

The importance of long-distance seed dispersal for the demography and distribution of a canopy tree species

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Abstract. Long-distance seed dispersal (LDD) is considered a crucial determinant of tree distributions, but its effects depend on demographic processes that enable seeds to establish into adults and that remain poorly understood at large spatial scales. We estimated rates of seed arrival, germination, and survival and growth for a canopy tree species (*Milusa horsfieldii*), in a landscape ranging from evergreen forest, where the species' abundance is high, to deciduous forest, where it is extremely low. We then used an individual-based model (IBM) to predict sapling establishment and to compare the relative importance of seed arrival and establishment in explaining the observed distribution of seedlings. Individuals in deciduous forest, far from the source population, experienced multiple benefits (e.g., increased germination rate and seedling survival and growth) from being in a habitat where conspecifics were almost absent. The net effect of these spatial differences in demographic processes was significantly higher estimated sapling establishment probabilities for seeds dispersed long distances into deciduous forest. Despite the high rate of establishment in this habitat, *Milusa* is rare in the deciduous forest because the arrival of seeds at long distances from the source population is extremely low. Across the entire landscape, the spatial pattern of seed arrival is much more important than the spatial pattern of establishment for explaining observed seedling distributions. By using dynamic models to link demographic data to spatial patterns, we show that LDD plays a pivotal role in the distribution of this tree in its native habitat.

Key words: hierarchical Bayesian model; individual-based model; long-distance dispersal; sapling establishment; seasonally dry forest; seed addition experiment; seed limitation; Thailand; tree demography.

INTRODUCTION

Adult recruitment from seeds dispersed long distances can have major consequences on plant population and community dynamics. For example, historical rates of long-distance seed dispersal (LDD) may explain the current distribution and diversity of many tree species (Svenning and Skov 2007, Lesser and Jackson 2013). Because LDD can enable range expansion of invasive species (Caughlin et al. 2012), plant migration in response to climate change (Corlett and Westcott 2013), and species persistence in fragmented landscapes (Uriarte et al. 2011), understanding LDD is also relevant for conservation and management (Trakhtenbrot et al. 2005). Recent advances in quantifying seed dispersal have revealed that LDD on the scale of kilometers may be relatively common (Nathan 2006). However, any effects of LDD on plant distributions depend on both the establishment of long-distance dispersed seeds into

adults, a process spanning many years, and transitions between multiple life stages for long-lived plants.

While paleoecological data, theoretical models, and data from invasive plant range expansion demonstrate the consequences of successful LDD events, there are also likely to be many cases in which LDD fails to result in established adults. LDD, which we define as dispersal beyond the spatial scale of the local patch (sensu Muller-Landau et al. 2003), could have high costs for establishment if seeds are dispersed out of favorable habitats and into unfavorable ones (Snyder and Chesson 2003, Kremer et al. 2012). Lower survival and growth for seeds dispersed into habitats with few conspecifics has been observed in forest and savannah (Hoffmann et al. 2004), landward and seaward habitats in sand dunes (Keddy 1982), and forest habitats in different successional states (Losos 1995). On the other hand, LDD may also result in benefits for establishment, if movement beyond the local patch allows seeds to escape high resource competition (Amarasekare 2003) or specialized pests (Fragoso et al. 2003, Muller-Landau et al. 2003). Evaluating the costs and benefits of LDD for seedling establishment probabilities has been identi-

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fied as an important, largely unresolved question in plant ecology (Trakhtenbrot et al. 2005).

Connecting the fate of LDD seeds to the distribution and abundance of plants requires estimating the degree to which abundance in a particular site is limited by rates of seed arrival vs. establishment (Muller-Landau et al. 2002). If low seed arrival limits adult abundance, the site is considered seed limited, remaining unoccupied due to lack of seed arrival rather than competition or suitable habitat (Clark et al. 2007). On the other hand, if survival and growth after seed arrival limit adult abundance, the site is considered establishment limited. Seed limitation is typically estimated from seed addition experiments (Munzbergova et al. 2006, Clark et al. 2007), or by comparing spatial patterns of natural seed arrival to spatial patterns of plant abundance, with the degree of positive correlation indicating the degree of seed limitation (Muller-Landau et al. 2002). Both of these methods are logistically challenging at spatial scales relevant to LDD. Seed addition experiments at large spatial scales require collecting and placing huge amounts of seed, and measuring natural rates of seed arrival at long distances from source populations is hindered by the rarity of LDD events (Clark et al. 1998). Consequently, few studies have quantified the relative importance of seed and establishment limitation at varying distances from a source population, the essential comparison underlying the potential for LDD to impact plant distributions (Diez 2007, Moore et al. 2011).

Patchy distributions of a given species could be a result of either seed or establishment limitation (Moore et al. 2011). This distinction is important for ecological theory because species coexistence in heterogeneous environments depends on the scale of dispersal relative to the scale of spatial variation in establishment (Snyder and Chesson 2003). Understanding the causes of patchiness also relates to biodiversity conservation in heterogeneous landscapes, such as managing woody encroachment into savannah (Hoffmann et al. 2012). If LDD seeds are able to establish into adults outside the source patch in these landscapes, chance LDD events and local extinction could result in stochastic shifts in tree distributions over time. One example of a tree population in a heterogeneous landscape is *Milusa horsfieldii* (Annonaceae), a canopy tree species, which, at our study site in Thailand, is abundant in evergreen forest and rare in deciduous forest (Baker 1997). This distribution could be due to spatially heterogeneous seed arrival, with low rates of LDD leading to seed limitation in the deciduous forest, or to spatially heterogeneous establishment, with low survival and growth in deciduous forest restricting recruitment to evergreen forest.

We quantified the importance of LDD in the current distribution of *Milusa* by using a unique, large-scale data set on demography to estimate seed and establishment limitation at varying distances from a source population of trees in evergreen forest. Because we estimated both seed arrival and establishment of seeds

into saplings, we were able to use an individual-based model (IBM) to integrate our spatial data on demography and dispersal into a dynamic framework. The IBM allowed us to determine the relative importance of seed and establishment limitation for the observed distribution of plants over multiple time scales, from 3 months to 15 years. Our study addresses three questions: (1) How does the probability of sapling establishment differ between seeds dispersed long vs. short distances? (2) How does seed arrival vary with distance from the source population? and (3) Is the current distribution of seedlings better predicted by observed rates of seed arrival or establishment? Our novel approach provides new insight into the demographic mechanisms that underlie the importance of LDD for tree distributions, enabling us to fill the knowledge gap between long-distance seed arrival and the abundance of established plants.

MATERIALS AND METHODS

Study site

The study site, the Huai Kha Khaeng Wildlife Sanctuary (HKK) in western Thailand, is part of the largest intact forest complex in mainland Southeast Asia, and it still contains viable populations of large mammalian seed dispersers (Bunyavejchewin et al. 2004). The landscape is a mosaic of three forest types: seasonally dry evergreen forest, mixed deciduous forest, and dry deciduous forest. These forest types are characterized by differences in canopy height and openness, leaf phenology, understory vegetation, and tree diversity (Baker 1997). Mosaics of these forest types are characteristic of many other sites in mainland Southeast Asia (Blanc et al. 2000). Previous research at the study site, including tree ring analysis, has suggested that the current patch of evergreen forest at the study site was established after a catastrophic disturbance event 250 years ago, and that periodic disturbance in general may be responsible for the patchy distribution of forest types (Baker et al. 2005). Ground fires, which occur roughly every 10–15 years and cause the mortality of small seedlings and saplings, likely represent one important periodic disturbance.

Study species

Milusa horsfieldii is one of the dominant tree species in seasonally dry evergreen forest at HKK (Bunyavejchewin et al. 2004), reaching heights of 35 m (Baker 1997), a maximum canopy diameter of 12–13 m, and fruiting from June to July. At the study site, *Milusa* is briefly deciduous during the dry season (Williams et al. 2008). Each roughly spherical, bright red fruit is ~20 mm in diameter and contains 1–5 seeds (average, 3.8) with an average diameter of 8.13 mm. The fruits do not have a noticeable odor. Seeds are dispersed by mammals, including civets (see Plate 1), macaques, and bears, with daily movements up to several kilometers and an occurrence in both evergreen and deciduous

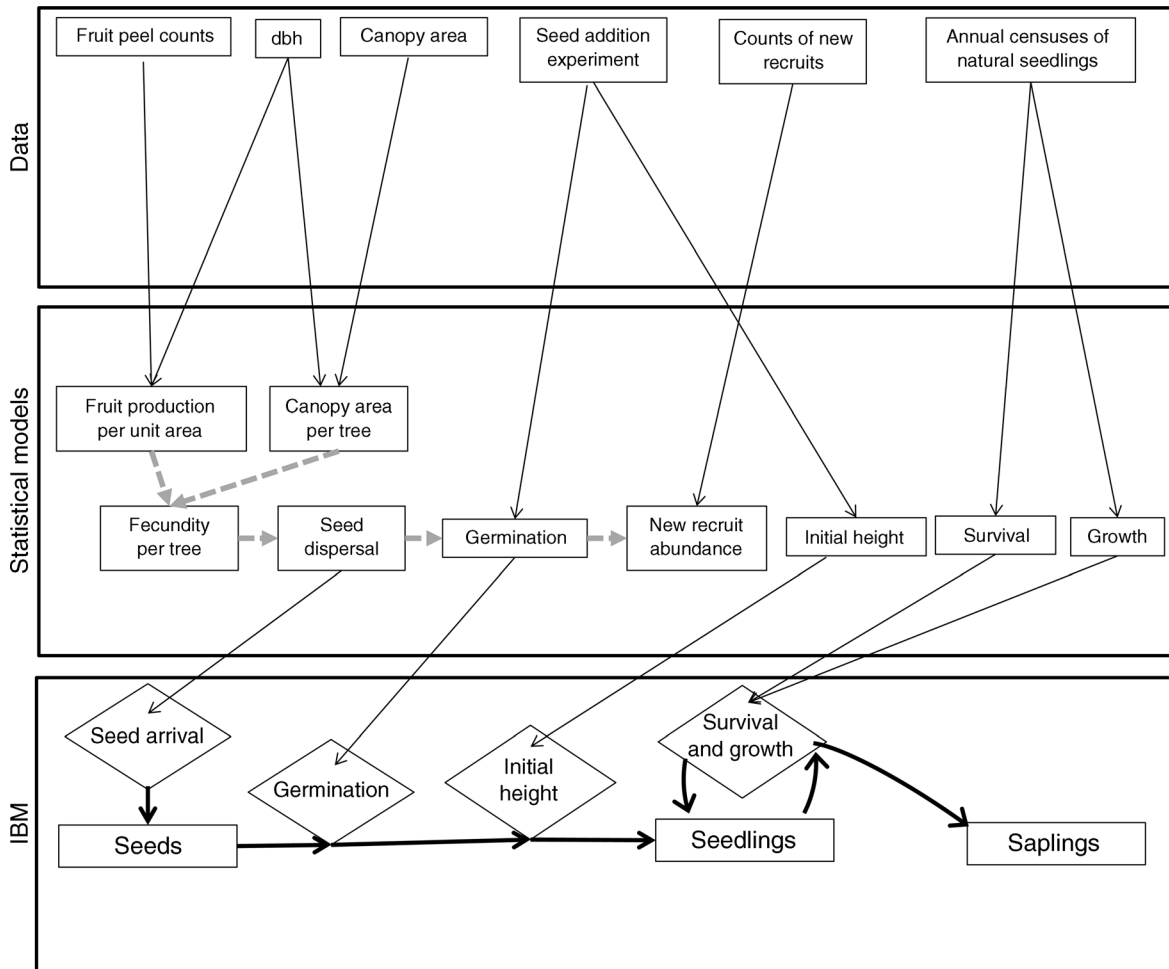


FIG. 1. Overview of study design, showing data and statistical models used as input to the individual-based model (IBM) that simulated seedling distributions. Thin black arrows between the three large rectangles represent connections between the data, statistical models, and IBM. Gray dotted arrows in the statistics rectangle represent connections between the statistical models used to estimate seed dispersal. The bottom rectangle shows the processes simulated by the IBM resulting in counts of seeds, seedlings, and saplings. The abbreviation dbh stands for diameter at breast height (1.3 m).

forests (Rabinowitz 1991, Kitamura et al. 2002, Ngo-prasert et al. 2011). While LDD can be operationally defined in terms of disperser movements (Trakhtenbrot et al. 2005), the gut passage times, home ranges, and habitat preferences of large, seed-dispersing mammals at HKK remain largely unknown. Therefore, we define LDD relative to the current spatial distribution of *Milusa* trees as seed dispersal beyond the scale of the local patches of evergreen forest at our study site, which occur on the scale of $\sim 1\text{--}3$ km. For further details on the study site and species, see Appendix A.

Study design

Our study consisted of three steps (Fig. 1). First, we collected demographic data on seeds and seedlings across a gradient from evergreen to deciduous forest. These data were collected in 93 24×24 m plots, randomly located along a 5-km transect (Fig. 2). We

then used these demographic data to parameterize statistical models for seed arrival and establishment. Finally, we used the statistical models as input for an IBM that combined information on seed arrival, germination, and survival and growth to dynamically simulate seedling distributions over multiyear periods. This study design allowed us to estimate seed and establishment limitation at varying distances from a source population of *Milusa* in seasonally dry evergreen forest.

Sapling establishment

We consider establishment to be the sequence of demographic transitions beginning with seed germination and ending at the sapling stage, with saplings defined as trees >1.6 m tall, a size threshold for surviving ground fires at our study site (Baker et al. 2008). To address Question 1, we quantified these

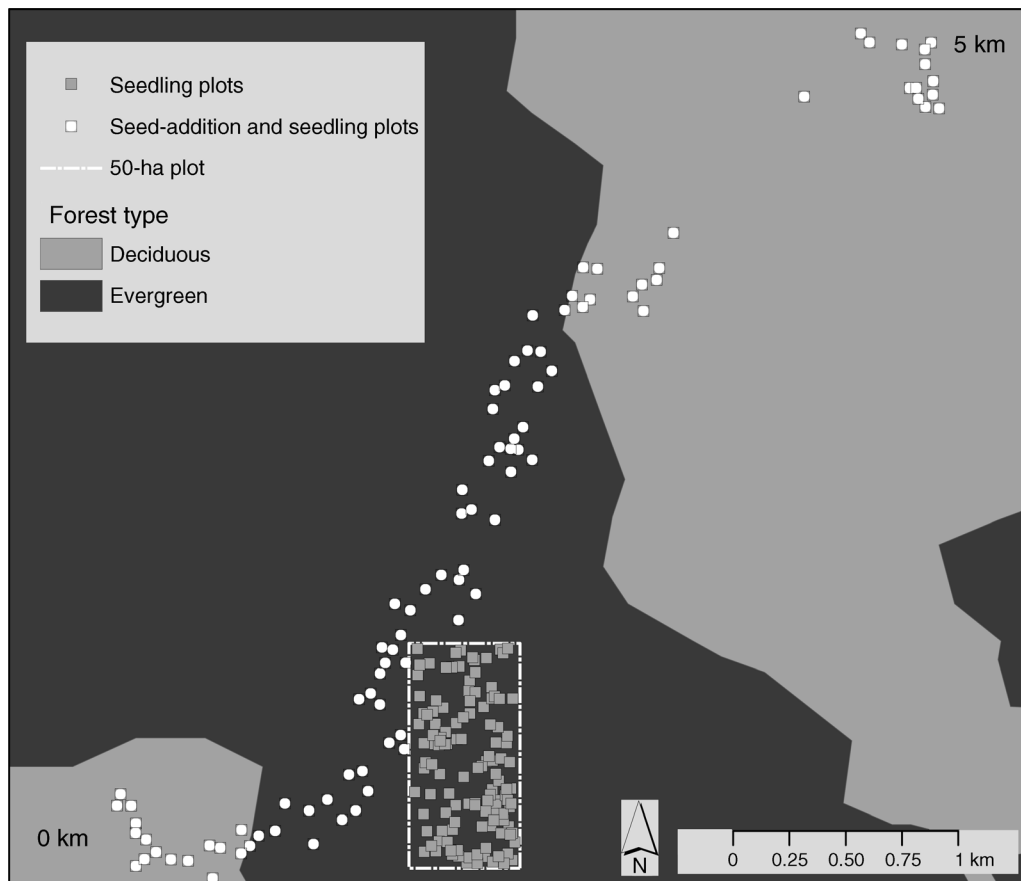


FIG. 2. Map of study region, including the transect with the 93 demographic plots (small white squares in figure), and the additional 124 plots located within the 50-ha forest dynamics plot that were used for natural seedling demography and new recruit abundance data (small gray squares). The labels 0 km and 5 km indicate the beginning and end of the transect, and correspond to the x-axis values in Fig. 3.

demographic transitions across the 5-km transect and then estimated how the probability of sapling establishment differs between seeds dispersed long vs. short distances. A challenge for quantifying seedling demography in regions where adult trees are absent is that seedlings are extremely rare. Therefore, in June 2009 we experimentally added the same number of seeds (65), in piles of 5, 15, and 45, to each of the 93 plots. Rates of secondary dispersal for *Miliusa* are negligible, and neither gut passage nor dung presence significantly affects germination rate (Wheeler 2009). A pilot study in which the fate of individual seeds was tracked over time revealed that three months after seed dispersal in June to July, all seeds had either died or become seedlings (Appendix A). Thus, we checked experimentally placed seeds for germination three months after seed placement, and we refer to three-month-old seedlings, both experimental and natural, as “new recruits.” Because seedlings generated from the seed-addition experiment represented only small-sized individuals, we also monitored survival and growth of naturally occurring seedlings using an adaptive sampling scheme, such that

the area sampled increased in plots where seedlings were rare. This scheme enabled us to census naturally occurring seedlings across a range of sizes, even in the deciduous forest where natural abundance was very low. We measured these naturally occurring seedlings annually from 2009 to 2011, yielding $n = 1443$ seedlings for survival data and $n = 819$ seedlings for growth data.

We used a hierarchical Bayesian approach to model germination, new recruit height, and seedling survival and growth as a function of environmental covariates measured within each plot, including presence of grass, light availability, and conspecific density. The purpose of using these environmental covariates was to improve the predictive power of our statistical models for tree vital rates. Environmental covariates were measured for each 1×1 m quadrat containing a seedling. Light was measured during the wet season using hemispherical photographs, grass was classified as present or absent, and conspecific density was quantified with two separate terms: the density of conspecific seedlings in quadrats, and the sum of the diameter at breast height (dbh, 1.3 m) values of all conspecific trees within 10 m of each

seedling (details in Appendix A). These variables were selected because they strongly influence seedling demography in similar systems (Hoffmann et al. 2004, Comita et al. 2010, Chanthorn et al. 2013). We included plot as a random effect in all models, representing unaccounted for spatial variation. For seedling survival and growth, we also included seedling height as a continuous predictor variable. Germination and survival were modeled as binomial random variables, and new recruit height and growth were modeled as normal random variables. A full description of these statistical models is provided in Appendix B.

While the statistical models provide insight into the spatial variation of each particular vital rate, we were interested in the multi-year process of sapling establishment, which combines all vital rates from seed germination to seedling growth into saplings. Consequently, we used an IBM to combine the statistical models for germination, new recruit height, and seedling survival and growth into a single dynamic model to predict sapling establishment. The IBM tracks size and survival of individual seedlings in 737 of the 1×1 m quadrats at the center of the 93 plots across the 5-km transect. Each quadrat is matched with environmental covariates (grass, light, conspecific adult density, and plot-level random effects) measured in 2011. Thus, sapling establishment per quadrat differs due to environmental covariates specific to a particular location along the transect. With the exception of conspecific seedling density, environmental covariates were assumed to remain constant throughout the IBM simulations. During each annual time step, the IBM simulates seed germination, assignment of new recruit height to new recruits (three-month-old seedlings), first-year survival of new recruits, and survival and growth of existing seedlings (those seedlings surviving from the previous year; Fig. 1). All parameters used in the IBM come from the demographic models and were estimated with field data. To propagate parameter uncertainty, we randomly drew 1000 parameter sets from the joint posterior distribution of parameters. To account for demographic stochasticity (Clark 2005, Evans et al. 2010), we ran the IBM 100 times for each of the 1000 parameter sets (details in Appendix B). We answered Question 1 by adding a single seed to each quadrat, running IBM simulations for 15 years, and at the end of this time period recording whether each seed had produced a sapling that reached the height threshold for fire resistance (1.6 m).

Seed arrival

Our second objective (Question 2) was to estimate plot-specific rates of seed arrival along the transect. Estimates of seed arrival are necessary to understand and model the dynamics of seedling distributions (Question 3). However, direct estimates of seed dispersal are impractical at long distances (>1 km) from source trees, due to the low density of seeds dispersed at such

distances. Indirect estimates based on counts of established seedlings are also problematic because different combinations of establishment probability and seed rain can result in similar seedling abundance (Caughlin et al. 2012). We addressed this problem by using direct observations of germination probability and fruit production, in addition to counts of naturally established recruits, to simultaneously estimate parameters describing seedling establishment, fecundity, and seed dispersal using a hierarchical Bayesian modeling approach. The combined model predicts the abundance of naturally established recruits in 1723 (1×1 m) quadrats, with 737 quadrats located within the 93 plots along the 5-km transect, and an additional 986 quadrats located within 124 plots in an adjacent 50-ha forest dynamics plot (Fig. 2; Appendix B). The abundance of newly recruited seedlings (three months after seed arrival) was modeled as a Poisson-distributed random variable with a mean ($\lambda_{k,j}^{\text{re}}$) equal to a germination probability ($\theta_{k,j}^{\text{ger}}$) multiplied by seed arrival ($\lambda_{k,j}^{\text{seeds}}$), where the index k represents quadrats, and the index j represents plots

$$\lambda_{k,j}^{\text{re}} = \theta_{k,j}^{\text{ger}} \times \lambda_{k,j}^{\text{seeds}}. \quad (1)$$

In Eq. 1, $\theta_{k,j}^{\text{ger}}$ is directly estimated from the seed addition experiment data. The seed arrival term ($\lambda_{k,j}^{\text{seeds}}$) includes seed arrival from nearby adult trees in a 20-m neighborhood ($\text{Nhoo}_{k,j}$) and from seed sources outside of the local neighborhood (Bath_j), along with a plot-level random effect ($\epsilon_j^{\text{seeds}}$)

$$\lambda_{k,j}^{\text{seeds}} = (\text{Nhoo}_{k,j} + \text{Bath}_j) \times \epsilon_j^{\text{seeds}}. \quad (2)$$

The Nhoo term accounts for seed production of neighboring trees, which was parameterized as a sigmoid function of dbh using data on seed production of fruiting trees (Appendix B: Fig. B2). The second term in Eq. 2, Bath_j , represents dispersal from seed sources outside the 20-m neighborhood, including landscape-scale seed availability. The Bath_j term was a function of linear distance along the transect, from the southwestern most point on the transect to the northeastern most point on the transect. Finally, the sum of the Bath and Nhoo terms was multiplied by a random effect, $\epsilon_j^{\text{seeds}}$, distributed as a lognormal random variable with a mean of 0 on the log scale. This random effect was able to be estimated because there are eight seed-addition quadrats per plot, and it was included to represent unexplained plot-scale variation in seed arrival (e.g., due to plot location relative to movement paths of seed-dispersing animals). The spatial scale of each of the data sources for the seed arrival model is displayed in Appendix B: Fig. B2. We used a Markov chain Monte Carlo algorithm in JAGS v. 3.2.0 (Plummer 2003) to generate samples from the joint posterior distribution of the seed arrival model (Eq. 1). Posterior samples for seed arrival to each plot (λ_j^{seeds}), which propagate uncertainty in

seedling establishment and fruit production, were one of the key inputs to the IBM experiments described below that were designed to quantify the relative effects of establishment probability and seed arrival on seedling distributions (details in Appendix B).

Quantifying seed and establishment limitation

To determine the relative importance of seed arrival and establishment in explaining the observed distribution of seedlings (Question 3), we combined the statistical models of establishment and seed arrival in the IBM. These IBM runs included the same processes for establishment used in the IBM runs focused on sapling establishment. However, in contrast to the IBM runs used to estimate sapling establishment, the second set of IBM runs described here used the statistical model for seed arrival to simulate seed arrival in each quadrat at each time step. Predicted distributions of seedlings generated in these IBM runs reflect spatial variation in seed arrival and establishment, parameter uncertainty, and conspecific density (which is a dynamic outcome of the IBM).

To test the relative importance of seed arrival and establishment for explaining the observed distribution of seedlings, we designed a simulation experiment with three treatments: (1) a full treatment with quadrat-specific establishment and seed arrival, (2) a homogeneous establishment treatment in which seed arrival was quadrat specific, but establishment (including survival, growth, germination, and new recruit height) was averaged across all quadrats, and (3) a homogeneous seed arrival treatment, in which establishment was quadrat specific, but each quadrat received the average number of seeds per quadrat. If differences in seed arrival, and hence seed limitation, are most important for determining observed seedling distributions, we would expect the treatment with variable seed arrival to have a better fit to the observed data than would the model with variable establishment but homogeneous seed arrival. In contrast, if the observed pattern of seedling distribution is better explained by differences in establishment, we would expect the treatment with variable establishment to perform better than would the model with variable seed arrival but homogeneous establishment. We compared output from the simulation experiment to observed abundance of both new recruits and older seedlings across a range of seedling sizes. For comparison with the distribution of new recruits, we ran the IBM for a single time step, including only seed arrival and germination. For comparison with the distribution of older seedlings, we initialized the IBM with zero seedlings in all quadrats, and then simulated seed arrival and establishment for 15 years. Comparing the relative predictive power of the full, homogeneous seed, and homogeneous establishment treatments for seedlings at multiple ages allowed us to leverage all our data and statistical models to determine the relative importance of seed arrival and establishment for the

distribution of seedlings. We ran each IBM experimental treatment 100 separate times for each of 1000 unique parameter sets (details in Appendix B). To compare IBM model output to observed data, we used mean-squared predicted error (MSPE) as a minimum posterior predictive loss criterion (Gelfand and Ghosh 1998).

RESULTS

Conspecific density and environmental covariates

Conspecific seedling and adult density were highest in evergreen forest ~1 km along the transect, and then declined with distance (Fig. 3; Appendix A: Fig. A3). No adults occurred in any plots beyond 3.20 km (in deciduous forest), and seedling density sharply decreased beyond 2.26 km. Thus, we refer to the region of high adult and seedling abundance between 0 and 2 km along the transect as the “source population,” and consider seed arrival to distances >2.26 km as LDD. Percent transmitted light and grass presence showed high spatial heterogeneity within forest types, but values of both covariates were higher (on average) in deciduous forest than in evergreen forest (Appendix A: Fig. A1).

Sapling establishment

Vital rates of individual plants (germination, seedling survival, and growth) revealed benefits for plants in deciduous forest at long distances from the source population (Appendix A: Fig. A3). While effects of environmental covariates varied in significance and magnitude between life stages, models generally revealed a positive effect of grass presence and light, and a negative effect of conspecific seedling and adult density (Appendix A: Fig. A2; Appendix B: Fig. B1). LDD had the strongest positive effect on germination rates; of the 6105 seeds in the seed addition experiment, 615 germinated to become new recruits, and most (>80%) of these new recruits were located in deciduous forest plots at distances >2 km from the source population (Appendix A: Fig. A3). In contrast, new recruit height showed only a small increase in deciduous forest, with a mean of 5.2 ± 1.42 cm (all error estimates are SD), compared to a mean of 4.71 ± 1.60 cm in evergreen forest. The 1443 naturally established seedlings represented a range of height from 3.5 to 180 cm, and a mean height of 18.3 ± 14.0 cm. Seedling survival and growth were highest in deciduous forest and lowest in evergreen forest (Appendix A: Fig. A3). However, models for seedling survival revealed that the effect of seedling height outweighed any effect of location on survival. For example, in the plot with the lowest predicted survival, located within evergreen forest, estimated median annual survival probability of a 3-cm seedling was 0.42 (95% credible interval [CI], 0.19–0.68), but for a 30-cm seedling in this plot, estimated median annual survival was 0.97 (95% CI, 0.90–0.99).

Simulations of survival and growth of single seeds for 15 years using the IBM indicated that 45% of quadrats had a mean probability of sapling establishment >0.01

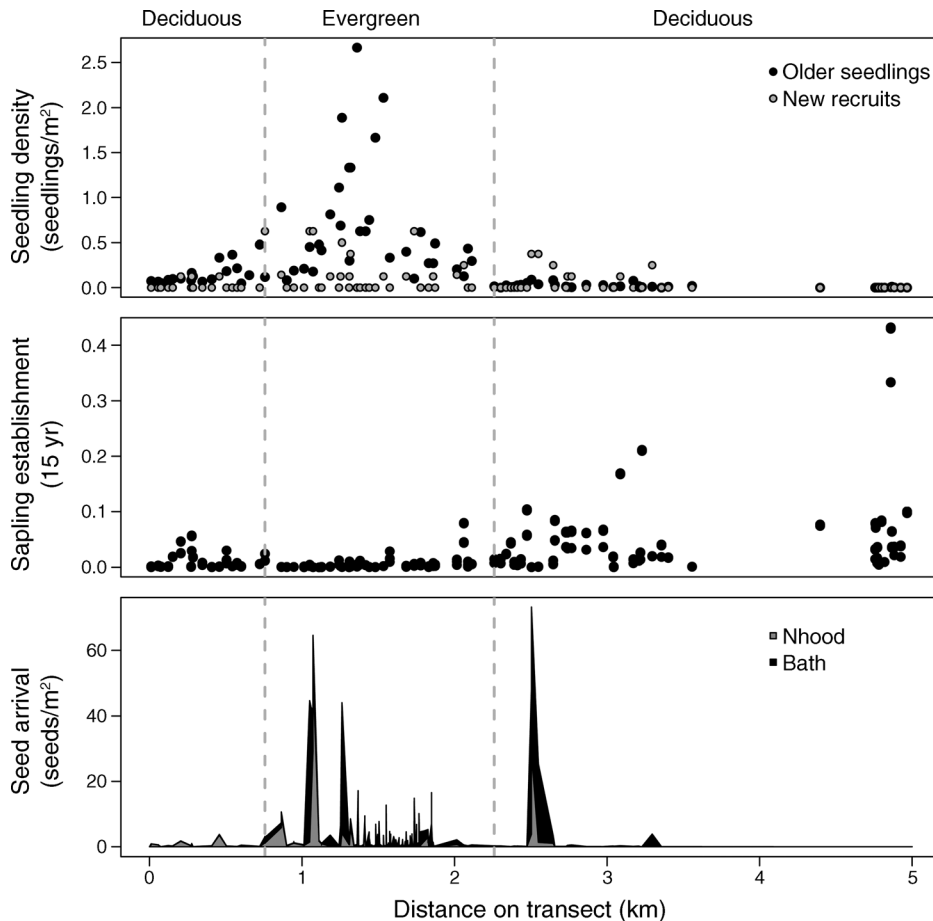


FIG. 3. Seedling density and predicted rates of sapling establishment and seed arrival along transect. The top panel displays naturally established seedling density (seedlings/m²), with gray dots representing new recruits and black dots representing older seedlings. The middle panel shows the posterior median probability of sapling establishment 15 years from present for each of 737 quadrats. The bottom panel shows the number of seeds per square meter predicted to arrive along the transect in a single fruiting season, with the black polygon indicating contribution of trees outside of 20 m (Bath term in Eq. 2) and the gray polygon indicating contribution of adult trees within 20 m to seed arrival (Nhood term in Eq. 2). Dashed gray lines represent boundaries between forest types.

(Fig. 3). Strikingly, 85% of the 261 quadrats located in evergreen forest had a mean probability of sapling establishment <0.01, suggesting that sapling establishment in this habitat is highly unlikely, even though evergreen forest is where adults and seedlings are most abundant (Fig. 3). Sapling establishment was highest in deciduous forest long distances from the source population, with a mean establishment probability >0.01 for 75% of 340 quadrats >2.26 km. Likewise, the 29 quadrats with the longest distances from the source population had mean sapling establishment probabilities >0.1.

Seed arrival

Estimated seed arrival was very heterogeneous, with several plots estimated to have received many seeds and most receiving close to zero (Fig. 3). Specifically, seed arrival was low in deciduous forest at distances >2.26 km, with 308 out of 340 of these quadrats predicted to

receive a median of <1 seed/m². Median seed production per tree ranged from 65 seeds (95% CI, 39–133) for a 20-cm dbh tree to 14 582 seeds (95% CI, 10 085–18 875) for a 100-cm dbh tree. Only a small proportion of seeds per tree, 7.90×10^{-5} (95% CI, 1.90×10^{-5} to 2.24×10^{-4}), were predicted to reach a 1×1 m quadrat within 20 m, reflecting the small size of this sampling unit. While the contribution to seed arrival from adult tree neighborhoods and sources >20 m from quadrats (Bath term) was similar, with means of 0.3 (95% CI, 0–1.5) and 0.4 (95% CI, 0–0.6) seeds, respectively, the plot-level random effect disproportionately increased seed arrival for quadrats with few adult trees within 20 m, leading to several plots with large numbers of seeds predicted to arrive from sources <20 m away (i.e., Bath term; Fig. 3).

Relative importance of seed and establishment limitation

Comparison of predicted seedling distribution from the IBM simulation experiment suggests that seed

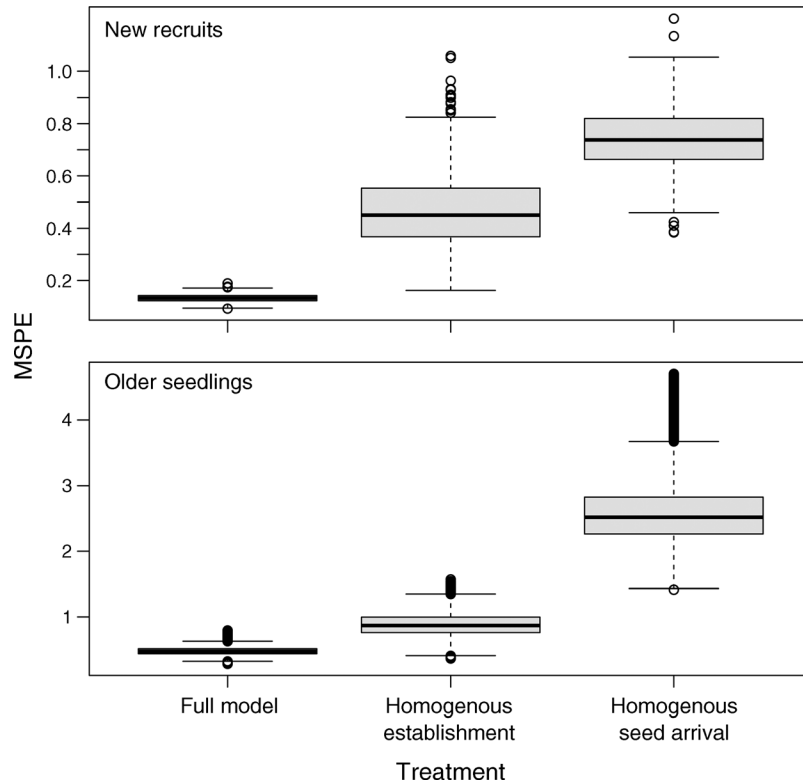


FIG. 4. Performance of different individual-based model (IBM) experiments in predicting the observed distribution of newly recruited (3-month-old, top panel) and older (3-month- to 15-year-old, bottom panel) seedlings after 15 years of simulated dynamics. Larger mean-squared predicted error (MSPE) indicates a worse fit between predicted and observed seedling distributions. The full model includes spatial variation in both establishment probability and seed arrival. The homogeneous establishment and seed arrival experiments remove spatial variation in the corresponding demographic factor. For each experiment, MSPE was calculated for each of 100 000 IBM runs to account for parameter uncertainty and demographic stochasticity. In the box-and-whisker plots, the thick black line represents the median, the horizontal lines on the box represent the first and third quartiles, the whiskers represent the minimum and maximum observations within 1.5 times the upper quartile, and the open circles represent outliers.

arrival is a more important determinant of seedling abundance than is establishment for both new recruits and older seedlings (Fig. 4). For both of these life stages, the full model, with quadrat-specific estimates of seed arrival and establishment, had the lowest MSPE, with a relatively small increase in MSPE for homogenous establishment but quadrat-specific seed arrival, and large increases in MSPE for models with homogenous seed arrival but quadrat-specific establishment. For the 15-year simulation, the MSPE of the homogenous seed model was 4.32 times higher than that of the full model, compared to the new recruit simulation in which MSPE of the homogenous seed model was 3.05 times higher than that of the full model. Therefore, spatial variation in seed arrival was more important for explaining the abundance of older plants compared to new recruits.

DISCUSSION

Our results suggest that the distribution of *Miliusa horsfieldii*, a canopy tree species in a landscape mosaic of forest types, is constrained by low rates of LDD. At our study site, *Miliusa* seedlings and adults are abundant in

evergreen forest and nearly absent in deciduous forest. We asked how sapling establishment and seed arrival differ at long vs. short distances from the source population, and whether the current distribution of seedlings is better predicted by observed rates of seed arrival or establishment. We found that individuals in deciduous forest far from the source population experienced multiple benefits (e.g., increased germination rate, new recruit height, seedling survival and growth) likely due to the near absence of conspecifics (Appendix A: Fig. A3). The net effect of these spatial differences in demographic processes is that estimated sapling establishment probabilities 15 years after seed dispersal are highest for seeds dispersed long distances (Fig. 3). The combination of high establishment probability and low abundance suggests that establishment does not constrain seedling abundance in the deciduous forest. Instead, we found that very low rates of seed arrival at long distances from the source population likely limit seedling abundance. To quantify how spatial differences in seed arrival and establishment generate seedling distributions, we used an IBM to



PLATE 1. A large Indian civet (*Viverra zibetha*) photographed in the act of dispersing *Miliusa* seeds at the study site. Large Indian civets are likely a vector for long distance seed dispersal >1 km (Rabinowitz 1991). Photo credit: T. T. Caughlin.

simulate seedling distributions across the entire landscape for 15 years and then compared results to the observed seedling distribution. The results suggest that seed limitation is much more important for explaining observed seedling distributions than is establishment limitation, even after 15 years of size-structured growth and survival (Fig. 4). Our central conclusion is that LDD plays a major role in structuring the distribution of this long-lived tree in its native landscape.

The IBM experiments suggest that arrival of even single seeds long distances from the source population can impact *Miliusa* distributions, with a mean probability of sapling establishment 15 years after seed dispersal of 4.9% for LDD seeds (Fig. 3). Consequently, quantifying rates of rare LDD events is critical for understanding plant population dynamics (Nathan 2006). Direct estimates of such events are logistically difficult, regardless of method (Nathan et al. 2008). Our approach illustrates a solution to this dilemma: the use of hierarchical Bayesian models to estimate seed arrival from data on seedling abundance and germination. Our seed arrival model includes terms both for local seed production and for landscape-level seed availability, enabling estimation of the very low (but nonzero) rate of seed arrival in deciduous forest, where adult trees are absent from local neighborhoods. Our model for seed dispersal reveals that while overall rates of LDD are very low, random plot-level variability in seed arrival is high, suggesting that some plots are likely to receive far larger numbers of seeds than are other plots, regardless of neighboring trees or distance from source population. These results could be explained by movement patterns of the large mammals that disperse *Miliusa* seeds, including civets and bears, which can produce hetero-

geneous patterns of dispersal with high seed deposition under trees where some of these dispersers sleep, in latrines, and along travel routes (Corlett 1998, Nakashima et al. 2010). A better understanding of how behavior and physiology of these mammals influences the spatial pattern of seed dispersal could provide valuable insight into the demography of the tree species they disperse.

A common criticism of using seed addition experiments to detect seed limitation is that the importance of seed arrival is likely to decrease over time for long-lived species, due to spatial differences in demographic performance between life stages (Schupp 1995), density dependence at later life stages (Kauffman and Maron 2006), or simply the loss of the pattern of initial seed dispersal from accumulation of chance mortality over time (Clark et al. 2007). By using an IBM to integrate seed arrival and establishment in a dynamic simulation, we were able to evaluate seed limitation on multiple time scales, from 3 months to 15 years. We linked the IBM output to the data by comparing observed and predicted seedling distributions and quantifying the contributions of spatial variation in seed arrival and establishment probability to the fit between predictions and observations. We found that even after 15 years of simulated demography, seed arrival was more important than establishment limitation in explaining the observed distribution of seedlings, suggesting that spatial patterns of seed dispersal have ecological relevance for at least 15 years. This surprising result is a consequence of both low rates of LDD (Fig. 3) and high rates of establishment for LDD seeds (Appendix A: Fig. A3). Because establishment success increases with distance from the source population, an increase in LDD can have important,

lasting, demographic consequences (i.e., seed arrival has its largest impacts far from the source population where seeds have a relatively high probability of establishing as saplings).

Understanding the dynamics of tree distributions in heterogeneous landscapes, such as the seasonally dry forests of Southeast Asia, is crucial for maintaining landscape biodiversity (Rabinowitz 1990). Although our results suggest that the seedling distribution of *Milusa* is determined largely by where seeds arrive, they raise a larger question: why are most *Milusa* trees, including adults, found in evergreen but not in deciduous forest at our study site? One possibility is that rare events such as fire or drought may have a larger negative effect in deciduous forest than in evergreen forest, ultimately restricting seedling and adult establishment in the former habitat. Our period of demographic monitoring did not include any such events; consequently, our models assume a constant environment, and we cannot make inferences about rare or extreme events. Nevertheless, our results suggest that sapling establishment in the deciduous forest is possible in a 10–15-year time period under current conditions, a period that is within the realm of possibility for a fire-free interval, considering there has been no wildfire at our site since 2004 (Baker et al. 2008). Alternately, the distribution of *Milusa* trees in the landscape could be driven by a stochastic combination of historic fire occurrence and chance seed dispersal events, an expectation supported by a disparate set of studies including remote sensing (Johnson and Dearden 2009), seedling transplant experiments (Baker 1997), and tree ring analysis (Baker et al. 2005). Our study provides insight into how LDD may be a demographic mechanism underlying stochastic changes in plant species distributions across an intact tropical forest landscape.

The importance of LDD for biodiversity conservation is expected to increase with habitat fragmentation and shifts in habitat suitability as a consequence of climate change (Trakhtenbrot et al. 2005, Corlett 2009, Corlett and Westcott 2013). For East Asia, climate change projections for the next 100 years suggest that movement on the scale of 1–3 km per century may be required for plant species to successfully track changing conditions (Corlett 2009, Corlett and Westcott 2013). Our results demonstrate that even for a species dispersed by long-ranging mammals, the rarity of LDD may be a major barrier to distributional shifts at this scale. Finally, our results directly show that changes in the spatial pattern of LDD can have a large effect on seedling distributions. Human actions that alter rates of LDD, such as overhunting of seed-dispersing mammals with long range movements, will likely have significant consequences for plant species distributions.

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SUPPLEMENTAL MATERIAL

Appendix A

Additional details on study site, species, and sampling protocol ([Ecological Archives E095-080-A1](#)).

Appendix B

Additional details on statistical methods ([Ecological Archives E095-080-A2](#)).