics for two of our three study species. The relative importance of these contrasting responses to conspecific density across the many hundreds of species in the tree community at our study site remains to be determined by future research.

### (b) Consistent positive conspecific density-dependent recruitment

All three species showed positive conspecific density-dependent trend at the seedling recruitment phase, in support

of the predator satiation hypothesis, and in contrast with the evidence of negative conspecific density-dependent patterns of seedling recruitment that are reported frequently in neotropical forests [2,3,39]. The three species produce seeds of varying size and quantity, which suggests that regardless of their reproductive strategy species of Dipterocarpaceae benefit from mast flowering via predator satiation, especially satiation of large mammals that are generalist frugivores [18]. These findings underscore that the importance and directionality of CDD may differ according to patterns of reproductive phenology and biogeographical context even within the single biome represented by lowland tropical forests. Despite this consistent effect, positive conspecific density-dependent recruitment was overshadowed by the effects of growth and survival on population growth rates for two of the three species, in support of our initial hypothesis that growth and survival have stronger influences on  $\lambda$  due to their continuous yearly impact relative to infrequent masting. Nonetheless, our model tested effects of conspecific density in the absence of additional variables, and the inclusion of environmental factors and interactions with heterospecific neighbours into dynamic models would improve estimates and help to disentangle the relative importance of recruitment and other demographic and environmental factors for population stability.

### (c) Variable conspecific density-dependent growth and survival

The role of conspecific neighbour density on growth and survival was species dependent. In general, the effect of CDD on survival was weaker for all species relative to the effect on growth. The results across species did not show expected patterns. *Shorea parvifolia* is commonly a light demanding, fast-growing species [24], and growth rate of species with these traits is generally considered to enhance their sensitivity to neighbour conspecific density [40]. Our contrasting result may be an indirect outcome of environmental factors, such that microsites that supported high seedling recruitment were also beneficial for growth and survival. Alternatively, higher conspecific densities could facilitate connections to common ectomycorrhizal networks that improve growth and survival via improved resource uptake and protection against pathogens and balance the negative effects of higher conspecific neighbour density [4].

There was evidence for strong negative conspecific density-dependent effects on growth (*D. lanceolata* and *P. malaanonan*) that led to large decreases in  $\lambda$ . This pattern supports our hypothesis of a transition from positive CDD at the recruitment phase (i.e. the seed to seedling transition) to negative conspecific density-dependent growth of seedlings and saplings. It is likely that direct competition for water or nutrients [41] or shading under the tree crown [24], rather than negative plant–soil feedbacks, contributed to these negative conspecific density-dependent effects on growth and survival, as only weak effects of soil pathogens on growth and survival have been documented in dipterocarp seedlings in Borneo [20]. The stronger effect of negative density dependence on growth than survival in these two species may be the result of their high survival rates in general relative to other dipterocarps [24]. The rank order of the survival response of species to density dependence found in our study is consistent with previous research on these species [15]: survival of *P. malaanonan* was most sensitive to

neighbours, while *D. lanceolata* and *S. parvifolia* were much more tolerant to dense neighbourhoods.

#### (d) Ontogenetic patterns in conspecific density dependence

Consistent with previous research [2,10,40], conspecific density-dependent effects faded with tree size, but the effects on growth and survival were observed on trees as large as 30 to 150 mm, especially in *D. lanceolata* and *P. malaanonan*. The mechanisms driving this effect are likely different between these two species. The high density of *P. malaanonan* (and its closely related congeneric *P. tomentella*) at our study sites and across the region may promote negative density-dependent effects, which is consistent with patterns reported previously in Borneo [13]. Despite research suggesting that negative plant–soil feedbacks are more limiting for rare species in some neotropical trees [39], the stronger negative effects of CDD on *P. malaanonan* indicates that negative CDD is probably limiting population growth of the most abundant species at our study sites. The cause of the sustained negative conspecific neighbour effects on *D. lanceolata* are unclear, but compared with other dipterocarps, seedling and sapling growth of *D. lanceolata* was the most sensitive to neighbour abundance in a parallel study at our study sites [15]. Our results, therefore, align with an emerging perspective that this species is disproportionately sensitive to conspecific neighbour density.

In contrast with these species, *S. parvifolia* was unaffected by conspecific neighbours above a diameter of 30 mm, which aligns with recent work suggesting it is insensitive to neighbour abundance [15]. However, this species produces many seeds in mast years. Therefore, in the period after a masting event, seedling densities may have a disproportionate influence on  $\lambda$  relative to other species. This pattern may be important in a mast-fruiting system where the seedling population comprises multiple even-aged cohorts. The common strategy of dipterocarps in Borneo is to tolerate shade while taking advantage of canopy gaps throughout their life cycle to reach higher canopy strata [24]. Therefore, seedling survival in the understorey environment between intermittent masting events likely plays an essential role in the population stability of masting systems that lack a soil seed bank.

## 5. Conclusion

We present an integrated assessment of the effects of conspecific neighbour density on vital rates and population growth rates in a tropical system that is defined by general flowering and mast fruiting. This comprehensive approach indicates that the effects of conspecific density range from positive to neutral to negative across species and within species across

vital rates. These conspecific density effects support the importance of predator satiation for seedling recruitment in this system but highlight a strong influence of negative conspecific density-dependent growth on seedlings, saplings and subcanopy trees that act collectively to reduce the population growth rates of two out of three species. Despite the predominance of neutral and positive CDD across vital rates in six out of nine combinations, negative CDD typically had larger effects on population growth rates, and these are likely to be important for limiting species dominance in tropical tree communities. The masting phenology and ectomycorrhizal status of our study species are shared by all species of the tree families that dominate lowland tropical forests in Southeast Asia (Dipterocarpaceae) and subtropical forests at higher latitudes (Fagaceae), which suggests that these findings may have widespread generality at a continental scale. However, their applicability to trees in other families and different biogeographical settings where these traits are absent remains to be determined.

**Data accessibility.** Data are available on Dryad Digital Repository: <https://doi.org/10.5061/dryad.cfxpnvx7s> [42].

The data are provided in the electronic supplementary material [43].

**Authors' contributions.** M.J.O.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, writing—original draft and writing—review and editing; A.H.: funding acquisition and writing—review and editing; R.T.K.: investigation; C.R.M.: data curation and investigation; R.O.: project administration and resources; C.D.P.: conceptualization and writing—review and editing; J.S.P.: resources and writing—review and editing; G.R.: project administration and resources; D.F.R.P.B.: formal analysis, methodology, resources and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

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## References

- Connell JH, Slatyer RO. 1977 Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**, 1119–1144. (doi:10.1086/283241)
- Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP. 2010 Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* **329**, 330–332. (doi:10.1126/science.1190772)
- Hülsmann L, Chisholm RA, Hartig F. 2021 Is variation in conspecific negative density dependence driving tree diversity patterns at large scales? *Trends Ecol. Evol.* **36**, 151–163. (doi:10.1016/j.tree.2020.10.003)



4. Bennet JA, Maherali H, Reinhart KO, Lekberg Y, Hart MM, Klironomos J. 2017 Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* **355**, 181–184. (doi:10.1007/978-1-4020-2625-6\_7)
5. Liang M, Johnson D, Burslem DFRP, Yu S, Fang M, Taylor JD, Taylor AFS, Helgason T, Liu X. 2020 Soil fungal networks maintain local dominance of ectomycorrhizal trees. *Nat. Commun.* **11**, 1–7. (doi:10.1038/s41467-020-16507-y)
6. Blundell AG, Peart DR. 2004 Seedling recruitment failure following dipterocarp mast fruiting. *J. Trop. Ecol.* **20**, 229–231. (doi:10.1017/S0266467403001123)
7. Maycock CR, Thewlis RN, Ghazoul J, Nilus R, Burslem DFRP. 2005 Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. *J. Veg. Sci.* **16**, 635–646. (doi:10.1111/j.1654-1103.2005.tb02406.x)
8. Visser MD, Jongejans E, van Breugel M, Zuidema PA, Chen YY, Rahman Kassim A, de Kroon H. 2011 Strict mast fruiting for a tropical dipterocarp tree: a demographic cost-benefit analysis of delayed reproduction and seed predation. *J. Ecol.* **99**, 1033–1044. (doi:10.1111/j.1365-2745.2011.01825.x)
9. Janzen DH. 1974 Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* **6**, 69–103. (doi:10.2307/2989823)
10. Silva Matos DM, Freckleton RP, Watkinson AR. 1999 The role of density dependence in the population dynamics of a tropical palm. *Ecology* **80**, 2635–2650. (doi:10.1890/0012-9658(1999)080[2635:TRODDI]2.0.CO;2)
11. Bagchi R *et al.* 2011 Impacts of logging on density-dependent predation of dipterocarp seeds in a South East Asian rainforest. *Phil. Trans. R. Soc. B* **366**, 3246–3255. (doi:10.1098/rstb.2011.0034)
12. Bagchi R, Press MC, Scholes JD. 2010 Evolutionary history and distance dependence control survival of dipterocarp seedlings. *Ecol. Lett.* **13**, 51–59. (doi:10.1111/j.1461-0248.2009.01397.x)
13. Webb CO, Peart DR. 1999 Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* **80**, 2006–2017. (doi:10.1890/0012-9658(1999)080[2006:SDDPCO]2.0.CO;2)
14. Oshima C, Tokumoto Y, Nakagawa M. 2015 Biotic and abiotic drivers of dipterocarp seedling survival following mast fruiting in Malaysian Borneo. *J. Trop. Ecol.* **31**, 129–137. (doi:10.1017/S026646741400073X)
15. O'Brien MJ, Escudero A. 2022 Topography in tropical forests enhances growth and survival differences within and among species via water availability and biotic interactions. *Funct. Ecol.* **36**, 686–698. (doi:10.1111/1365-2435.13977)
16. Bell T, Freckleton RP, Lewis OT. 2006 Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecol. Lett.* **9**, 569–574. (doi:10.1111/j.1461-0248.2006.00905.x)
17. Bagchi R, Swinfield T, Gallery RE, Lewis OT, Gripenberg S, Narayan L, Freckleton RP. 2010 Testing the Janzen–Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecol. Lett.* **13**, 1262–1269. (doi:10.1111/j.1461-0248.2010.01520.x)
18. Granados A, Brodie JF, Bernard H, O'Brien MJ. 2017 Defaunation and habitat disturbance interact synergistically to alter seedling recruitment. *Ecol. Appl.* **27**, 2092–2101. (doi:10.1002/eap.1592)
19. Curran LM, Leighton M. 2000 Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* **70**, 101–128. (doi:10.1890/0012-9615(2000)070[0101:VRTSVI]2.0.CO;2)
20. Cannon PG, O'Brien MJ, Yusah KM, Edwards DP, Freckleton RP. 2020 Limited contributions of plant pathogens to density-dependent seedling mortality of mast fruiting Bornean trees. *Ecol. Evol.* **10**, 13 154–13 164. (doi:10.1002/ece3.6906)
21. Laliberté Etienne, Lambers Hans, Burgess Treena I, Wright S. Joseph. 2015 Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytologist* **206**(2), 507–521. (http://dx.doi.org/10.1111/nph.2015.206.issue-2)
22. Adler PB, Dalgleish HJ, Ellner SP. 2012 Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *J. Ecol.* **100**, 478–487. (doi:10.1111/j.1365-2745.2011.01930.x)
23. Kettle C, Maycock C, Burslem D. 2012 New directions in dipterocarp biology and conservation: a synthesis. *Biotropica* **44**, 658–660. (doi:10.1111/j.1744-7429.2012.00912.x)
24. Philipson CD *et al.* 2014 A trait-based trade-off between growth and mortality: evidence from 15 tropical tree species using size-specific relative growth rates. *Ecol. Evol.* **4**, 3675–3688. (doi:10.1002/ece3.1186)
25. Davies SJ *et al.* 2021 ForestGEO: understanding forest diversity and dynamics through a global observatory network. *Biol. Conserv.* **253**, 108907. (doi:10.1016/j.biocon.2020.108907)
26. Kettle CJ *et al.* 2011 Seeing the fruit for the trees in Borneo. *Conserv. Lett.* **4**, 184–191. (doi:10.1111/j.1755-263X.2010.00161.x)
27. Kettle C, Maycock CR, Ghazoul J, Hollingsworth P, Khoo E, Sukri R, Burslem D. 2011 Ecological implications of a flower size/number trade-off in tropical forest trees. *PLoS ONE* **6**, e0016111. (doi:10.1371/journal.pone.0016111)
28. Ashton P, Givnish T, Appanah S. 1988 Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* **132**, 44–66. (doi:10.1086/284837)
29. Appanah S. 1993 Mass flowering of dipterocarp forests in the aseasonal tropics. *J. Biosci.* **18**, 457–474. (doi:10.1007/BF02703079)
30. Bebbier DP, Brown ND, Speight MR. 2004 Dipterocarp seedling population dynamics in Bornean primary lowland forest during the 1997–8 El Niño–Southern Oscillation. *J. Trop. Ecol.* **20**, 11–19. (doi:10.1017/S0266467404006133)
31. Curran LM, Caniago I, Paoli GD, Astianti D, Kusneti M, Leighton M, Nirarita CE, Haeruman H. 1999 Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* **286**, 2184–2188. (doi:10.1126/Science.286.5447.2184)
32. Spedicato G. 2017 Discrete time Markov chains with R. *R Journal* **9**, 84–104.
33. Naito Y *et al.* 2008 Size-related flowering and fecundity in the tropical canopy tree species, *Shorea acuminata* (Dipterocarpaceae) during two consecutive general flowerings. *J. Plant Res.* **121**, 33–42. (doi:10.1007/s10265-007-0116-x)
34. Sun IF, Chen YY, Hubbell SP, Wright SJ, Noor NSM. 2007 Seed predation during general flowering events of varying magnitude in a Malaysian rain forest. *J. Ecol.* **95**, 818–827. (doi:10.1111/j.1365-2745.2007.01235.x)
35. Philipson CD *et al.* 2020 Active restoration accelerates the carbon recovery of human-modified tropical forests. *Science* **369**, 838–841. (doi:10.1126/science.aay4490)
36. Uriarte M, Turner BL, Thompson J, Zimmerman JK. 2015 Linking spatial patterns of leaf litterfall and soil nutrients in a tropical forest: a neighborhood approach. *Ecol. Appl.* **25**, 2022–2034. (doi:10.1890/15-0112.1)
37. Janzen DH. 1970 Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528. (doi:10.1086/282687)
38. Connell JH. 1970 On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of population* (eds PJ den Boer, GR Gradwell), pp. 296–310. Wageningen, The Netherlands: Centre for Agricultural Publishing and Documentation.
39. Mangan SA, Schnitzer SA, Herre EA, Mack KML, Valencia MC, Sanchez EI, Bever JD. 2010 Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**, 752–755. (doi:10.1038/nature09273)
40. Zhu Y, Queenborough SA, Condit R, Hubbell SP, Ma KP, Comita LS. 2018 Density-dependent survival varies with species life-history strategy in a tropical forest. *Ecol. Lett.* **21**, 506–515. (doi:10.1111/ele.12915)
41. O'Brien MJ, Reynolds G, Ong R, Hector A. 2017 Resistance of tropical seedlings to drought is mediated by neighbourhood diversity. *Nat. Ecol. Evol.* **1**, 1643–1648. (doi:10.1038/s41559-017-0326-0)
42. O'Brien MJ, Hector A, Kellenberger RT, Maycock CR, Ong R, Philipson CD, Powers JS, Reynolds G, Burslem DFRP. 2022 Data from: demographic consequences of heterogeneity in conspecific density dependence among mast fruiting tropical trees. Dryad Digital Repository. (doi:10.5061/dryad.cfxpvnv7s)
43. O'Brien MJ, Hector A, Kellenberger RT, Maycock CR, Ong R, Philipson CD, Powers JS, Reynolds G, Burslem DFRP. 2022 Demographic consequences of heterogeneity in conspecific density dependence among mast fruiting tropical trees. FigShare. (https://doi.org/10.6084/m9.figshare.c.6011798)