



## Research

**Cite this article:** Caughlin TT, Ferguson JM, Lichstein JW, Zuidema PA, Bunyavejchewin S, Levey DJ. 2015 Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proc. R. Soc. B* **282**: 20142095.  
<http://dx.doi.org/10.1098/rspb.2014.2095>

Received: 22 August 2014  
 Accepted: 14 October 2014

**Subject Areas:**

ecology, environmental science, plant science

**Keywords:**

seed dispersal, overhunting, tree population, tropical forest dynamics, extinction, spatial model

**Author for correspondence:**

T. Trevor Caughlin  
 e-mail: [trevorcaughlin@ufl.edu](mailto:trevorcaughlin@ufl.edu)

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2014.2095> or via <http://rsob.royalsocietypublishing.org>.

# Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages

T. Trevor Caughlin<sup>1,2</sup>, Jake M. Ferguson<sup>1</sup>, Jeremy W. Lichstein<sup>1</sup>, Pieter A. Zuidema<sup>3</sup>, Sarayudh Bunyavejchewin<sup>4</sup> and Douglas J. Levey<sup>1,5</sup>

<sup>1</sup>Department of Biology, University of Florida, PO Box 118525, Gainesville, FL 32611, USA

<sup>2</sup>Conservation Ecology Program, King Mongkut's University of Technology Thonburi, 49 Soi Tientalay 25, Bangkhuntien-Chaitalay Road, Thakham, Bangkhuntien, Bangkok 10150, Thailand

<sup>3</sup>Forest Ecology and Forest Management Group, Wageningen University and Research Centre, PO Box 47, 6700 AA Wageningen, The Netherlands

<sup>4</sup>Royal Thai Forest Department, Chatuchak, Bangkok 10900, Thailand

<sup>5</sup>Division of Environmental Biology, National Science Foundation, Arlington, VA 22230, USA

Overhunting in tropical forests reduces populations of vertebrate seed dispersers. If reduced seed dispersal has a negative impact on tree population viability, overhunting could lead to altered forest structure and dynamics, including decreased biodiversity. However, empirical data showing decreased animal-dispersed tree abundance in overhunted forests contradict demographic models which predict minimal sensitivity of tree population growth rate to early life stages. One resolution to this discrepancy is that seed dispersal determines spatial aggregation, which could have demographic consequences for all life stages. We tested the impact of dispersal loss on population viability of a tropical tree species, *Miliusa horsfieldii*, currently dispersed by an intact community of large mammals in a Thai forest. We evaluated the effect of spatial aggregation for all tree life stages, from seeds to adult trees, and constructed simulation models to compare population viability with and without animal-mediated seed dispersal. In simulated populations, disperser loss increased spatial aggregation by fourfold, leading to increased negative density dependence across the life cycle and a 10-fold increase in the probability of extinction. Given that the majority of tree species in tropical forests are animal-dispersed, overhunting will potentially result in forests that are fundamentally different from those existing now.

## 1. Introduction

Animal populations in tropical forests are threatened by overhunting, even in areas that are otherwise protected [1–3]. Large frugivores, including most primates and ungulates, are often the first animals to disappear [1,4]. If animal-mediated seed dispersal is important for maintaining viable populations of trees, overhunting may lead to tropical forest degradation, including loss of biodiversity and decreased biomass [5–7]. Comparisons between hunted and non-hunted sites generally reveal lower rates of seed dispersal and lower seedling abundance of animal-dispersed tree species in hunted sites [8–11]. The most comprehensive study to date tracked changes in a tree community as hunting increased over a 15-year period and found increased spatial aggregation and decreased sapling recruitment for animal-dispersed tree species, leading to an overall decline in sapling biodiversity [12]. While these empirical studies provide convincing evidence of short-term negative impacts of overhunting on tree populations, there is a discrepancy between these empirical results and the general finding of demographic studies

that in long-lived plants, population dynamics are minimally sensitive to changes in recruitment [13–15]. If the effects of seed disperser loss on tree vital rates are limited to early life stages, overhunting may result in only slight decreases in tree population growth rates [5]. This discrepancy between our understanding of tree population dynamics and empirical evidence for tree population declines after disperser loss is problematic as it does not allow us to forecast or project effects of overhunting on tree population viability.

One way that loss of seed dispersers could have long-term consequences for tree population dynamics is by changing the pattern of spatial aggregation for all subsequent life stages. Negative density dependence (NDD)—here defined as a reduction in growth and/or survival with increased conspecific density at spatial scales of 0–20 m—is a demographic mechanism for how increases in spatial aggregation could result in decreased population size. NDD is recognized as a widespread and pervasive force in regulating populations of tropical trees [16–19]. If increased spatial aggregation owing to loss of seed dispersal increases NDD throughout the tree life cycle, overhunting could lead to decreased tree population viability. On the other hand, if spatial aggregation has a negative effect only on early life stages or is advantageous for certain life stages but disadvantageous for others [20], seed dispersal may have only minimal effects on demography. Distinguishing between these possibilities requires quantifying NDD and its population-level consequences for multiple tree life stages.

While the importance of size and stage for structuring tropical tree populations has long been recognized [13,14,21], nearly all research on NDD in tropical forests has quantified effects on growth or survival for only one or two life stages. Most empirical research on NDD in tree species has focused on seeds [18] and seedlings [22], although several studies have also detected NDD for later life stages, including saplings [19,23] and adult trees [24]. Few studies have integrated effects of NDD across life stages [25,26], and no studies, to our knowledge, have directly quantified the effects of NDD across all tree life stages, from seeds to adults. Multiple reviews have recognized this knowledge gap and called for research to integrate effects of seed dispersal across the tree life cycle [6,27–29]. However, repeated calls to ‘close the seed dispersal loop’ have gone unanswered owing to the challenge of obtaining spatial data for multiple life stages and the complexity of spatially explicit population models [29].

Here we evaluate the threat of overhunting to tropical tree population viability, using spatial data to simulate consequences of seed dispersal across the tree life cycle. Our focal species, *Miliuma horsfieldii*, is a dominant component of the canopy at our study site, and has seeds dispersed by large mammals, including bears, civets and primates [30,31], which have been extirpated from many other forests in the region [1]. We quantified NDD using spatial data on more than 10 000 *Miliuma* individuals spanning all life stages, from seeds to reproductive adults. We then constructed a spatially explicit individual-based model (IBM) to simulate *Miliuma* population dynamics, allowing us to compare the probability of tree extinction between our study site with an intact disperser community and a scenario in which animal seed dispersers are hunted to extinction. Our study is unique in evaluating the importance of spatial aggregation throughout a tree species’ entire life cycle and demonstrates

that loss of seed dispersal can have unexpectedly large impacts on tree population viability.

## 2. Material and methods

### (a) Study site

The study site, the Huai Kha Khaeng Wildlife Sanctuary (HKK), is located in western Thailand and forms part of the largest intact forest complex in mainland Southeast Asia. HKK still contains viable populations of large mammalian seed dispersers, including gibbons, bears and elephants [32], although like all other sites in mainland Southeast Asia, some species (e.g. rhinoceroses) have been extirpated or have experienced severe declines [1]. Mean annual rainfall is approximately 1500 mm, with a five- to six-month dry season from November to April. Our study site is centred around a 50 ha Forest Dynamics Plot in which all woody stems greater than or equal to 1 cm diameter at breast height (DBH) have been tagged, mapped and measured every 5 years since 1994, according to Center for Tropical Forest Science standard protocols [33].

### (b) Study species

*Miliuma horsfieldii* (Annonaceae) is a canopy tree species that reaches heights of 35 m [34]. It is a dominant species in the 50 ha Forest Dynamics Plot, with the most stems greater than 10 cm DBH of any tree species and comprises 8.7% of tree basal area in the plot [33]. From June to July, *Miliuma* produces roughly spherical fruits approximately 20 mm in diameter, each containing one to five seeds with an average diameter of 8.13 mm [35]. Seeds are dispersed by large mammals, including gibbons, civets and bears [30,31]. Rates of secondary seed dispersal at our study site are negligible, and there is no seed bank; three months after dispersal, all seeds have either germinated or died [35]. *Miliuma* produces shade-tolerant seedlings that form a long-lived seedling bank in the understory [36].

### (c) Demographic data

We used spatially explicit data on *Miliuma* seed germination, and survival and growth of seedlings (less than 1 cm DBH) and saplings plus trees (greater than 1 cm DBH; hereafter ‘trees’). Survival and growth data on trees come from a 15-year dataset from the Forest Dynamics Plot in which 2049 *Miliuma* individuals were marked, measured and mapped to the nearest 0.1 m between 1994 and 2009. Survival and growth of seedlings were determined from 1500 tagged seedlings censused annually in 3 × 3 m plots from 2009 to 2011. Seedling growth was measured as the annual change in seedling height measured to the highest meristem (cm). Data on seed germination were collected using a seed addition experiment in 95 experimental plots along a 5 km transect adjacent to the Forest Dynamics Plot. In these plots, a total of 6500 marked seeds were added and monitored for survival until all seeds had either germinated or died [36]. We quantified conspecific tree neighbourhoods by mapping reproductive trees (DBH > 20 cm) within the neighbourhood of all *Miliuma* seeds, seedlings and trees. Conspecific seedling neighbourhoods were quantified by counting all conspecific seedlings in 1 × 1 m quadrats containing tagged seeds and seedlings. We estimated fecundity and seed dispersal parameters by combining data on seed production by sampled reproductive adults, germination probability and the spatial distribution of newly germinated seedlings relative to adults (see electronic supplementary material, text S1, and [36] for details).

### (d) Models

We modelled *Miliuma* population dynamics in three steps. First, we used empirical data and hierarchical Bayesian statistical

techniques to parametrize submodels for vital rates, including effects of NDD at all life stages. Second, we incorporated these submodels into an IBM to simulate population dynamics. Third, we used our IBM to conduct a population viability analysis (PVA) and compare extinction probability in simulated *Miliusa* populations with and without animal-mediated seed dispersal.

For each life stage (seeds, seedlings and trees), we used our field data to estimate parameters for submodels for vital rates including both NDD and size as predictor variables. There are five vital rate submodels: germination, seedling survival and growth, and tree survival and growth, each with separate parameters for size and NDD. We used similar functional forms for submodels for all life stages, including functions for individual size,  $F(\text{size})$ ; NDD,  $N(\text{neighbourhood})$  and conspecific seedling density  $S(\text{seedling density})$ . Survival was modelled as a binomial random variable, with probability of survival equal to

$$P(\text{survival}) = \text{logit}^{-1}[F(\text{size}) + N(\text{neighbourhood}) + S(\text{seedling density})]. \quad (2.1)$$

The distributions of growth rates for trees and seedlings were positively skewed, but with some negative values (e.g. due to trunk decay) and were thus modelled as skew-normal distributions with expectation

$$E(\text{growth}) = F(\text{size}) \times \exp[N(\text{neighbourhood}) + S(\text{seedling density})]. \quad (2.2)$$

We estimated model parameters using a Bayesian Markov chain Monte Carlo (MCMC) algorithm [37] run for 110 000 iterations with a burn-in period of 10 000 iterations and four chains. We used non-informative priors for all parameters. Convergence was assessed with the Gelman–Rubin diagnostic with a threshold of 1.1 [38]. We evaluated whether including NDD terms improved model fit based on posterior predictive loss [39]. Submodels included random effect terms to account for non-independence between census periods (for tree data) and plots (for seed and seedling data). For more details on statistical estimation of submodel parameters, see electronic supplementary material, text S1.

### (e) Negative density dependence in vital rates

For all life stages, the conspecific tree neighbourhood function— $N(\text{neighbourhood})$  developed by Uriarte *et al.* [23] for tropical forests—depended on the distance to each neighbour tree and the size of each neighbour tree relative to the size of the focal individual

$$N(\text{neighbourhood}) = \frac{\alpha}{\text{size}} \sum_{i=1}^n \frac{\text{DBHneighbour}_i}{\text{distance}_i^d}, \quad (2.3)$$

where size is the size of the focal individual (height for seedlings; DBH for trees),  $\text{DBHneighbour}_i$  is the DBH of the  $i$ th neighbour tree,  $\text{distance}_i$  is the distance from neighbour  $i$  to the focal individual, and  $\alpha$  and  $d$  are parameters estimated separately for each submodel (germination, seedling survival and growth, and tree survival and growth). Based on preliminary analyses, we selected the following distance thresholds for different life stages to identify neighbour trees: 10 m radius for seed germination, 20 m radius for seedling survival and growth, and 25 m radius for tree survival and growth.

For seed germination and seedling growth and survival, NDD effects also included a linear function of conspecific seedling density

$$S(\text{seedling density}) = \beta \times \text{seedling density}, \quad (2.4)$$

where  $\beta$  is a free parameter fit separately for seed germination and seedling growth and survival, and *seedling density* is the number of conspecific seedlings in  $1 \times 1$  m plots containing

the focal individual. We assumed that seedling density would have a negligible effect on trees and so did not include conspecific seedling density in submodels for tree survival and growth.

### (f) Size dependence in vital rates

For growth and survival of trees, we used the Hossfeld function for  $F(\text{size})$  (equation (2.5)), which allows growth and survival to initially increase and later decrease with increasing size, as commonly observed in tree populations [21,24]

$$F(\text{size}) = \frac{R \times G \times \text{DBH}^{R-1}}{(G + (\text{DBH}^R/P)^2)}, \quad (2.5)$$

where size is the DBH of the focal tree,  $G$  and  $P$  are parameters fit separately for growth and survival, and we set  $R = 2$  based on a previous study of six tropical tree species [21]. Preliminary analyses revealed high correlations between parameters  $R$  and  $P$ , which precluded fitting  $R$  as a free parameter.

For seedling survival and growth,  $F(\text{size})$  was a linear function with an intercept and a slope parameter multiplied by seedling height.

$$F(\text{size}) = \mu + \beta \times \text{height}. \quad (2.6)$$

For the seed germination model, we assumed seed germination was independent of seed or parent-tree size.

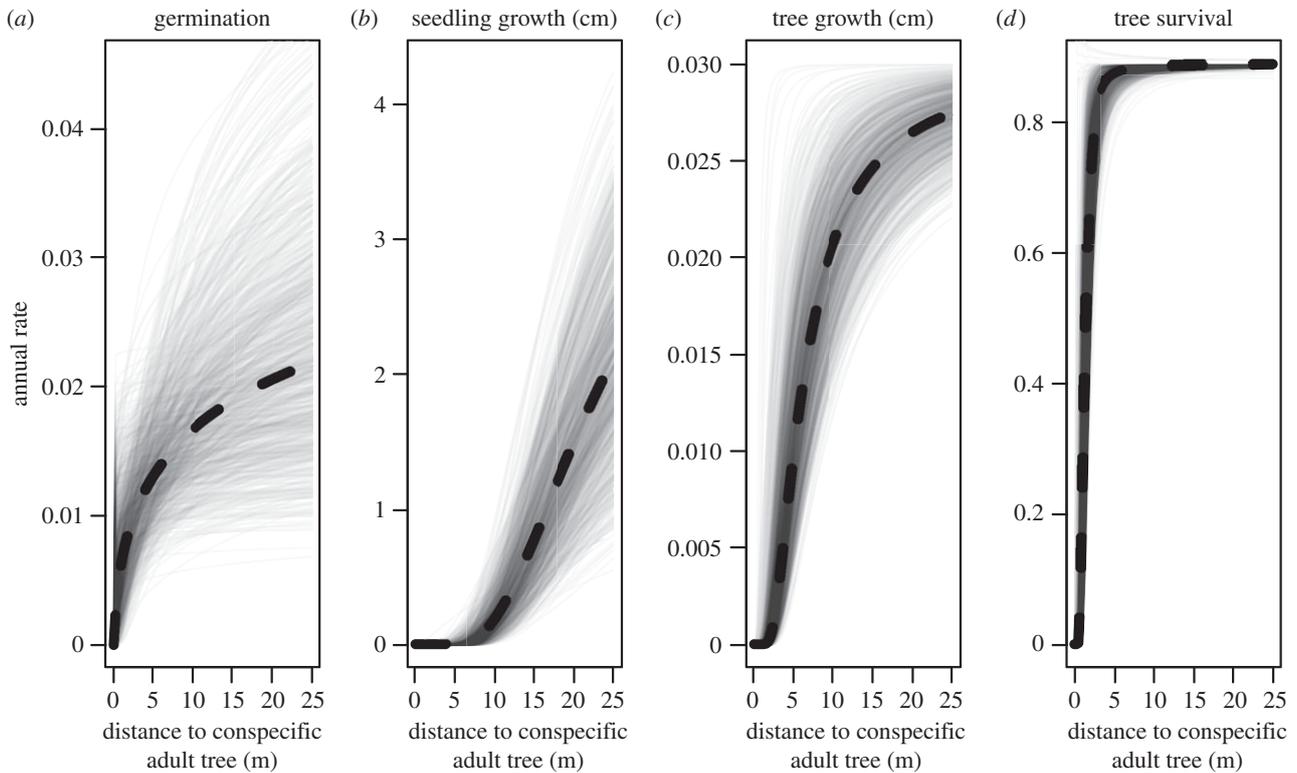
### (g) Seed dispersal

In addition to submodels for the effect of conspecific neighbourhood on survival and growth, our spatially explicit simulations also require information on seed dispersal. We modelled seed dispersal distances with a two-dimensional Student's  $t$  distribution with 3 d.f., which has been shown to provide a good fit to seed dispersal data from animal-dispersed trees in tropical forests [40,41]. To fit this dispersal kernel for the intact community of animal dispersers at our study site, we used data and methods described in [36] and electronic supplementary material, text S1.

### (h) Modelling population dynamics with an individual-based model

To understand the importance of seed dispersal for tree population dynamics, we used an IBM to explicitly track the position and size of trees over time. The IBM connects the submodels for vital rates into a single dynamical framework, enabling inference on consequences of seed dispersal and NDD for population viability. At annual time steps within a 4 ha area ( $200 \times 200$  m), the IBM stochastically determines survival and growth of existing trees and seedlings, production and dispersal of seeds and germination of seeds into seedlings. All parameters in the IBM were estimated using the submodels for vital rates (see previous section). Each run of the IBM was initialized with the size and location of trees in one of the eight 4 ha subplots from the 1994 census of the 50 ha plot. Owing to the finite size of the simulated area (4 ha), we assumed a toroidal surface with wrap-around edges. At each of the IBM's annual time steps, we recorded three different outputs: total population size as a measure of population density, basal area as a measure of biomass and spatial aggregation. We quantified spatial aggregation as the average density of neighbours in a 10 m radius of each tree ( $\Omega$ ) divided by mean population density in the 4 ha area (see [42,43];  $\Omega > 1$  indicates spatial aggregation,  $\Omega = 1$  indicates random spacing and  $\Omega < 1$  indicates regular spacing. For more details on the IBM model see electronic supplementary material, text S2).

We performed a global sensitivity analysis [44,45] to quantify the impact of parameter uncertainty on IBM predictions of total population size after 100 years. Global sensitivity analyses perturb



**Figure 1.** (a–d) Consistent negative effects of neighbourhood conspecific tree density on vital rates of *Miliusa* seeds, seedlings and trees greater than 1 cm DBH. Each panel shows effect of distance from a 90 cm DBH conspecific adult tree on individual growth and survival. For seedlings, we estimated effects for a 5 cm high seedling, the minimum size observed in the data, and for trees we estimated effects for a 1 cm DBH individual. Black lines represent median values for spatial functions. Each grey line is one of 1000 draws from the posterior distribution of parameters, collectively representing uncertainty.

all parameters simultaneously, and account for uncertainty in parameter estimation, nonlinear responses and interactions between parameters. Because all of the parameters were estimated with field data, we were able to use samples from the posterior distribution of each parameter as input to different runs of the IBM for the global sensitivity analysis. We decomposed variance in IBM output into main (additive) effects of each parameter, as well as total effects, which include interactions between parameters [46]. Effect sizes in the global sensitivity analysis increase with both the uncertainty in the posterior distribution and the sensitivity of the IBM outcome to changes in each parameter; i.e. effects are largest for parameters with both large posterior uncertainty and strong influence on population dynamics. For more details on the global sensitivity analysis see electronic supplementary material, text S3.

### (i) Population viability analysis

We quantified the consequences of animal-mediated seed dispersal loss for the viability of *Miliusa* populations by comparing predictions from the IBM described above (based on empirically predicted seed dispersal) to predictions from a modified IBM in which seeds were not dispersed beyond the projected crown area of reproductive *Miliusa* trees. The ‘no dispersal’ IBM assumes that if large frugivores go extinct, seeds will remain beneath parent-tree canopies, a reasonable assumption given the lack of secondary seed dispersal for *Miliusa* at HKK [35]. A pilot study suggested comparable rates of germination for dispersed seeds and undispersed seeds in intact fruits beneath parent trees, however, we note that for many tree species undispersed seeds are likely to have lower germination rates owing to inhibition from chemicals in fruit pulp [47]. For the PVA, we ran the IBM 1000 times for each scenario and compared the probability of extinction over 100 years between the no dispersal IBM and the natural seed dispersal IBM. We defined extinction as zero

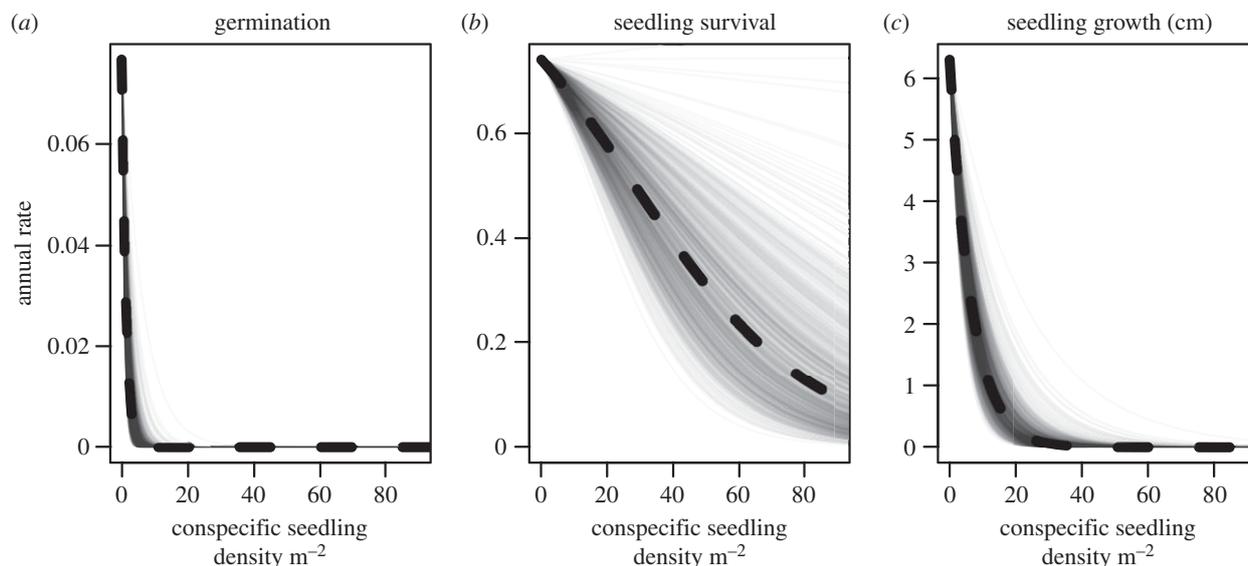
individuals in any size class. Note that we were interested in the relative difference in population viability between scenarios and not absolute values which may be influenced by stochastic disturbances that we did not quantify or simulate [48]. Simulations for both scenarios drew from posterior samples estimated from data; thus, our PVA can be considered robust to variability in data collection and parameter estimation [44].

## 3. Results

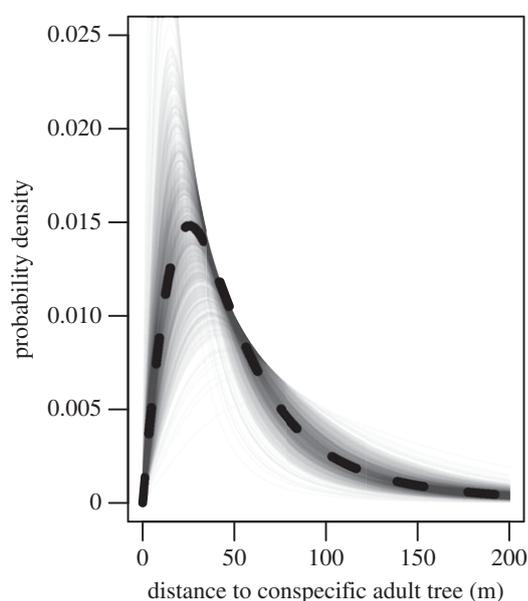
### (a) Demographic processes with an intact disperser community

We detected NDD for all sizes and life stages, although the strength and spatial scale of NDD effects varied greatly among life stages (figure 1). Survival and growth submodels revealed a significant negative effect of tree neighbourhood for all vital rates except seedling survival. Conspecific neighbour trees caused the largest decreases in germination and seedling growth, with suppressed growth and germination even at distances greater than 20 m from a large neighbour (figure 1). For seeds and seedlings, conspecific seedling density in  $1 \times 1$  m plots had strong effects on survival and growth, with germination predicted to be near zero at conspecific seedling densities greater than  $10 \text{ seedlings m}^{-2}$ , and seedling growth near zero at densities greater than  $20 \text{ seedlings m}^{-2}$  (figure 2).

In the presence of an intact animal disperser community, most estimated *Miliusa* seed dispersal distances were greater than tens of metres, so that most seeds escaped severe NDD effects near their parent tree. While the majority of seeds were predicted to be dispersed less than 50 m from neighbour



**Figure 2.** (a–c) Consistent negative effects of *Miliusa* conspecific seedling density on seed germination, seedling survival and growth. For seedlings, we estimated effects for a 5 cm high seedling, the minimum size observed in the data. Black and grey lines as in figure 1.



**Figure 3.** High probability of seed dispersal distances far beyond parent tree for *Miliusa* in a faunally-intact forest. Black and grey lines as in figure 1.

trees, there was an appreciable frequency of seed dispersal at long distances, with a 0.16 median probability (95% credible interval (CI), 0.02–0.31) of seed dispersal greater than 100 m from the parent tree (figure 3). A consequence of seed dispersal occurring at larger spatial scales than NDD is that recruitment is suppressed around large trees, but areas with few reproductive adults quickly fill with seedlings and saplings (figure 4).

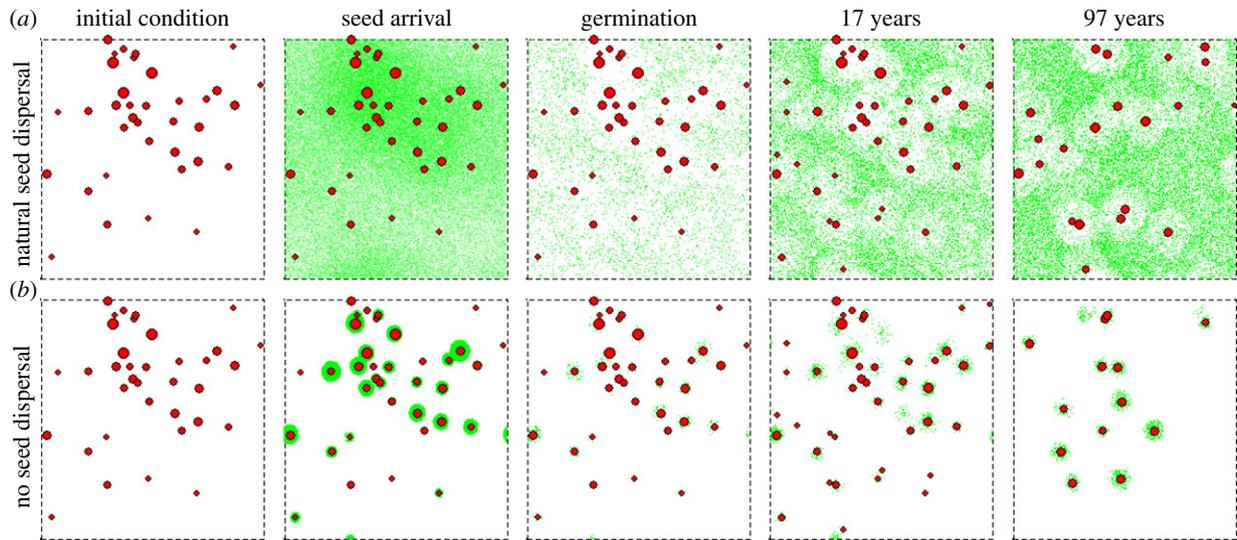
Our IBM revealed that total population size tended to increase rapidly in the first 40 years, and then stabilize at approximately 25 000 individuals (figure 5). Basal area generally declined over the 100-year period, while spatial aggregation ( $\Omega$ ) typically remained near one, indicating a lack of aggregation or overdispersion (electronic supplementary material, figure S1). However, parameter uncertainty generated wide variance in IBM dynamics across 10 000 replicate runs, with some runs exhibiting exponential-like

population growth, some overcompensatory dynamics and some extinction (figure 5).

The global sensitivity analysis revealed that despite the differences in strength of NDD between life stages (figure 1), NDD has impacts throughout the life cycle, in part due to the demographic importance of large individuals. Main effects from the global sensitivity analysis reveal that a single parameter for size-dependent tree survival ( $G$  in equation (2.5)) contributed the most variance (greater than 70%) in total population size. This result indicates that survival rates of large trees exerted a strong influence on predicted population dynamics. The main effects of NDD showed highest sensitivities for NDD on seedling growth, which contributed 15% of variance in total population size, and NDD on tree growth and survival, which contributed 7.8% and 5.2% of variance in total population size, respectively. However, the total sensitivities, which include interactions between parameters, suggest approximately equal importance of NDD for all life stages. Full results from the global sensitivity analysis are presented in electronic supplementary material, text S3.

## (b) Population viability with and without animal-mediated seed dispersal

Output from the IBM simulation with no animal-mediated seed dispersal exhibited fundamental differences from the IBM with animal-mediated seed dispersal (figure 6). Median  $\Omega$  increased nearly fourfold in simulations with no dispersal; as  $\Omega$  was calculated using data only on trees greater than 1 cm DBH, the large difference between dispersal scenarios indicates that the spatial distribution generated by seed dispersal has a long-lasting effect. Without dispersal, median total population size decreased by an order of magnitude, from 22 149 to 2840 individuals, while median basal area decreased by about half, from  $4.74 \times 10^{-5}$  to  $2.5 \times 10^{-5} \text{ m}^{-2}$ . Most importantly, without animal-mediated seed dispersal, the probability of extinction in a 100-year period increased by over 10-fold from 0.5% in the simulation with natural seed dispersal to 7% in the simulation with no animal-mediated seed dispersal (figure 5).

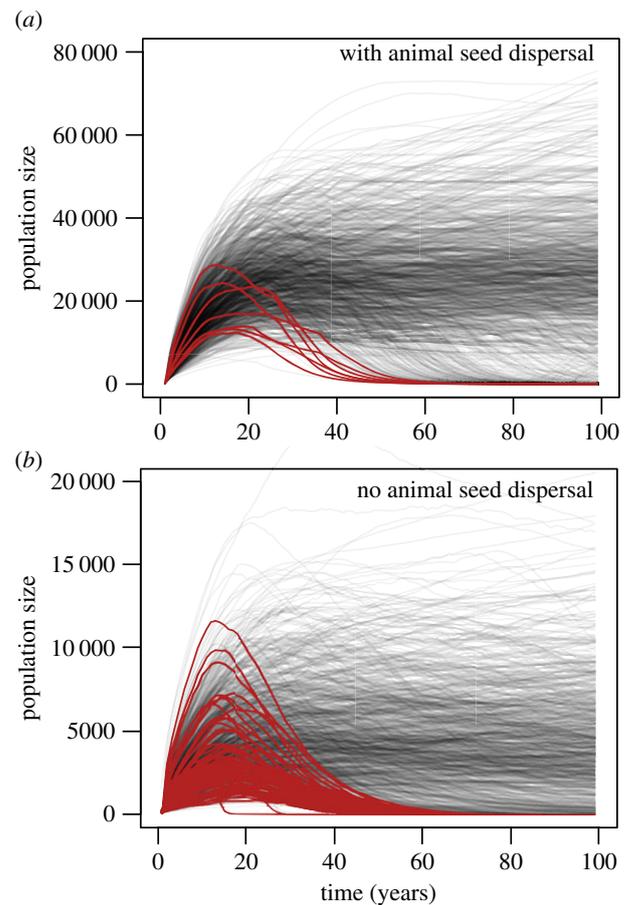


**Figure 4.** Loss of animal-mediated seed dispersal changes spatial distributions of *Miliusa* populations. This figure shows the location and size of seedlings and reproductive individuals (DBH > 20 cm) for representative runs of an IBM with current seed dispersal by animals (a) and without animal-mediated seed dispersal (b). Red circles represent reproductive trees, with circle size proportional to tree size. Green dots represent seedlings. The model begins with initial conditions determined by data from a 50 ha plot (initial conditions panel), then shows the pattern of seed arrival during the first year of the simulation (seed arrival panel), followed by the location of first-year seedlings immediately after germination (germination), and finally, adult trees and seedlings 17 and 97 years into the model runs.

## 4. Discussion

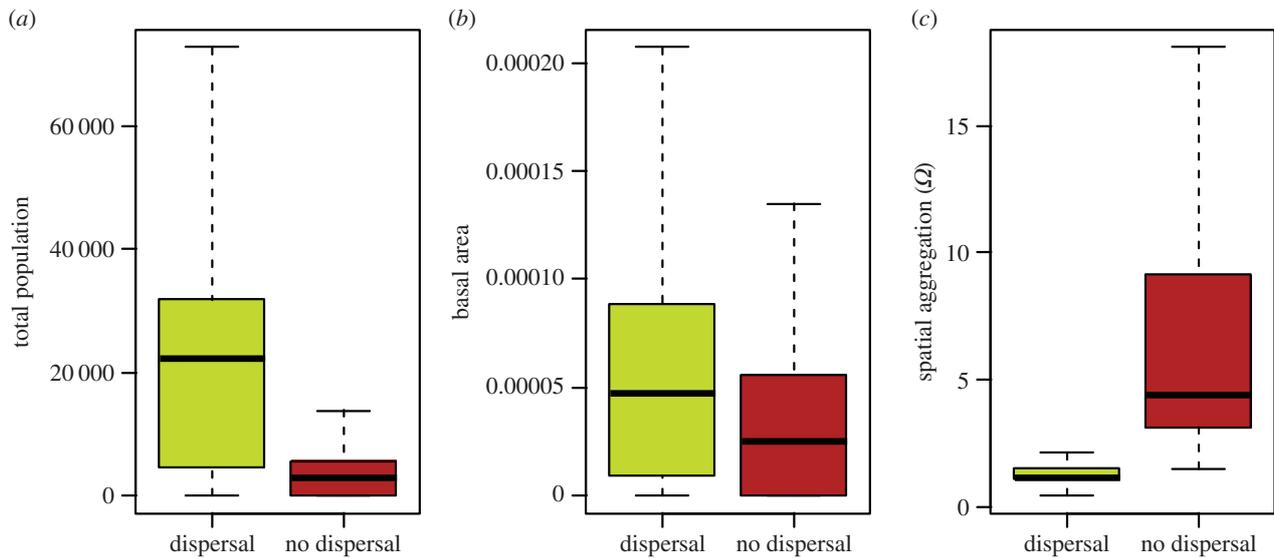
Local extinction of the large-bodied mammals that disperse *Miliusa* seeds is ongoing in Thai forests and reflects a global trend of tropical forest defaunation [1,5]. We demonstrate that loss of seed dispersal will have a large negative impact on population viability of this abundant canopy tree species. From a population perspective, the importance of any single seed is minimal: a *Miliusa* tree can live for hundreds of years and produce greater than 100 000 seeds, and the vast majority of these individuals will die before reaching reproductive maturity. However, the importance of seed dispersal for tree population dynamics is significant, because survival and growth of *all* life stages—seeds, seedlings and trees—are negatively impacted by conspecific neighbours. Without animal-mediated seed dispersal, conspecific spatial aggregation ( $\Omega$ ) increases by a factor of four (figure 4), and the probability of extinction increases by more than an order of magnitude. These results suggest that NDD throughout the life cycle is probably a demographic mechanism underlying observed declines in abundance of animal-dispersed tree species after extirpation of seed dispersers [12,49]. More generally, these results demonstrate the pervasive impact of seed dispersal for dynamics of all tree life stages, not just seeds and seedlings.

Our study is the first tree population dynamics study, to our knowledge, to quantify NDD across all life stages, enabling us to compare the effects of conspecific density across *Miliusa*'s life cycle. NDD effects were typically stronger for small individuals in early life stages, with the strongest measured effects of NDD for seed germination and seedling growth (figure 2). Many authors have focused on the effects of NDD on seedling mortality [22,50], which has an immediate and obvious effect on seedling abundance. Results from our global sensitivity analysis suggest that NDD effects on seedling growth and tree survival are also relevant for population dynamics. Both our statistical models and our sensitivity analysis highlight the importance of quantifying NDD across the entire tree life cycle.



**Figure 5.** Loss of animal-mediated seed dispersal decreases population viability of *Miliusa* by an order of magnitude. Results for each scenario are based on 1000 runs of an IBM, each simulated for 100 years. (a) Displays population trajectories from IBM runs with natural seed dispersal, while the (b) IBM runs with no animal-mediated seed dispersal. Red lines show populations that have gone extinct.

The spatial scale of seed dispersal relative to NDD is crucial for *Miliusa* population dynamics. For our study population in a faunally-intact forest, current seed dispersal



**Figure 6.** (a–c) Loss of animal-mediated seed dispersal decreases total population size, basal area and spatial aggregation of simulated *Miliusa* populations. Results are based on 1000 runs of an IBM, each simulated for 100 years. Boxes delineate first to third quartiles, the thick black line with boxes shows the median, and ‘whiskers’ represent minimum and maximum observations within 1.5 times of the upper and lower quartiles.

distances enable *Miliusa* seeds to escape neighbourhoods with high densities of conspecifics. Indeed, most seeds are estimated to disperse greater than 30 m from their parent tree (figure 1). The long range of animal-mediated seed dispersal estimated in our study is similar to estimates for mammal-dispersed tree species in other faunally-intact tropical forests [3,40,51], and far exceeds the spatial scale of NDD effects observed in this study and others [22,23,26]. Thus, the presence of an intact community of animal dispersers appears critical for seeds to escape the effects of NDD [3]. If loss of animal-mediated seed dispersal results in seed deposition near or beneath the parent crown, as seems likely for *Miliusa*, very few seeds would be likely to escape NDD, because the scale of NDD can be tens of metres greater than the crown radius of the parent tree [26]. Theoretical models for spatial plant population dynamics show that lower population size is a predictable consequence of decreasing the scale of seed dispersal relative to the scale of NDD [52]; our empirical study shows that this theoretical prediction is relevant to tropical forest conservation. Our results suggest that quantifying the growth and survival consequences of seed dispersal loss only for early life stages may greatly underestimate effects of overhunting. For example, a recent model for the impact of overhunting on an animal-dispersed tree species assumed seed dispersal affected vital rates of only seeds and seedlings and concluded that local extinction of large-bodied dispersers resulted in only slight decreases in tree population growth rate [5]. Similar to that study and others that employ size-structured models for tree population dynamics [14,21], we found high sensitivity of total population density to size-dependent survival, which highlights the importance of adult survival to population dynamics. Our spatially explicit model demonstrates that these previous sensitivity analyses of size-structured populations do not contradict empirical evidence for major impacts of overhunting on tree demography over decadal timescales, including declines in animal-dispersed tree abundance [12] and rapid evolutionary changes in seed size [49]. Our results indicate that the most appropriate way to measure the demographic importance of seed dispersal for

tree populations may be to quantify how spatial distribution affects multiple life stages.

Focusing on a single, data-rich species enabled us to include a high level of detail in our demographic models but also raises the question of how generalizable our results are to other tropical tree species. Many of the characteristics of *Miliusa* that lead to low population viability without animal-mediated seed dispersal are likely to be similar for other tree species. Community-wide studies that have quantified NDD in tropical forests have revealed strong NDD for most species at the seed stage [18], seedling stage [22] and for trees greater than 1 cm DBH [19,53]. Most tropical tree species (70–90%) are animal-dispersed [54], and seed dispersal distances of *Miliusa* in the faunally-intact Thai forest that we studied are on the same scale as many other tropical tree species [40,41,51]. A potential difference between *Miliusa* and some animal-dispersed tropical tree species is the lack of mammalian seed predation and secondary seed dispersal by rodents on *Miliusa* seeds, both of which may compensate for loss of large-bodied seed dispersers [55,56].

Our PVA shows that overhunting poses a serious threat to persistence of a common tree species, with an order of magnitude increase in the probability of extinction in the absence of animal seed dispersers. Overhunting of frugivorous animals is widespread throughout tropical regions [12,57], and many tropical tree species are animal-dispersed. Therefore, loss of animal-dispersed tree species, such as *Miliusa*, is likely to lead to major changes in tree community composition and forest dynamics. Implementation of policies to manage hunting, including regulating wildlife trade, enforcing existing laws and improving monitoring of protected areas will be necessary to maintain ecosystem integrity in tropical forests.

**Data accessibility.** Data on trees greater than 1 cm DBH: CTFS network <http://www.ctfs.si.edu/>. Data on seed and seedling demography: Dryad <http://dx.doi.org/10.5061/dryad.v82b7>.

**Acknowledgements.** The Huai Kha Khaeng Forest Dynamics Plot is part of the Center for Tropical Forest Science, a global network of large-scale demographic tree plots. We acknowledge the Royal Thai Forest Department for supporting and maintaining the project in

Huai Kha Khaeng Wildlife Sanctuary, Thailand. We thank Tommaso Savini, George Gale, Robert Dorazio, Emilio Bruna, Mart Vlam and Kaoru Kitajima for helpful comments on the manuscript. Research was conducted with the permission of the National Research Council of Thailand.

**Funding statement.** This research was funded by the National Science Foundation under grant no. 0801544 in the Quantitative Spatial Ecology, Evolution and Environment Program at the University of Florida, and a Graduate Research fellowship under grant no.

DGE-0802270. The Huai Kha Khaeng 50-ha plot project has been financially and administratively supported by many institutions and agencies. Direct financial support for the plot has been provided by the Royal Thai Forest Department and the National Parks Wildlife and Plant Conservation Department, the Arnold Arboretum of Harvard University (under NSF award no. DEB-0075334, and grants from USAID and the Rockefeller Foundation), the Smithsonian Tropical Research Institute and the National Institute for Environmental Studies, Japan.

## References

- Corlett RT. 2007 The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica* **39**, 292–303. (doi:10.1111/j.1744-7429.2007.00271.x)
- Harrison RD. 2011 Emptying the forest: hunting and the extirpation of wildlife from tropical nature reserves. *BioScience* **61**, 919–924. (doi:10.1525/bio.2011.61.11.11)
- Terborgh J. 2013 Using Janzen–Connell to predict the consequences of defaunation and other disturbances of tropical forests. *Biol. Conserv.* **163**, 7–12. (doi:10.1016/j.biocon.2013.01.015)
- Peres CA, Palacios E. 2007 Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* **39**, 304–315. (doi:10.1111/j.1744-7429.2007.00272.x)
- Brodie JF, Helmy OE, Brockelman WY, Maron JL. 2009 Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecol. Appl.* **19**, 854–863. (doi:10.1890/08-0955.1)
- Beckman NG, Rogers HS. 2013 Consequences of seed dispersal for plant recruitment in tropical forests: interactions within the seedscape. *Biotropica* **45**, 666–681. (doi:10.1111/btp.12071)
- Poulsen JR, Clark CJ, Palmer TM. 2013 Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biol. Conserv.* **163**, 122–130. (doi:10.1016/j.biocon.2013.03.021)
- Cordeiro NJ, Howe HF. 2001 Low recruitment of trees dispersed by animals in African forest fragments. *Conserv. Biol.* **15**, 1733–1741. (doi:10.1046/j.1523-1739.2001.99579.x)
- Nunez-Iturri G, Olsson O, Howe HF. 2008 Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru. *Biol. Conserv.* **141**, 1536–1546. (doi:10.1016/j.biocon.2008.03.020)
- Markl JS, Schleuning M, Forget PM, Jordano P, Lambert JE, Traveset A, Wright SJ, Böhning-Gaese K. 2012 Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conserv. Biol.* **26**, 1072–1081. (doi:10.1111/j.1523-1739.2012.01927.x)
- Effiom EO, Nuñez-Iturri G, Smith HG, Ottosson U, Olsson O. 2013 Bushmeat hunting changes regeneration of African rainforests. *Proc. R. Soc. B* **280**, 20130246. (doi:10.1098/rspb.2013.0246)
- Harrison RD, Tan S, Plotkin JB, Slik F, Detto M, Brenes T, Itoh A, Davies SJ. 2013 Consequences of defaunation for a tropical tree community. *Ecol. Lett.* **16**, 687–694. (doi:10.1111/ele.12102)
- Alvarez-Buylla ER, Garcia-Barrios R, Lara-Moreno C, Martinez-Ramos M. 1996 Demographic and genetic models in conservation biology: applications and perspectives for tropical rain forest tree species. *Annu. Rev. Ecol. Syst.* **27**, 387–421. (doi:10.1146/annurev.ecolsys.27.1.387)
- Franco M, Silvertown J. 2004 A comparative demography of plants based upon elasticities of vital rates. *Ecology* **85**, 531–538. (doi:10.1890/02-0651)
- Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C, Franco M. 2014 Functional traits explain variation in plant life history strategies. *Proc. Natl Acad. Sci. USA* **111**, 740–745. (doi:10.1073/pnas.1315179111)
- Janzen DH. 1970 Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528. (doi:10.1086/282687)
- Connell JH. 1971 On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dyn. Popul.* **298**, 312.
- Harms KE, Wright SJ, Calderón O, Hernández A, Herre EA. 2000 Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**, 493–495. (doi:10.1038/35006630)
- Peters HA. 2003 Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecol. Lett.* **6**, 757–765. (doi:10.1046/j.1461-0248.2003.00492.x)
- Schupp EW. 1995 Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J. Bot.* **82**, 399–409. (doi:10.2307/2445586)
- Zuidema PA, Jongejans E, Chien PD, Durning HJ, Schieving F. 2010 Integral projection models for trees: a new parameterization method and a validation of model output. *J. Ecol.* **98**, 345–355. (doi:10.1111/j.1365-2745.2009.01626.x)
- Comita LS, Hubbell SP. 2009 Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology* **90**, 328–334. (doi:10.1890/08-0451.1)
- Uriarte M, Canham CD, Thompson J, Zimmerman JK. 2004 A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecol. Monogr.* **74**, 591–614. (doi:10.1890/03-4031)
- Hurst JM, Allen RB, Coomes DA, Duncan RP. 2011 Size-specific tree mortality varies with neighbourhood crowding and disturbance in a montane nothofagus forest. *PLoS ONE* **6**, e26670. (doi:10.1371/journal.pone.0026670)
- 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)
- Swamy V, Terborgh J, Dexter KG, Best BD, Alvarez P, Cornejo F. 2011 Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest. *Ecol. Lett.* **14**, 195–201. (doi:10.1111/j.1461-0248.2010.01571.x)
- Wang BC, Smith TB. 2002 Closing the seed dispersal loop. *Trends Ecol. Evol.* **17**, 379–386. (doi:10.1016/S0169-5347(02)02541-7)
- Howe H, Miriti M. 2004 When seed dispersal matters. *BioScience* **54**, 651–660. (doi:10.1641/0006-3568(2004)054[0651:WSDM]2.0.CO;2)
- Muller-Landau HC. 2007 Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica* **39**, 372–384. (doi:10.1111/j.1744-7429.2007.00290.x)
- Kitamura S, Yumoto T, Poonswad P, Chuailua P, Plongmai K, Maruhashi T, Noma N. 2002 Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* **133**, 559–572. (doi:10.1007/s00442-002-1073-7)
- Ngoprasert D, Steinmetz R, Reed DH, Savini T, Gale GA. 2011 Influence of fruit on habitat selection of Asian bears in a tropical forest. *J. Wildl. Manag.* **75**, 588–595. (doi:10.1002/jwmg.83)
- Bunyavechewin S, LaFrankie JV, Ashton PS. 2000 *Population ecology of trees in Huai Kha Khaeng Wildlife Sanctuary, Thailand: data from the 50-ha forest dynamics plot*. Balboa, Panama: Smithsonian Tropical Research Institute.
- Bunyavechewin S, Baker PJ, LaFrankie JV, Ashton PS. 2004 Huai Kha Khaeng Forest dynamics plot. In *Tropical forest diversity and dynamism: findings from a large-scale plot network* (eds EC Losos, EG Leigh), pp. 482–491. Chicago, IL: University of Chicago Press.
- Baker PJ. 1997 Seedling establishment and growth across forest types in an evergreen/deciduous forest mosaic in western Thailand. *Nat. Hist. Bull. Siam Soc.* **45**, 17–41.

35. Wheeler J. 2009 Who dung it? The impact of seed dispersal by mammals on the fate of *Milusa lineata* (Annonaceae) seeds in a dry evergreen forest, Huai Kha Khaeng Wildlife Sanctuary, Thailand. BA thesis, New College of Florida, Sarasota, Florida.
36. Caughlin TT, Ferguson JM, Lichstein JW, Bunyavejchewin S, Levey DJ. 2013 The importance of long-distance seed dispersal for the demography and distribution of a canopy tree species. *Ecology* **95**, 952–962. (doi:10.1890/13-0580.1)
37. Plummer M. 2003 JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In *Proc. 3rd Int. workshop on distributed statistical computing* (eds K Hornik, F Leisch, A Zeileis), Vienna, Austria. See [www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf](http://www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf).
38. Gelman A, Rubin DB. 1992 Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 457–472. (doi:10.1214/ss/1177011136)
39. Gelfand AE, Ghosh SK. 1998 Model choice: a minimum posterior predictive loss approach. *Biometrika* **85**, 1–11. (doi:10.1093/biomet/85.1.1)
40. Clark JS, Silman M, Kern R, Macklin E, Lambers JH. 1999 Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* **80**, 1475–1494. (doi:10.1890/0012-9658(1999)080[1475:SDNAFP]2.0.CO;2)
41. Muller-Landau HC, Wright SJ, Calderón O, Condit R, Hubbell SP. 2008 Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* **96**, 653–667. (doi:10.1111/j.1365-2745.2008.01399.x)
42. Condit R *et al.* 2000 Spatial patterns in the distribution of tropical tree species. *Science* **288**, 1414–1418. (doi:10.1126/science.288.5470.1414)
43. Flügge AJ, Olhede SC, Murrell DJ. 2012 The memory of spatial patterns: changes in local abundance and aggregation in a tropical forest. *Ecology* **93**, 1540–1549. (doi:10.1890/11-1004.1)
44. Ellner SP, Fieberg J. 2003 Using PVA for management despite uncertainty: effects of habitat, hatcheries, and harvest on salmon. *Ecology* **84**, 1359–1369. (doi:10.1890/0012-9658(2003)084[1359:UPFMDU]2.0.CO;2)
45. Fieberg J, Jenkins KJ. 2005 Assessing uncertainty in ecological systems using global sensitivity analyses: a case example of simulated wolf reintroduction effects on elk. *Ecol. Model.* **187**, 259–280. (doi:10.1016/j.ecolmodel.2005.01.042)
46. Saltelli A, Ratto M, Andres T, Campolongo F, Cariboni J, Gatelli D, Saisana M, Tarantola S. 2008 *Global sensitivity analysis: the primer*. New York, NY: Wiley-Interscience.
47. Robertson AW, Trass A, Ladley JJ, Kelly D. 2006 Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Funct. Ecol.* **20**, 58–66. (doi:10.1111/j.1365-2435.2005.01057.x)
48. Morris WF, Doak DF. 2002 *Quantitative conservation biology: theory and practice of population viability analysis*. Sunderland, MA: Sinauer Associates.
49. Galetti M *et al.* 2013 Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* **340**, 1086–1090. (doi:10.1126/science.1233774)
50. Poulsen JR, Clark CJ, Bolker BM. 2012 Experimental manipulation of seed shadows of an Afrotropical tree determines drivers of recruitment. *Ecology* **93**, 500–510. (doi:10.1890/10-2430.1)
51. Clark CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT. 2005 Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology* **86**, 2684–2694. (doi:10.1890/04-1325)
52. Law R, Dieckmann U. 2000 Moment approximations of individual-based models. In *The geometry of ecological interactions: simplifying spatial complexity* (eds U Dieckmann, R Law, JAJ Metz), pp. 252–270. Cambridge, UK: Cambridge University Press. (doi:10.1017/CBO9780511525537.017)
53. Stoll P, Newbery DM. 2005 Evidence of species-specific neighborhood effects in the Dipterocarpaceae of a Bornean rain forest. *Ecology* **86**, 3048–3062. (doi:10.1890/04-1540)
54. Howe HF, Smallwood J. 1982 Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* **13**, 201–228. (doi:10.1146/annurev.es.13.110182.001221)
55. Wright SJ, Zeballos H, Dominguez I, Gallardo MM, Moreno MC, Ibáñez R. 2000 Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conserv. Biol.* **14**, 227–239. (doi:10.1046/j.1523-1739.2000.98333.x)
56. Kurten EL. 2013 Cascading effects of contemporaneous defaunation on tropical forest communities. *Biol. Conserv.* **163**, 22–32. (doi:10.1016/j.biocon.2013.04.025)
57. Wilkie DS, Bennett EL, Peres CA, Cunningham AA. 2011 The empty forest revisited. *Ann. NY. Acad. Sci.* **1223**, 120–128. (doi:10.1111/j.1749-6632.2010.05908.x)