Temporal and spatial variability in seedling dynamics: a cross-site comparison in four lowland tropical forests

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Abstract: Spatial and temporal variation in seedling dynamics was assessed using records of community-wide seedling demography collected with identical monitoring methods at four tropical lowland forests in Panama, Malaysia, Ecuador and French Guiana for periods of between 3 and 10 y. At each site, the fates of between 8617 and 391 777 seedlings were followed through annual censuses of the 370–1008 1-m^2 seedling plots. Within-site spatial and inter-annual variation in density, recruitment, growth and mortality was compared with among-site variability using Bayesian hierarchical modelling to determine the generality of each site's patterns and potential for meaningful comparisons among sites. The Malaysian forest, which experiences community-wide masting, was the most variable in both seedling density and recruitment. However, density varied year-to-year at all sites ($CV_{among\ years\ at\ site} = 8$–43%), driven largely by high variability in recruitment rates (CV = 40–117%). At all sites, recruitment was more variable than mortality (CV = 5–64%) or growth (CV = 12–51%). Increases in mortality rates lagged 1 y behind large recruitment events. Within-site spatial variation and inter-annual differences were greater than differences among site averages in all rates, emphasizing the value of long-term comparative studies when generalizing how spatial and temporal variation drive patterns of recruitment in tropical forests.

Key Words: Barro Colorado Island, El Niño, masting, Nouragues, Pasoh, recruitment, seedling demography, Yasuní

INTRODUCTION

There has been increasing recognition that cross-site comparisons are needed to determine how differences in climate, underlying geology and biogeographical history lead to differences in biotic interactions, diversity and dynamics in seemingly similar forests (Condit *et al.* 1999, Corlett & Primack 2006, Pitman *et al.* 2002). Most studies of tropical forest dynamics, however, focus on single study sites, and in many cases, only a handful of species present at a site. Results from such studies are of limited generality, since tropical forest sites can differ in a number

of ecologically significant ways (LaFrankie *et al.* 2006, see reviews in Primack & Corlett 2005).

Comparative studies are becoming more common with the establishment of coordinated networks of forest plots throughout the tropics, such as the Center for Tropical Forest Science (CTFS), which oversees large mapped forest dynamics plots in Asia, Africa and Latin America (Condit 1995, Losos & Leigh 2004). Similarly, RAINFOR is coordinating efforts to monitor forest biomass and dynamics in plots across Amazonia (Malhi *et al.* 2002). These networks employ standardized methodologies to facilitate comparative studies of how forest dynamics differ among sites. Thus far, however, such comparative, dynamic studies have been restricted to adult trees or large saplings (Condit *et al.* 1999, 2006; Wills & Condit 1999), missing critical processes occurring during early stages in the plant life cycle. In tropical forests, processes affecting the seedling stage act as a strong selective filter

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Table 1. Study site and seedling census characteristics. Site characteristics are drawn from Losos & Leigh (2004) for BCI (Panama), Pasoh (Peninsular Malaysia) and Yasuní (Ecuador), and from Bongers *et al.* (2001) for Nouragues (French Guiana).

Site	Location	Forest type	Rainfall (mm y^{-1})/ mo < 100 mm	Richness (no. spp.)/ area of FDP (ha)	Adults (dbh $\geq$ 10 cm) density (ha^{-1})/ basal area (m^2 ha^{-1})	Seedling census period	No. census stations/ seedling plots
BCI	9°9′N 79°51′W	semi-deciduous lowland moist	2551/4	300/50	429/27.8	1994–2004	200/600
Pasoh	2°58′N 102°18′E	mixed dipterocarp lowland	1571/0	816/50	531/25.7	2001–2006	320/741–1008
Yasuní	0°41′S 76°24′W	evergreen lowland wet	3081/0	1100/25	702/27.3	2002–2006	200/600
Nouragues	4°05′N 52°40′W	evergreen lowland wet	2990/2	803/100[a]	495/29.4	2004–2006	160/370

[a]Based on tree checklist for a ∼100-ha area, not complete census data.

in regeneration, controlling patterns of recruitment and influencing forest composition (Harms *et al.* 2000, Uriarte *et al.* 2005, Wright *et al.* 2005). Quantitatively rigorous cross-site comparisons of seedling dynamics are therefore essential for understanding variations in regeneration pathways and forest dynamics both within and among tropical forests (Corlett & Primack 2006).

In any one forest, seedling recruitment may be highly variable through time at both the population (Connell & Green 2000, DeSteven & Wright 2002, Schupp 1990) and community levels (Norden *et al.* 2007), with community-wide masting events in South-East Asian forests providing an extreme example of such temporal variability (Sakai 2002). Within a site, seedling recruitment also varies in space because of limited seed dispersal (Dalling *et al.* 1998, 2002; Makana & Thomas 2004), spatial variation in environmental conditions (Montgomery & Chazdon 2002, Palmiotto *et al.* 2004, Uriarte *et al.* 2005) and variation in biotic interactions (Augspurger 1983, Schupp 1988, Webb & Peart 1999). Ostensibly, seedling dynamics also vary among sites. However, because of the lack of cross-site comparisons, it is unknown how variation in seedling dynamics among sites compares to the considerable variation known to occur within sites.

In order to assess recruitment variability both within and among forests, we have employed identical methodologies for monitoring seedling dynamics at four diverse tropical forest sites. These sites, located in central Panama, western Amazonia, the Guiana Shield and Peninsular Malaysia, are all situated in closed canopy, moist to wet lowland forests that rarely experience major disturbance events such as hurricanes or fires. Here we compare annual, community-wide fluctuations in seedling recruitment at these four forests and explore the consequences of variable recruitment for understorey seedling densities, which change through the addition of newly recruited seedlings and loss of seedlings due to mortality and growth into larger size classes. In each forest we ask how seedling dynamics vary in space in any given year and how mean vital rates vary among years within

a site. We then compare this within-site variability to variation in seedling dynamics among the four forests in order to determine the generality of results from any one site and to assess our ability to make meaningful comparisons among sites.

STUDY SITES

Three of the four study sites are part of the Center for Tropical Forest Science network of Forest Dynamics Plots (FDP): Barro Colorado Island (Panama), the Pasoh Forest Reserve (Peninsular Malaysia) and the Yasuní Scientific Station (Ecuador). These sites all have large-scale (50-ha) permanent forest dynamics plots, in which all free-standing trees and large shrubs $\geq$ 1 cm dbh (trunk diameter at 1.3 m) are inventoried using similar methods. Detailed site descriptions and methodology can be found in Losos & Leigh (2004). The fourth study site is located at the Nouragues Biological Station (French Guiana) and is described in detail by Bongers *et al.* (2001).

Barro Colorado Island (BCI) is a 1500-ha island situated in Lake Gatun, a man-made lake that forms a portion of the Panama Canal. BCI is the most seasonal of the four sites, experiencing a pronounced dry season from January to April (Table 1). Nouragues, in central French Guiana, also has seasonal rainfall but most precipitation falls between March and June and only two months of the year receive less than 100 mm of rain. Both Yasuní, located in the upper Amazon basin in eastern Ecuador, and Pasoh, in Peninsular Malaysia, have aseasonal rainfall distributions. Yasuní has the highest annual rainfall of all the sites, however, and Pasoh the lowest.

Of the four sites, only Pasoh has supra-annual masting events, in which the majority of species and individuals flower and fruit together every 3–7 y. During the course of this study, two relatively small back-to-back masting events occurred in 2002 followed by a larger event in 2005 (Chen 2007, Sun *et al.* 2007). Peak fruiting times at the other three sites are related to seasonality in rainfall and solar irradiation with annual peaks observed at

Nouragues (March and April) and BCI (March, April and May) but no consistent strong peaks at Yasuní (Persson 2006).

METHODS

Field methodology

All four sites have a network of seed traps used in studies of phenology that are arrayed in a stratified random design along each site's trail network (Chen 2007, Norden *et al.* 2007, Persson 2006, Wright & Calderón 1995). We placed three 1-m^2 seedling plots (or 2–3 plots at Nouragues) 2 m from each seed trap in the three directions away from the trail. The trap and its surrounding plots comprise a census station. There were 160–320 stations per forest, separated by a minimum distance of 16.6–20.5 m. The number of stations differed among years at Pasoh because 86 stations were added in the study's second year and some stations were made inaccessible in certain years by large treefalls.

Seedling plots have been censused annually at BCI since 1994 (SJW), at Pasoh since 2001 (YC), at Yasuní since 2002 (MRM) and at Nouragues since 2004 (NN) (Table 1). In each census, we marked all seedlings (0–50 cm in height) of woody species within the plots with a unique tag number and measured the height of all surviving and newly recruited seedlings to quantify recruitment, growth and mortality rates. Peaks in seedling germination vary among sites and in relation to the seedling census schedule. Therefore, the average age of newly recruited seedlings varies from 6–10 mo among sites. Due to the difficulty of identifying seedlings in these highly diverse forests, species identifications are still underway at the three newer sites. In the analyses presented here, we combined all species to examine patterns at the level of the seedling assemblage.

Analyses

In all analyses we calculated measures of seedling dynamics at the level of the census station, considering the seedling plots as replicates at each station. We use 'station' to refer to seedling census stations within a particular study site and 'site' to refer to the four different forests. We used a hierarchical Bayesian model that accounts for the influence of differing sample sizes and also partitions the variation among plots within stations as well as among stations. The method uses a Gibbs Sampler and Metropolis-Hastings algorithms and is described in detail by Condit *et al.* (2006) for a similar analysis of adult and sapling growth and mortality at several CTFS sites. An important benefit of this method is its ability to assign variance in seedling dynamics to different processes

happening at different scales. A more general discussion of the advantages of this approach can be found in Clark (2005).

We used a similar procedure for each parameter analysed. At each station *i*, we estimated a parameter of interest, p_i, using observed counts of seedlings (alive, newly recruited, or newly dead), seedling growth or mortality rates. The values of p_i varied among stations, following a distribution that we modelled as either normal or log-normal. Our goal was to estimate each p_i as well as parameters μ (mean) and σ (standard deviation) describing the distribution of p_i across stations (i.e. variation in space) using the likelihood equations described below. This approach assumes non-informative (i.e. uniform) Bayesian prior distributions. In each analysis, we executed 5500 iterations of the Metropolis-Hastings algorithms and then discarded the first 500. The remaining 5000 values comprised the posterior distributions for parameters of interest. We used the mean of each resultant posterior distribution as our best estimate of a parameter and the 2.5[th] and 97.5[th] percentile to bracket the 95% credible interval on that estimate (Gilks *et al.* 1996). For comparisons among years or sites, we define values of a parameter whose 95% credible intervals do not overlap as significantly different. We conducted all analyses using the statistical language R, version 2.3.1 (R Development Core Team, http://www.r-project.org).

Seedling density

For seedling plot *j* within census station *i* we calculated seedling density as the number of individuals, N_{ij}, counted per 1-m^2 plot, observed at each census. We assumed that the probability of observing a value of $N_{ij} = x$ follows a negative binomial distribution, a random sampling process described by the mean, γ, and a parameter, *k*, that allows for clumping in the observations. We assumed *k* was constant across stations within a site, a characterization of the average degree of dispersal limitation, topography and other features of a given site.

We assumed γ_i follows a log-normal distribution across stations within the forest, described by the mean, μ, and standard deviation, σ, of the natural logarithm of seedling density (Figure 1a). The probability of observing a particular γ_i depends on variability within and among stations:

$$P(N_{ij}|\mu, \sigma, k, \gamma) = \prod_i \prod_j \int \text{NBinom}(N_j|\gamma_i, k)$$
$$\cdot \text{LNormal}(\gamma_i|\mu, \sigma)\,d\gamma \qquad (1)$$

In this analysis, the mean of the posterior distribution of μ represents our forest-wide estimate of density at each site in each census year, and the mean of the posterior distribution of σ represents the best estimate for spatial

variance in density at a site. We quantified the range of spatial variation in observed seedling density throughout a site within a year using the 95% prediction interval of $\mu \pm 2\sigma$ (using the mean estimates of μ and σ).

Seedling recruitment, mortality and growth

Over each census interval we analysed the counts of new seedling recruits, seedling deaths and seedlings that grew out of our 50-cm size restriction. We estimated the density of these three groups following the same steps used in the analysis of overall seedling density described above.

We next modelled mortality and relative growth rates in separate analyses. The per capita mortality rate was modelled separately, because increased seedling densities can lead to increases in seedling deaths, without any change to the per capita mortality rate. At each census station we used the observed number of surviving seedlings, S, from the seedlings present in the previous census, N, to estimate the annual station survival probability, θ_i, using a binomial distribution. The negative natural logarithm of θ_i is m_i, the annual per capita mortality rate, and we modelled m_i using a log-normal distribution.

$$P(S|N, \mu, \sigma) = \prod_i \int \text{Binom}(S_i|N_i, \theta_i)$$
$$\cdot \text{LNormal}(\theta_i|\mu, \sigma)\, d\theta \qquad (2)$$

Next, we estimated the distribution of relative growth rates, λ, which we calculated as the natural logarithm of the ratio of height before and after each census interval, standardized to an annual rate. We calculated the growth λ_{ij} of individual j at station i, then described variation in λ_j within stations using a bi-exponential distribution, a symmetric model with long tails allowing for both negative and positive growth and described by mean c and the exponential rate of decay, a (Figure 1b). Negative growth in seedlings is quite common due to stem breakage or damage from falling branch debris, browsing or trampling by animals and insect clipping or grazing.

We described the mean growth rate, c_i, using a normal distribution (with mean μ and standard deviation σ) because the observed station means were symmetrically distributed with a short tail of extreme values. As in the other analyses, the distribution of c_i depends on both within and among station variation:

$$P(c_i|\lambda_{ij}, a_i, \mu, \sigma) = \int \text{Biexp}(\lambda_{ij}|a_i, c_i)$$
$$\cdot \text{Norm}(c_i|\mu, \sigma)\, dc \qquad (3)$$

We updated μ and σ in this case with a Gibbs sampler that used random draws to an inverse gamma distribution, an analytical solution for the posterior probability of a normal distribution, in place of the Metropolis algorithm (Condit *et al.* 2006).
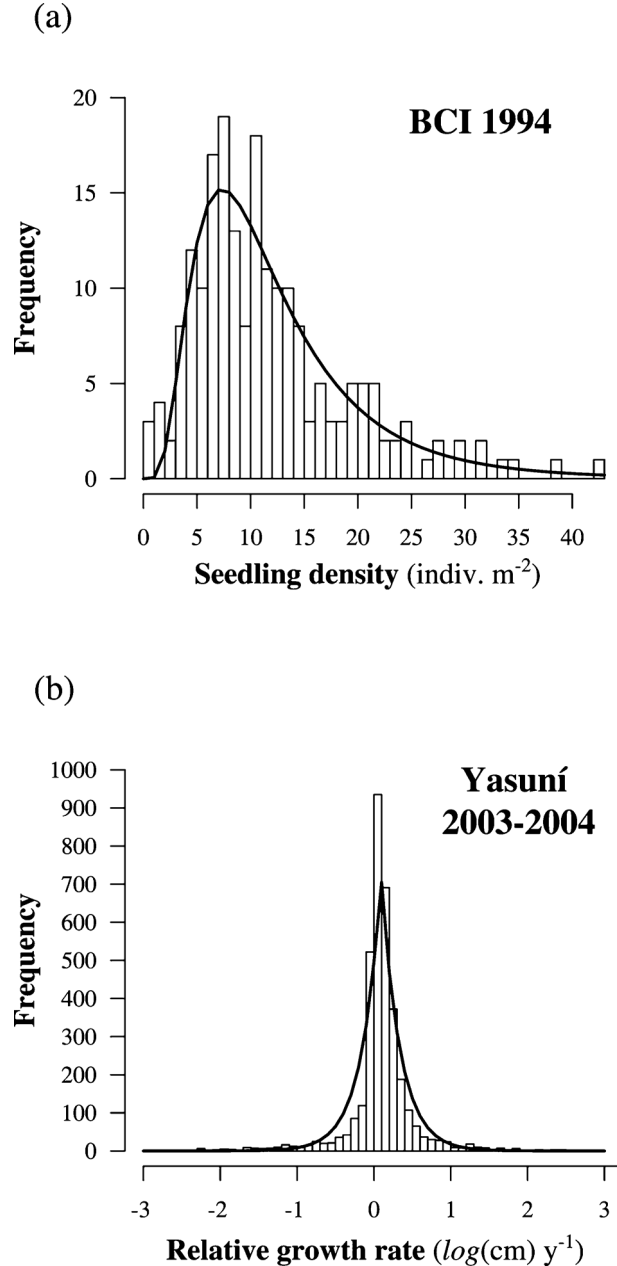
(a)

(b)

Figure 1. Sample distributions of seedling density and growth. Histogram of station-level seedling densities at BCI during the 1994 census with an overlaid log-normal distribution described by estimates of μ (mean seedling density) and σ (standard deviation of station seedling densities) (a). Histogram of forest-wide individual relative growth rates at Yasuní with an overlaid bi-exponential distribution described by estimates of μ (mean relative growth rate) and a (exponential decay constant) from the 2003–2004 census interval (b).

RESULTS

Seedling density

The mean seedling density across all years ranged from 8.9 seedlings m^{-2} at Pasoh to 12.2 seedlings
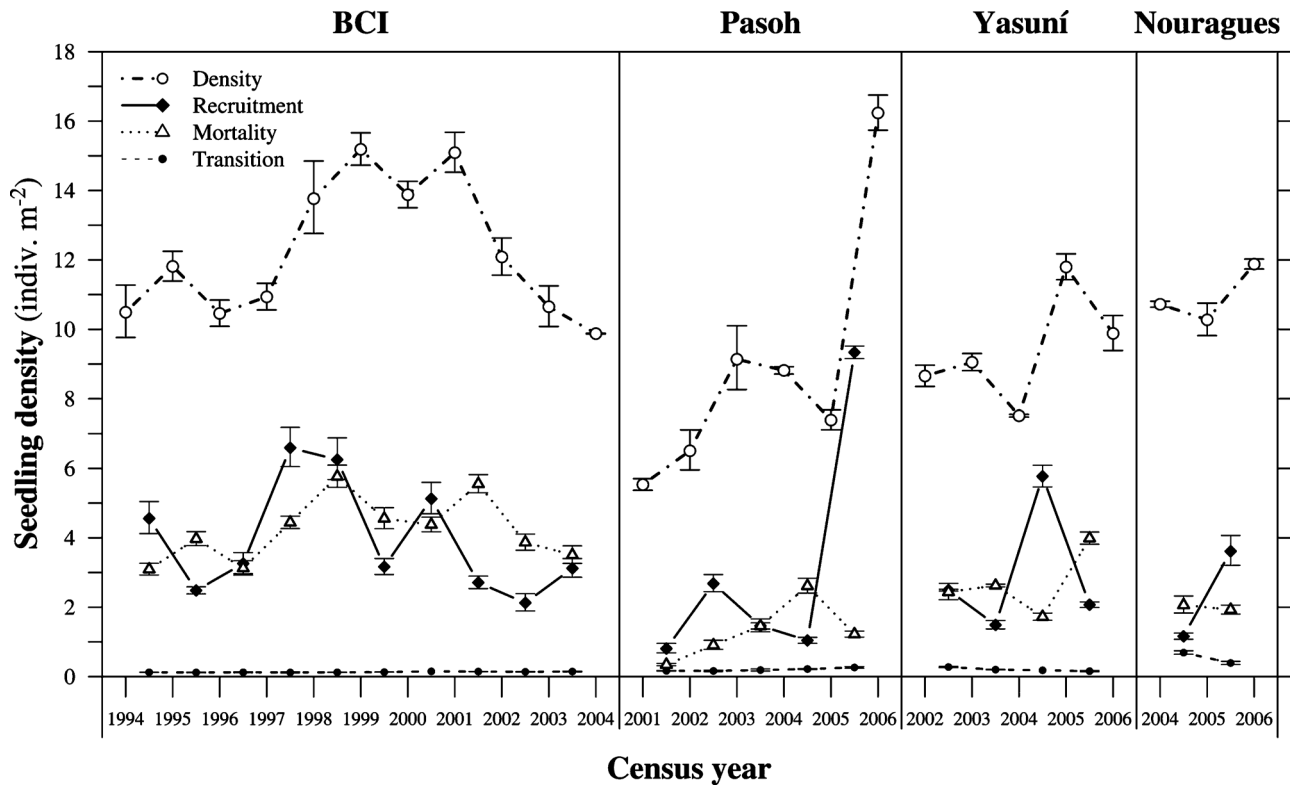
Figure 2. Inter-annual variation in seedling demography (1994–2006). Points represent the density of individuals in any census year of all seedlings ≤ 50 cm (Density), seedlings newly recruited over the census interval (Recruitment), seedlings that died over the census interval (Mortality) and seedlings that survived and grew > 50 cm (Transition). Points for recruitment, growth and mortality are offset relative to density because they were calculated for the interval between censuses. The error bars represent the 95% credible interval on each estimate. The points and error bars were estimated on the log-scale, but are back-transformed in their presentation here.

m^{-2} at BCI. Year-to-year fluctuations within sites were much greater than differences in seedling density among sites (Figure 2). In most cases, the mean seedling density in any single year fell outside the 95% confidence limits around mean density values from other years, demonstrating statistically significant inter-annual differences. In general, most years at BCI and Nouragues exhibited significantly higher seedling densities than were seen at Pasoh and Yasuní (Figure 2), although there was some overlap. Most notably, values at Pasoh spanned the range of densities seen at all other sites, with the most recent Pasoh masting event producing the highest densities in the study and the first two years at Pasoh exhibiting the lowest densities of all the sites. This led to a per cent coefficient of variation (CV) in density that was much higher at Pasoh (CV = 42.8%) than at BCI, Yasuní and Nouragues (CV = 16.0% 17.0%, 7.6%, respectively).

Seedling recruitment

As with overall seedling density, there was high variability among years in the density of new seedlings recruiting at each site (Figure 2). The mean density of new recruits over

all years ranged from 2.4 seedlings m^{-2} at Nouragues to 3.9 seedlings m^{-2} at BCI, with Yasuní and Pasoh having intermediate densities of 3.0 and 3.1 seedlings m^{-2}, respectively. However, the ranges of recruit densities observed at different sites overlapped considerably (Figure 2). The CVs for inter-annual variation in recruitment (CV: BCI = 40.4%, Yasuní = 65.0%, Nouragues = 72.6%, Pasoh = 117%) were much higher than the CVs for density at each site, and again, Pasoh exhibited the greatest variability among years.

Seedling mortality

Mortality, as measured by the counts of seedling deaths, also displayed considerable inter-annual variability at all sites (Figure 2). The coefficients of variation, ranging from 4.8% at Nouragues to 64.2% at Pasoh, were lower than the CV for recruitment at each site. Mortality over each interval at BCI was significantly higher than mortality observed over each interval at Pasoh and Nouragues and over all but one census interval at Yasuní. Estimates of annual mortality rate were highly correlated with the average density of seedling deaths at each site (e.g. at

BCI, Pearson's correlation $= 0.80$, $P < 0.01$). Thus, the inter-annual patterns of seedling mortality were similar whether examining the counts of seedling deaths or the mortality rate constant, and we graphically present mortality as measured by counts of seedling deaths (Figure 2).

Seedling growth

Very few seedlings grew out of the < 50-cm height category each year, and the density of transitions was very small compared to variability in recruitment and mortality (Figure 2). Out-growth thus contributed little to inter-annual changes in density. Mean annual relative growth rates varied little among sites, ranging from $0.08 \, log$(cm) y^{-1} at Nouragues to $0.11 \, log$(cm) y^{-1} at Pasoh and Yasuní. At BCI, Pasoh and Yasuní annualized relative growth rates demonstrated less inter-annual variability than was observed in the density of recruits or deaths. At Nouragues, relative growth rate declined by 50% in the second census interval, compared to the first, leading to a very high CV for relative growth (CV $= 51.2$%) compared to the other sites (CV: Pasoh $= 12.4$%, Yasuní $= 15.9$%, BCI $= 16.6$%).

Within-site spatial variation

In every census year at each of the four sites, there was considerable among-station variability in all demographic parameters. For example, observed seedling densities at BCI ranged from 1.0 to 42.7 m^{-2} in 1994, with a median density of 10.3 m^{-2} (Figure 1a). At Pasoh, seedlings recruited to census stations with densities ranging from 0 to 39.0 recruits m^{-2} (median $= 3$ seedlings m^{-2}) over the 2005–2006 interval, the period with the highest recruitment levels in our study. Seedling relative growth rates at Yasuní ranged from –4.6 to 2.8 log(cm) y^{-1} (median $= 0.8 \, log$(cm) y^{-1}) over the 2003–2004 census interval (Figure 1b). At all sites, the 95% prediction interval (spanned by $\mu \pm 2\sigma$) in any year was greater than the range of the mean annual values observed throughout the study (Figure 3), indicating that spatial variation exceeded temporal variation for all measures.

DISCUSSION

Temporal variation within sites

Year-to-year variation in seedling density and demography within each forest was much more conspicuous than differences among the four study sites, and much of the variation within each site was due to large inter-annual fluctuations in recruitment. We found particularly high inter-annual variability in seedling
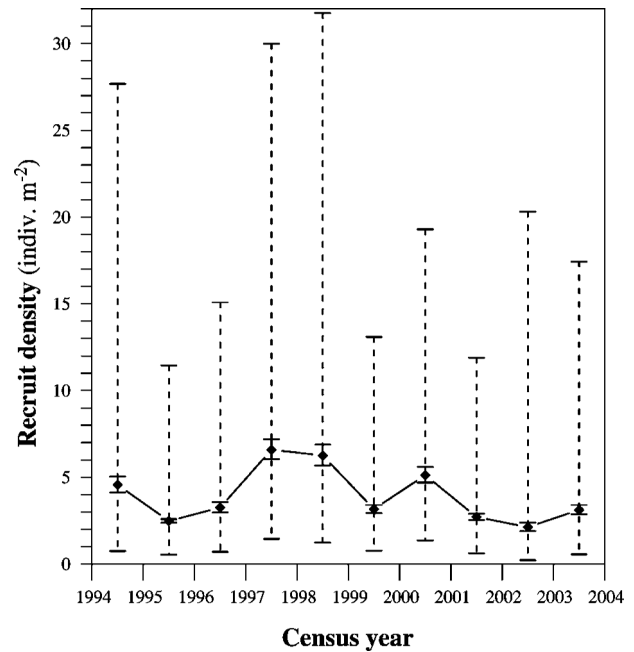

Figure 3. Spatial variation in recruitment at BCI. Mean annual density of new seedlings recruiting in each census interval. Solid error bars are the 95% credible interval on the mean density estimate, as in Figure 2. Dashed error bars show the spatial variation in recruitment across the forest within each year, representing the 95% prediction interval estimated using $\mu \pm 2\sigma$. The points and error-bars were estimated on the log-scale but are back-transformed in their presentation here to represent the number of recruits m^{-2}.

recruitment and density at Pasoh, the only forest experiencing supra-annual, community-wide masting events. Recruitment levels during the 2006 mast at Pasoh far exceeded the rates observed at the other three sites in all years. At the same time, non-mast years at Pasoh had lower densities of new recruits than any other site. However, BCI, which is not considered a masting site, also showed considerable fluctuations in seedling recruitment and density over time. At this site, recruitment in the census intervals of 1997–1998 and 1998–1999 was significantly greater than recruitment at Pasoh following the smaller masting event in 2002 (Figure 2).

Such pulses in recruitment at these two sites are probably due to variation in climatic conditions, which drives inter-annual variability in seed production. For example, in South-East Asia, droughts associated with the shift from La Niña to El Niño conditions are thought to trigger mass flowering (Sakai *et al.* 2006). At BCI, intra-annual patterns of flowering and fruiting are driven by seasonal patterns of light availability with community-wide peaks in reproduction timed to coincide with the periods of highest solar irradiance (Zimmerman *et al.* 2007). Among years at BCI, there is increased solar irradiation during El Niño events, which significantly enhances fruit production and drives variability in recruitment among years (Wright & Calderón 2006). Indeed, there is clear evidence that, over the length

of the BCI study, inter-annual variability in seedling recruitment was high due to large recruitment events following increases in fruit production during the 1997 El Niño event (Wright *et al.* 1999, 2005).

Similar to the other sites, Yasuní experienced high temporal variability in recruitment, though the cause is unknown, and long-term climate records from this region of the Amazon are sparse (Malhi & Wright 2004). The shorter study period at Nouragues showed quite different recruitment levels leading to high recruitment variability at that site as well, which is consistent with a previous study from Nouragues showing that seedling density fluctuates considerably over time (Norden *et al.* 2007). These findings show that high inter-annual variability in recruitment is not exclusive to masting communities. In future years, we may find increased variability among years at Yasuní and Nouragues, the sites with the shortest duration of seedling studies, because longer studies increase the likelihood of observing rare events.

At all sites, we found higher variability in recruitment than in mortality or growth rates at all sites, implicating recruitment as a more important driver of inter-annual differences in seedling density. Each year that experienced an increase in seedling density from increased recruitment was followed by a year where seedling mortality increased (Figure 2). This increase occurred both in the absolute number of deaths and in the annual mortality rate, the latter indicating a lower per capita probability of survival than in years when recruitment was lower. At least some of this increase in mortality likely is due to the higher proportion of first-year recruits in the seedling assemblage following periods of high recruitment, since newly recruited seedlings tend to have higher mortality rates than more established seedlings. Our results demonstrate that community-wide recruitment pulses are followed by periods of higher mortality for established seedlings, but that seedling mortality does not immediately damp inter-annual fluctuations in seedling recruitment. In fact, it is the lag between high recruitment and increased mortality that causes seedling densities to fluctuate from year to year. These fluctuations may have little impact on the density of individuals in larger size classes, however, because growth out of the < 50 cm seedling class varied little year to year. Still, temporal variation in recruitment for different species may have important consequences for species diversity (Chesson 1985, Grubb 1977).

Spatial variation within sites

Our results show large spatial variability in seedling dynamics at all study sites. This within-site spatial variation exceeded both the temporal variation observed at each site and the variation among the four forests. The large spatial variation in seedling density and recruitment at the community level likely arise from limited seed dispersal distances and the spatial patterning of adult trees, which typically result in a patchy distribution of seeds across the landscape (Hubbell *et al.* 1999, Muller-Landau *et al.* 2002, Nathan & Muller-Landau 2000). Movement patterns of seed dispersers also affect dispersal distances and dispersion patterns of seeds and seedlings at multiple spatial scales across the landscape (Fragoso 1997, Julliot 1997).

In addition, successful germination and seedling recruitment, as well as subsequent growth and mortality rates, are affected by spatial variation in abiotic resources and interactions with the local biotic neighbourhood. Light availability is patchy in tropical forests, even under closed canopies, and the recruitment, growth and survival of many species can be strongly affected by subtle differences in light levels (Montgomery & Chazdon 2002). Seedling growth rates can also differ significantly among soil types and along fertility and moisture gradients, which can vary over relatively short distances (Hall *et al.* 2003, Palmiotto *et al.* 2004). Natural enemies also drive spatial variation in seedling recruitment and survival if seed predators and herbivores cause disproportionately high seed and seedling mortality near fruiting adult trees and enhance survival far from seed sources (Connell 1971, Janzen 1970). Future analyses will explore the importance of seed arrival and the influences of the biotic and abiotic environment on species-specific rates of seedling recruitment, survival and growth at each of the four study sites.

Variation among sites

Large spatial and temporal variation within sites eclipsed variation in seedling density and dynamics among sites, yet some general trends did emerge. BCI and Nouragues, the two seasonal sites, tended to support higher seedling densities than the two aseasonal sites. Seasonal rainfall regimes have been shown to support lower sapling densities than less-seasonal sites (ter Steege *et al.* 2003). Consistent with this, tree densities were lower at BCI and Nouragues compared with Pasoh and Yasuní (Table 1). High seedling densities in seasonal sites may therefore be due to a higher availability of resources, e.g. free space and light, on the forest floor and reduced asymmetric competition with saplings and adults (Harms *et al.* 2004, Wright 2002). Indeed, the density of established seedlings across four Neotropical forests has been shown to be negatively correlated with the abundance of understorey palms, which may be better competitors for light or space in the dark understorey (Harms *et al.* 2004).

BCI had the highest seedling mortality rates overall, with all years exceeding the mortality observed at the other sites, except for the 2005–2006 interval at Yasuní. Pasoh had the lowest mortality rates in the study. Condit *et al.* (1999) also found higher sapling and adult tree

mortality rates at BCI as compared to Pasoh and attributed the differences to the many pioneer species in the BCI flora. The higher seedling mortality at BCI may also be due to the strong seasonality. Seedlings may be particularly vulnerable to drought stress because they lack roots able to access deeper than superficial sources of water (Paz 2003). On BCI, seedling mortality is higher during the 4-mo dry season compared to the wet season (Comita & Engelbrecht, unpubl. data), supporting the idea that seedling mortality rates are highest at BCI due to seasonal droughts. The highest seedling mortality rate at BCI occurred over the 1998–1999 interval, a year when BCI experienced a harsh dry season following the 1997–1998 El Niño event (Condit *et al.* 2004).

When comparing the two aseasonal sites, Yasuní and Pasoh, we found that seedlings at Yasuní, which receives far greater annual rainfall, suffered higher mortality rates. This higher mortality at Yasuní may be because the effect of damping-off diseases on tropical tree seedlings is much greater in wetter than drier sites (Gilbert 2002). In addition, seedlings at Pasoh may receive some survival advantage relative to Yasuní from herbivore satiation during high recruitment years caused by community-level masting (Curran & Webb 2000).

Conclusions

The present study represents the first rigorous comparison of seedling dynamics at multiple tropical forest sites. Our results demonstrate considerable spatial and temporal variation in seedling dynamics, particularly recruitment, within all sites. This considerable within-site variability was greater than variation observed among the four sites, despite differences in climate, biogeographic history and phenology. The evolutionary and ecological diversity of our study forests suggests that all tropical forests are likely to experience significant spatial and temporal variation in seedling recruitment and subsequent seedling survival. The impact of these recruitment pulses to long-term fluctuations in community composition and species diversity will become clearer as we follow these cohorts into the future and examine the performance of particular species in the community. The significant variation within and among sites in seedling dynamics emphasizes the need for long-term comparative studies across additional tropical forests.

ACKNOWLEDGEMENTS

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