3 Assessing Recruitment Limitation: Concepts, Methods and Case-studies from a Tropical Forest

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Introduction

Seed production and seed dispersal are critically important processes in population dynamics, precisely because they are almost never completely successful – that is, because not all sites suitable for a given species are reached by its seeds. The failure of seeds to arrive at all suitable sites limits population growth rates and abundances, a phenomenon called seed limitation (Crawley, 1990; Eriksson and Ehrlen, 1992; Turnbull *et al.*, 2000). Seed limitation has important consequences for population and community dynamics and for species diversity at multiple scales (Tilman, 1994; Hurtt and Pacala, 1995; Pacala and Levin, 1997; Zobel *et al.*, 2000).

Seed limitation can arise from limited seed numbers and/or limited dispersal of available seeds. The total number of seeds available, determined by a species' adult abundance and fecundity, places an upper limit on the number of sites that can possibly be reached by seeds and determines overall mean seed density (Clark *et al.*, 1998). The variance in seed density depends primarily upon the shapes and sizes of seed shadows and the clumping or contagion of the seed rain (Clark *et al.*, 1998). If adult trees are clumped (as they often are, Condit *et al.*, 2000), seed limitation will be further increased (Ribbens *et al.*, 1994).

To assess the consequences and importance of restricted seed rain, we need to quantify seed limitation and compare it with establishment limitation (also known as site limitation) – the limitation of a plant population by the number of sites suitable for establishment or, more generally, by the suitability of sites for establishment (Eriksson and Ehrlen, 1992; Clark *et al.*, 1998; Nathan and Muller-Landau, 2000). Plant ecologists have long recognized the contribution of both these factors, although they have differed on the issue of their relative importance, with profound

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implications for how one views plant communities (Clark *et al.*, 1999). In particular, if establishment limitation dominates, then species relative abundances are determined mainly by their regeneration niches and the relative abundances of microhabitats (Grubb, 1977). In contrast, if seed limitation dominates, then fewer sites are won by the best possible competitor in that microhabitat and more by whichever species happens to arrive (Hubbell and Foster, 1986; Cornell and Lawton, 1992).

While the consequences of establishment limitation are well understood, the mechanisms and implications of seed limitation are less widely appreciated. Seed limitation essentially slows rates of change in abundance – species cannot increase as quickly if they do not reach all suitable sites (nor, as a result, can their competitors decrease as quickly). Further, dispersal limitation in particular reduces the frequency of interspecific competition and increases the frequency of intraspecific competition, because propagules of a species are aggregated rather than equally distributed across sites, further reducing potential rates of changes in population size (Pacala and Levin, 1997). These forces will operate even in the face of strong niche differences. For example, even if all species have strict competitive rankings in every available habitat and are able to win only within their preferred habitat, seed limitation will increase the probability that the best competitor is not present at a given site and that the site will be won instead by a lesser competitor that is present. This results in more stochastic dynamics on the community level, despite deterministic dynamics at each site (Hurtt and Pacala, 1995). Whether species are equivalent or differentiated by life-history trade-offs, model communities in which dispersal is localized maintain higher total diversity (albeit lower local diversity) than those in which dispersal is global (Hubbell, 2001; Chave *et al.*, 2002).

Despite its importance to plant populations and communities and its obvious link to seed dispersal, few studies of dispersal explicitly quantify seed limitation and its components (but see Clark *et al.*, 1998). In this chapter, we first outline methods for measuring seed limitation, establishment limitation and their components. These methods are applicable to any study that quantifies seed rain at an unbiased sample of locations in a community or explicitly measures the shapes of seed shadows. Then we apply these methods to several species in a tropical forest to evaluate their usefulness. Finally, we assess the implications of observed seed and establishment limitation for tropical forest diversity and conservation.

General Methods for Quantifying Recruitment Limitation and its Components

Recruitment limitation is the reduction in a species' abundance from the maximum set by the environment that can be attributed to limited numbers of recruits. That is, how much smaller is the abundance than it would be if there were unlimited numbers of recruits? To apply this very general definition, we must specify whose abundance (e.g. adults, juveniles), and which stage recruits (e.g. seeds, seedlings) are of interest. In the theoretical literature, recruitment limitation means limitation of the adult population by arrival of the mobile, dispersing stage; in this case, recruitment limitation can be directly juxtaposed with total establishment limitation, which reflects all post-dispersal processes (Hurtt and Pacala, 1995; Pacala, 1997). This accords with the use of the term in the marine literature, where it was introduced to describe limitation of adult density by the rate of larval arrival (Chesson, 1998). In the terrestrial plant literature, the term has been used in different ways corresponding to different definitions of recruit: in some cases, recruits are seeds and recruitment limitation is simply seed limitation (Tilman, 1997; Hubbell *et al.*, 1999); in others, recruits are an older juvenile class such as seedlings and recruitment limitation thus reflects a combination of seed limitation and early establishment limitation (Ribbens *et al.*, 1994; Clark *et al.*, 1998). Here, we use the more specific terms seed limitation and seedling limitation, respectively, to describe these two cases, and use recruitment limitation in the general sense, to encompass limitation by any stage recruits of a measure of the abundance of any later stage.

We start by defining seed limitation and establishment limitation of adult abundance, where establishment means establishment to adulthood, including all post-arrival processes (e.g. germination, competition, herbivory). We can assess seed and establishment limitation in two distinct ways: (i) seed addition experiments; and (ii) measurement of seed rain and establishment patterns. These provide different but complementary measures of each type of limitation.

Seed addition experiments

The most straightforward way to assess seed limitation of a population is to experimentally add large numbers of seeds of that species, and compare the results with controls in which no seeds are added. Many such experiments have been conducted; of those reviewed by Turnbull *et al.* (2000), approximately half found an increase in density following sowing, evidence that the populations are seed-limited. To determine how much larger population density would be if seed availability were not limiting would require addition experiments using optimal densities of seeds – that is, seed densities at which adult density is maximized (this may mean simply seed densities greater than a threshold value above which further addition of seeds does not result in further increases in adults, or it might mean densities within a limited range above which yield actually decreases due to overcompensating density dependence). From such experiments, we can calculate exactly the reduction in population density due to reduced (or excessive) numbers of seeds alone, in the context of all other limitations imposed during establishment. By analogy with the concept of realized niches (niche size in the context of all other factors), Nathan and Muller-Landau (2000) termed this realized seed limitation:

$$\text{Realized seed limitation} = 1 - \frac{\text{adult density in control plots}}{\text{adult density in seed addition plots}}$$

The fraction essentially gives actual adult density (density under actual seed densities and actual establishment conditions) as a proportion of potential density, given optimal seed densities and actual establishment conditions. Note that experiments that add seeds at non-optimal densities will allow for estimation of a lower bound on realized seed limitation, since adult densities in the addition plots will not be as large as they could be.

Seed addition experiments also provide information on the total limitation of population size by factors other than seed availability. Because seed numbers are not limiting in the addition plots, any difference in adult density from the maximum possible must be due to limitation by other factors acting on early establishment and survival to adulthood. Maximum possible density could be determined from maximum densities observed in the field, experimental monocultures or, potentially, calculations based on organism size and total resource availability. We can then calculate the reduction in population density due to establishment factors from the maximum possible if neither seed availability nor establishment were limiting. By analogy with the concept of fundamental niches, this is termed fundamental establishment limitation (Nathan and Muller-Landau, 2000):

$$\text{Fundamental establishment limitation} = 1 - \frac{\text{adult density in seed addition plots}}{\text{maximum possible adult density}}$$

The numerator of the fraction in this equation is essentially potential density given optimal seed densities and actual establishment conditions, while the denominator is potential density given optimal seed densities and optimal establishment conditions. Experiments in which seeds are added at non-optimal densities provide an upper bound on fundamental establishment limitation.

Measurement of seed rain and establishment patterns

Another way to assess seed limitation is to measure patterns of seed rain in the field or to simulate patterns of seed arrival, to determine the proportion of sites that are reached by seeds (Ribbens *et al.*, 1994; Clark *et al.*, 1998; Hubbell *et al.*, 1999). Where there are no seeds, there can be no subsequent seedlings or adults, regardless of establishment conditions. Thus, the proportion of all sites at which seeds do not arrive is a measure of fundamental seed limitation – seed limitation measured as if no other factors were limiting. To assess fundamental seed limitation of adult density, we define a site as the area occupied by a single adult and observe or estimate seed rain to sites that constitute an unbiased sample of the community. Following Nathan and Muller-Landau (2000), we then define:

$$\text{Fundamental seed limitation} = 1 - \frac{\text{sites reached by seeds}}{\text{total number of sites}}$$

(see also Ribbens *et al.*, 1994; Clark *et al.*, 1998). The numerator above is essentially the potential adult density given actual seed arrival patterns and optimal establishment conditions; the denominator is potential adult density given seeds everywhere and optimal establishment conditions. Optimal establishment conditions would be conditions under which an adult establishes at every site receiving one or more seeds.

If both seed arrival and subsequent establishment are measured, we can also obtain an estimate of establishment limitation. Where seeds arrive but establishment does not occur, establishment must be limiting. Thus, the proportion of sites receiving seeds at which establishment does not occur is a measure of realized establishment limitation – establishment limitation in the context of other limiting factors. To assess realized establishment limitation, we observe or estimate seed rain to sites constituting an unbiased sample of the community, and then observe or estimate establishment at sites sampling the community (preferably, but not necessarily, the same sites). We then define:

$$\text{Realized establishment limitation} = 1 - \frac{\text{sites in which establishment occurs}}{\text{sites reached by seeds}}$$

(Nathan and Muller-Landau, 2000). The numerator above is actual density (under actual seed arrival patterns and actual establishment conditions); the denominator is potential density given actual seed arrival patterns and optimal establishment conditions (see Box 3.1).

Further decomposing limitation

Both seed and establishment limitation reflect a variety of factors and thus can be decomposed into corresponding component limitations. For example, seed limitation arises from both limited numbers of seeds and limited distribution of available seeds. We can separate these two influences quantitatively by considering what would happen if available seeds were distributed uniformly across sites. Clark *et al.* (1998) pioneered such analyses by decomposing what we call fundamental seed limitation into source limitation and dispersal limitation. Their source limitation, which we call fundamental source limitation, is failure of seeds to reach sites due simply to insufficient seed numbers: there are not enough seeds to go around, even if all seeds are uniformly distributed among sites (Clark *et al.*, 1998). Clark *et al.* (1998) calculate this as:

$$\text{Fundamental source limitation} = 1 - \frac{\begin{array}{c}\text{sites that would be reached by seeds}\\ \text{if seeds were uniformly distributed}\end{array}}{\text{total number of sites}}$$

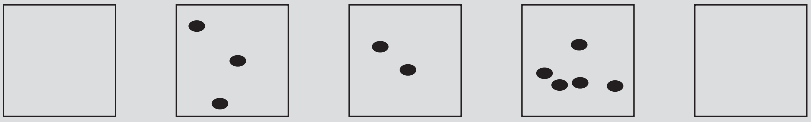
Source limitation is contrasted with dispersal limitation – seed limitation due to non-uniform distribution of seeds among sites (Clark *et al.*, 1998). Non-uniform distribution of seeds is nearly ubiquitous, because seeds are dispersed limited distances from their sources and are often dispersed in clumps (Clark *et al.*, 1998) and because adult trees are themselves clumped, increasing the number of sites that are very far from any sources (Ribbens *et al.*, 1994). Clark *et al.* (1998) quantify dispersal limitation of seed arrival, which we call fundamental dispersal limitation, as:

$$\text{Fundamental dispersal limitation} = 1 - \frac{\text{sites reached by seeds}}{\begin{array}{c}\text{sites that would be reached by seeds}\\ \text{if seeds were uniformly distributed}\end{array}}$$

(see Box 3.1 for a worked example).

Box 3.1. Calculating recruitment limitation from observational data.

Data on seed arrival and subsequent seedling establishment at an unbiased sample of sites allow us to assess fundamental seed limitation and its components, as well as realized seedling establishment limitation. Consider, for simplicity, an example of $n = 5$ sites, of which $a = 3$ receive seeds. (Much larger sample sizes are needed for statistically significant estimates, of course; the small numbers used here are for illustration only.)



Fundamental seed limitation – the proportion of sites not receiving seeds – can then be defined as:

$$\text{Seed limitation} = 1-\frac{a}{n} = 1-\frac{3}{5} = 0.4$$

at this spatiotemporal scale (see main text for a discussion of how to choose an appropriate scale).

We can calculate the limitation due solely to seed number by considering how many sites would be reached if seeds were distributed uniformly, with an expectation of s/n seeds per site. Following Clark *et al*. (1998), we can define uniform distribution stochastically as a Poisson seed rain with equal expectation everywhere – that is, a random distribution. Then the proportion of sites at which no seeds arrive under such a distribution is simply the Poisson probability of zero events given an expectation of s/n events, that is:

$$\text{Source limitation (stochastic)} = \exp\left(-\frac{s}{n}\right) = \exp\left(-\frac{10}{5}\right) = 0.14$$

Note that under this stochastic definition, source limitation is non-zero even though there are more seeds than sites. An alternative, deterministic interpretation of a uniform distribution would distribute seeds evenly, and thus non-independently, across all sites to the degree possible without producing fractional seeds per site. In this case, we have

$$\text{Source limitation (deterministic)} = \max\left\{1-\frac{s}{n},0\right\} = \max\left\{1-\frac{10}{5},0\right\} = 0$$

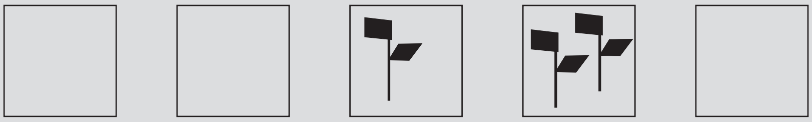
Thus, source limitation is zero when there are more seeds than sites, as here, and is the proportion of sites that would not receive a seed if no more than one seed were deposited on each site otherwise. In the results presented in this chapter, we apply the stochastic definition.

By comparing the proportion of sites reached by seeds in reality with the proportion of sites that would be reached by seeds if dispersal were uniform, we can assess the influence of restricted dispersal of seeds among sites as:

$$\text{Dispersal limitation} = 1-\frac{a/n}{1-\text{source limitation}}$$

(Clark *et al*., 1998). For our example, this is 0.3 for the stochastic definition of a uniform distribution and 0.4 for the deterministic definition.

From a study of seedling establishment finding that seedlings recruit in $r = 2$ of $n = 5$ sites,



we can calculate fundamental seedling limitation as:

$$\text{Seedling limitation} = 1-\frac{r}{n} = 1-\frac{2}{5} = 0.6$$

Given information on both seed arrival and seedling establishment at the same spatiotemporal scale, the reduction in seedling site occupancy due to failure of establishment in sites where seeds arrive can be quantified as:

$$\text{Establishment limitation} = 1-\frac{r}{a} = 1-\frac{2}{3} = \frac{1}{3}$$

Calculations of establishment limitation can be made even if seedling recruitment is not measured in the same sites as seed arrival, as long as site sizes are the same in both studies and both sets of sites are an unbiased sample of the area.

Like fundamental seed limitation, realized seed limitation can also be broken down into contributions due to source and dispersal limitation. This requires seed redistribution experiments, in which all seeds produced in an area are collected and redistributed uniformly across sites. Comparison with controls in which seeds dispersed naturally would allow calculation of realized dispersal limitation – the decrease in population caused by clumping of dispersed seeds. Comparison with seed addition experiments in which optimal seed densities were added would allow calculation of realized source limitation – the decrease in population caused by limited seed numbers alone, in the absence of limited dispersal. Such seed redistribution experiments have rarely been conducted (but see Augspurger and Kitajima, 1992).

Dispersal limitation could be further decomposed into contributions due to clumping of adults, variance in seed production among adults, short dispersal distances of seeds and so forth. For example, we can examine the contribution of clumping of adults by simulating or experimentally manipulating seed rain under actual spatial patterns of adults as well as under uniform spatial patterns, all other things being equal. Establishment limitation can similarly be broken down into contributions at different stages or by different agents, by examining the proportion of sites occupied at different stages or with and without particular agents (e.g. herbivores, pathogens, physical damage).

Generalizing and applying limitation measures

The methods described above can be adapted to examine limitation of and by other stages as well – for example, instead of examining limitation of adult density by seed availability, we could examine limitation of juvenile density by seed availability or limitation of adult biomass by seedling availability. Of course, the relative magnitudes of seed and establishment limitation for juveniles may be very different from that for adults, because factors act differently at different stages (Schupp, 1995). In particular, seed limitation of juveniles will generally be larger than seed limitation of adults because there is more scope for establishment factors to manifest themselves in the longer time to adulthood. It may be possible to extrapolate from limitation of juvenile densities to limitation of adult densities by using information on later survival patterns.

Both sets of methods for calculating seed and establishment limitation essentially divide the number of missed opportunities (sites a species does not capture) between those missed due to failure of seed arrival and those missed due to failure of establishment. They differ in how they attribute failure at sites in which both seed rain and establishment conditions are more than minimally adequate but less than optimal – sites in which one or more seeds arrive but no establishment occurs in nature, and yet establishment does occur when seeds are added at optimal numbers. Realized seed limitation will almost always be greater than fundamental seed limitation because the probability of having an adult establish almost always increases as additional seeds (above one) are added and thus the proportion of sites not receiving seeds is smaller than the proportion of sites in which no adults establish because of limited seed availability overall. Similarly, realized establishment limitation will almost always be greater than fundamental establishment limitation, because the proportion of sites in which establishment is totally impossible is smaller than the proportion of sites receiving any seeds in which establishment does not occur. The relationship between fundamental and realized limitation will also depend upon the correlation, if any, between seed arrival and establishment conditions across sites. Directed dispersal alone produces a strong positive correlation between seed arrival and establishment conditions; negatively density-dependent survival alone results in a negative correlation.

Choosing spatiotemporal scales

Definition of a suitable scale at which to calculate limitation measures depends in large part on the stage whose limitation is being assessed. To assess seed limitation of adult populations, addition experiments or seed-rain measurement should be conducted on a spatial scale similar to the area occupied by an adult, and on a temporal scale similar to the time it takes for an adult to establish (as in Ribbens *et al.*, 1994). On the other hand, for examining limitation of seedling or sapling densities in the same forest, the appropriate scale would be smaller – a seedling might occupy only 0.1 m × 0.1 m, a sapling 1 m × 1 m (as in Clark *et al.*, 1998). Choice of temporal scale can likewise be based on the age of the class whose limitation is being evaluated. It may be useful to examine seed and establishment limitation at spatial or temporal scales smaller than those occupied by an establishing individual of the focal stage, however, in order to take account of heterogeneity of seed rain and establishment conditions at such smaller scales. For any given system or species, there will be a range of spatiotemporal scales at which limitation measures provide useful information; in general, no single scale will be most appropriate for all questions because processes change across scales (Kollmann, 2000).

Limitation measures change both absolute and relative values with scale. The proportion of 1 m^2 sites receiving seeds will obviously be smaller than the proportion of 25 m^2 sites receiving seeds. Further, the scale of the analysis will affect the relative magnitude of different components of limitation. Source limitation is a declining function of the total seed fall expected per sample plot, which will increase with area and time period. Seed limitation will also decline with increasing sample plot size or time period, but much less quickly, because real seed rain is spatiotemporally autocorrelated. Thus, dispersal limitation will become a proportionately larger component of seed limitation as the scale increases – at some point, plots are large enough (or time periods long enough) for uniform distribution of seeds to result in all plots receiving seeds, and thus any failure of seeds to arrive is attributed entirely to limited dispersal. Because limitation measures are scale-dependent, the spatiotemporal scale should be given for every measure reported, measures should be calculated for multiple scales when possible and the utmost care should be taken in comparing limitation measures between species and systems when absolute or relative scales vary.

Case-studies from Barro Colorado Island

Fundamental seed limitation can be calculated from either of two kinds of data routinely collected in studies of seed dispersal.

1. We can make calculations of observed seed limitation in a set of randomly or regularly spaced sites (e.g. seed traps), providing an unbiased sample of the area in respect of distance to and density of source trees (see Box 3.1).

2. We can make calculations of projected limitation, given sufficient information on adult density, spatial pattern and seed shadows to allow projection of seed rain across the area of interest (Ribbens *et al.*, 1994; Clark *et al.*, 1998).

In this section, we use data on seed arrival to calculate both observed and projected seed limitation and its components at the 0.5 m^2 scale and periods of 1–12 years for four tropical tree species varying in life history and abundance. We then combine estimates of 1 m^2 seed limitation (obtained via extrapolation) with data on seedling abundances to calculate seedling limitation and establishment limitation at the 1 m^2 scale and periods of 1–6 years.

The spatial scales examined here were chosen for the seed and seedling censuses because they seemed appropriate for sampling heterogeneity in seed rain and establishment conditions in a tropical forest. They are of the order of scales at which seed rain and establishment conditions vary and over which seedlings compete – that is, small enough for seed rain and establishment conditions within sites to be relatively homogeneous and large enough to encompass competitors for the same regeneration site (although not large enough to encompass all competitors for the same canopy position). The temporal scales used in calculating the limitation measures are of the order of the time it takes for an open regeneration site to be pre-empted in this forest and for seedlings and saplings to establish.

Study site and species

The case-studies we present are from a seasonally moist tropical forest on Barro Colorado Island (BCI), Panama. Annual rainfall averages 2600 mm, with a dry season from late January through mid-April. The geology and hydrology of the 1500 ha island are described in Dietrich *et al.* (1982) and its flora and vegetation in Croat (1978) and Foster and Brokaw (1982). The study was conducted within the 50 ha Forest Dynamics Plot on the central plateau (described in Hubbell and Foster, 1983).

The target species were chosen to provide a diverse sampling of the range of abundances, dispersal characteristics and adult spatial patterns present among tree species on BCI (Table 3.1): *Beilschmiedia pendula* (Sw.) Hemsl. (*Lauraceae*), *Cordia alliodora* (Ruiz & Pav.) Oken (*Boraginaceae*), *Terminalia amazonia* (J. F. Gmel.) Exell (*Combretaceae*) and *Trichilia tuberculata* (Triana & Planch.) C. DC. (*Meliaceae*).

Data collection

Seed-fall data were collected from 200 seed traps placed along trails within the 50 ha Forest Dynamics Plot (Wright *et al.*, 1999). Each seed trap consists of a square, 0.5 m^2 polyvinyl chloride (PVC) frame supporting a shallow, open-topped, 1 mm nylon-mesh bag, suspended 0.8 m above the ground on four PVC posts. Beginning in January 1987 and continuing to the present, seed traps have been emptied weekly and all seeds, fruits and seed-bearing fruit fragments > 1 mm in diameter have been identified to species. The count of mature fruits was multiplied by the total number of seeds per fruit (S.J. Wright, unpublished data) and was added to the count of

Table 3.1. Demographic and life-history characteristics of the focal species. Tree density is the density of trees greater than 10 cm diameter at breast height (dbh) on the Forest Dynamics Plot in 1995. Adult size is the estimated minimal size of first reproduction (R.B. Foster and S.J. Wright, unpublished data). Adult density is the density of trees greater than the threshold adult size on the Forest Dynamics Plot. Seedling density is the average density of first-year seedlings per year as estimated from 7 years of censuses of 600 1 m^2 plots. Seed density is the density of seeds arriving per year as estimated from 13 years of censuses of 200 0.5 m^2 seed traps. Regeneration habitat of *Beilschmiedia* from Hubbell and Foster (1983) and Welden *et al.* (1991), of *Cordia* from Augspurger (1984) and Welden *et al.* (1991), of *Terminalia* from Augspurger (1984) and of *Trichilia* from Welden *et al.* (1991). Seed masses of *Beilschmiedia* from Wenny (2000), of *Cordia* and *Terminalia* from Augspurger (1986) and of *Trichilia* from S.J. Wright (unpublished data). Dispersers from Croat (1978), Leighton and Leighton (1982) and S.J. Wright (unpublished data).

	Beilschmiedia pendula	*Cordia alliodora*	*Terminalia amazonia*	*Trichilia tuberculata*
Tree density (ha^{-1})	5.9	1.3	0.56	34
Adult size (cm dbh)	20	13	20	20
Adult density (ha^{-1})	3.6	1.1	0.40	17
Seedling density (ha^{-1})	1.5×10^3	1.1×10^2	0	6.8×10^3
Seed density (ha^{-1})	6.8×10^3	1.9×10^4	7.1×10^4	2.5×10^5
Dioecious	No	No	No	Yes
Regeneration habitat	Prefers slopes, shade-tolerant	Requires gaps	Requires large gaps	Generalist, very shade-tolerant
Seed mass (g)	12.89	0.0063	0.0041	0.15
Dispersers	Mammals, large birds and a bat	Wind	Wind	Mammals and large birds

simple seeds to obtain the estimated total number of seeds falling into the traps. To avoid having partial data for a fruiting season, only data collected in the 12 complete phenological fruiting years of each species falling between 1 January 1987 and 1 January 2000 were used in the analyses here.

Seedling data were collected from 600 seedling plots, three matched to each seed trap (Harms *et al.*, 2000). Each seedling plot is 1 m × 1 m and located 2 m distant from its associated seed trap on one of the sides away from the nearest trail. Beginning in January–March 1994 and continuing annually until the present, all seedlings < 50 cm tall were measured and, if new, identified and marked.

Observed seed limitation

Observed seed limitation, source limitation and dispersal limitation were calculated directly from the data for the 200 seed traps (see Box 3.1 for methods). Measures were calculated at the 0.5 m^2 scale of the traps and for temporal periods of 1, 2, 3, 4, 6 and 12 years for non-overlapping subsets of the data (Fig. 3.1). We used the stochastic definition of a uniform distribution in calculating source and dispersal limitation (see Box 3.1). We found considerable interannual variation in limitation measures, a reflection of interannual variation in seed production (Wright *et al.*, 1999) and seed dispersal (unpublished analyses).

Comparing seed limitation measures among the species, we observe patterns consistent with their abundances, distributions and life histories (Tables 3.1 and 3.2, Fig. 3.1). *Beilschmiedia* is quite common but concentrated on the slopes of the plot (Hubbell and Foster, 1983). Its seeds fail to reach a large proportion of the plot (high seed limitation), even at the larger temporal scales at which population-level production of its large seeds is adequate to reach most sites (low source limitation). *Cordia* is not very common and only moderately well dispersed (Augspurger, 1986). It also shows high levels of seed limitation, despite high seed production (of small seeds) per adult. *Terminalia*, while rare, produces its tiny seeds in very large numbers and disperses them very well (Augspurger, 1986). It has low seed limitation even at the 1-year scale, and almost no seed limitation at the 6- and 12-year scales. *Trichilia* is abundant throughout the BCI plot but not very well dispersed (Muller-Landau *et al.*, 2001). It also has relatively low seed limitation; what seed limitation it does have is due entirely to dispersal limitation.

Projected seed limitation

We calculated projected seed limitation and its components from simulations of seed rain across the plot, with the simulations based on fitted functions for seed production and seed dispersal.

Data on the locations and numbers of seeds in seed traps and on locations and sizes of adults in the 50 ha plot were used to fit the probability of seed arrival as a function of distance from an adult tree and to fit fecundity as a function of tree size. Starting from a set of parameters specifying these functions, expected seed rain into a given trap was calculated as the sum of contributions from conspecific adult trees on the plot. These contributions were determined by tree sizes and distances to traps, according to the parameter values. We then searched for parameter values that produced the best fit to the observed seed rain, using maximum likelihood methods (Ribbens *et al.*, 1994; Clark *et al.*, 1998). Likelihood ratio tests were used to determine whether the best-fit model was significantly better than a null model that assumed uniform expected seed rain across the plot. Seed dispersal kernels giving expected seed rain as a function of distance from source tree were fitted with negative exponential functions (Turchin, 1998), and fecundity was assumed to be proportional to basal area (as in Ribbens *et al.*, 1994). We used a negative binomial distribution to model variation in annual seed fall into each trap, thus allowing for contagion or clumping of seeds due to factors not included in the model (Clark *et al.*, 1998).

Using the fitted functions for seed production and seed dispersal, we then simulated seed rain to one in every 50 sites of size 0.5 m^2 across the entire 50 ha plot, and calculated seed

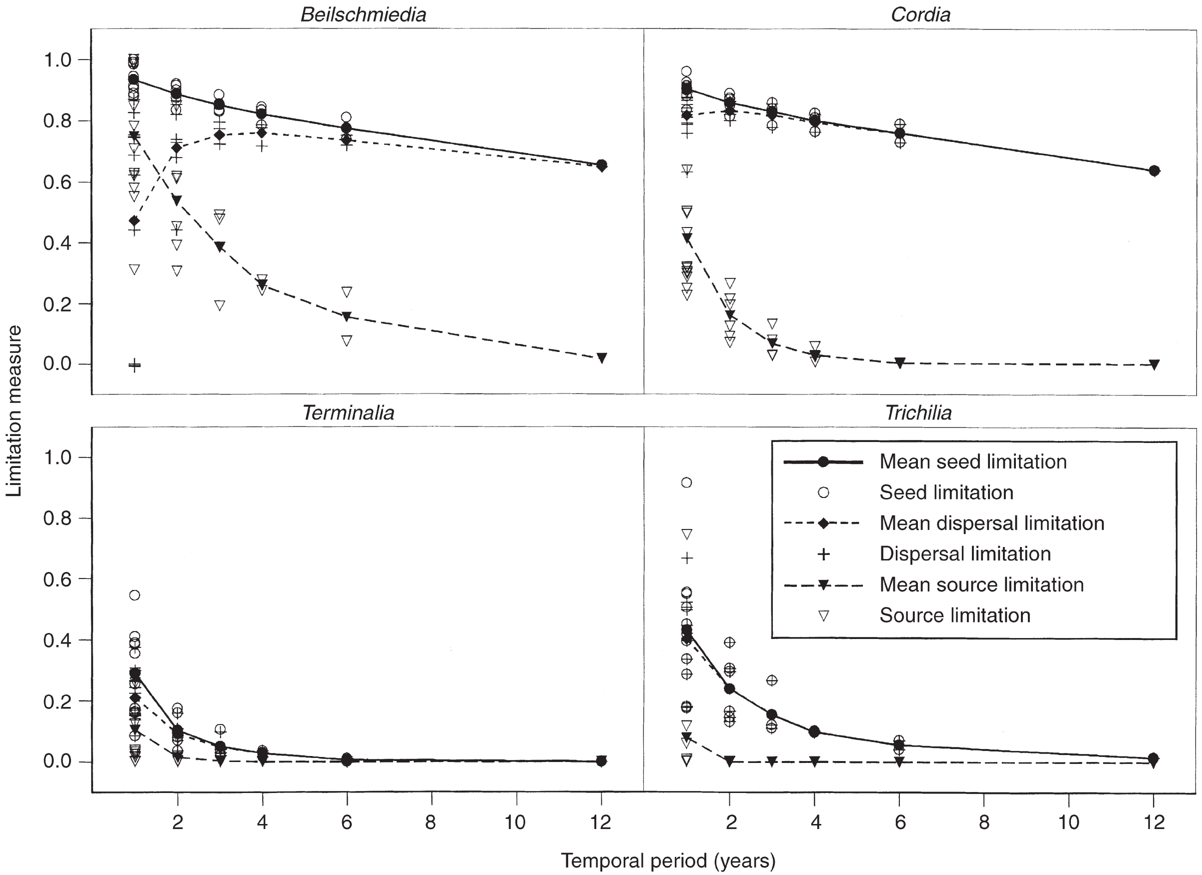


Fig. 3.1. Fundamental seed limitation (the proportion of sites not receiving seeds), source limitation (the proportion of sites that would not receive seeds if all were distributed randomly) and dispersal limitation (the proportion of sites that would have been reached under random dispersal but are not actually reached) at the spatial scale of 0.5 m^2 and temporal scales of 1–12 years, as calculated from the seed-trap data. Values for individual years or non-overlapping blocks of years are shown with open symbols; mean values across periods are shown with filled symbols.

limitation measures from the simulated seed rain. We refer to these as measures of projected seed limitation because they are calculated, not from direct observations, but from estimates of seed rain, themselves based on a model that was fitted to the data. One advantage of projected measures is that they can be calculated across a much larger area than could realistically be sampled; thus, we calculate projected limitation for simulated seed rain across the whole plot, as well as for simulated seed rain only to the 200 traps. There were some small differences between projections to the 200 traps and to the plot as a whole, reflecting the fact that traps happen to sample sites on average closer to *Beilschmiedia* and further from *Cordia* than the plot as a whole (Table 3.2).

Projected limitation measures were always within the range of observed limitation measures for the same species and scales, although sometimes quite different from the mean of observed values (Table 3.2). For all species, projected seed limitation closely matched mean observed seed limitation. Projected source limitation was quite different from mean observed source limitation, except in the case of *Beilschmiedia*. The poor match for *Cordia* was due to much lower projected mean seed arrival per site than was observed among the 200 traps, where a single trap received more seeds than all other traps combined (thus, projected source limitation may actually better represent source limitation for the plot as a whole). For *Terminalia* and *Trichilia*, mean seed densities were well fitted, but mean observed source limitation was much higher than projected source limitation because of huge interannual variation in mean seed densities. The non-linear dependence of source limitation upon seed density makes the mean of source limitation for years with varying seed density much higher than source limitation for a year with mean seed density – mean observed seed limitation reflects the former, while projected seed limitation effectively reflects the latter. *Beilschmiedia* source limitation values matched, despite considerable interannual variation in seed density, because source limitation is a nearly

Table 3.2. Observed and projected seed rain and limitation measures at the 0.5 m^2 spatial scale and 1-year temporal scale. Observed values were calculated separately for 12 different years and are given as mean ± standard deviation [minimum, maximum].

Tree species	Observed (200 traps)	Projected (200 traps)	Projected (whole plot)
Beilschmiedia pendula			
Seeds per site	0.34 ± 0.34 [0.00, 1.17]	0.30	0.23
Seed limitation	0.93 ± 0.05 [0.88, 1.00]	0.92	0.92
Source limitation	0.75 ± 0.22 [0.31, 1.00]	0.74	0.79
Dispersal limitation	0.47 ± 0.37 [–0.01, 0.87]	0.68	0.63
Cordia alliodora			
Seeds per site	0.97 ± 0.41 [0.12, 1.49]	0.48	0.65
Seed limitation	0.90 ± 0.03 [0.84, 0.96]	0.90	0.89
Source limitation	0.41 ± 0.19 [0.23, 0.89]	0.62	0.52
Dispersal limitation	0.82 ± 0.07 [0.63, 0.89]	0.75	0.76
Terminalia amazonica			
Seeds per site	3.57 ± 2.52 [1.23, 9.96]	3.73	3.66
Seed limitation	0.29 ± 0.13 [0.09, 0.55]	0.28	0.27
Source limitation	0.10 ± 0.11 [0.00, 0.29]	0.02	0.03
Dispersal limitation	0.21 ± 0.08 [0.08, 0.37]	0.26	0.25
Trichilia tuberculata			
Seeds per site	12.47 ± 12.36 [0.30, 37.31]	13.86	13.09
Seed limitation	0.43 ± 0.20 [0.18, 0.92]	0.43	0.44
Source limitation	0.08 ± 0.21 [0.00, 0.74]	0.00	0.00
Dispersal limitation	0.40 ± 0.14 [0.18, 0.67]	0.43	0.44

linear function of seed density for seed densities below 1. (*Beilschmiedia* and *Cordia* values were mostly within this range; *Terminalia* and *Trichilia* densities were mostly much higher.) Projected dispersal limitation was relatively close to the mean observed dispersal limitation for all species but *Beilschmiedia*. Mean observed dispersal limitation in *Beilschmiedia* was depressed by 4 years with zero dispersal limitation; in these years, only three or fewer seeds were captured, each in different traps.

Observed establishment limitation

We calculated observed seedling limitation – the proportion of plots in which seedlings did not emerge – at the 1 m^2 scale of the seedling plots and for temporal periods of 1, 2, 3 and 6 years (see Box 3.1 for methods). Because seed data and seedling data were collected at different spatial scales, realized establishment limitation could not be calculated exactly, but only bounded. First, we calculated bounds on seed limitation at the 1 m^2 scale from data at the 0.5 m^2 scale, by considering the probability that seeds arrive in the two halves of the 1 m^2 plots. Seed arrival in the two halves will almost certainly be correlated; in the absence of any data on this correlation, we made calculations based on the extreme assumptions of perfect positive correlation and no correlation. If seed arrival in adjacent 0.5 m^2 plots is perfectly positively correlated, then seed limitation at the 1 m^2 scale is equal to seed limitation at the 0.5 m^2 scale. If seed arrival is entirely uncorrelated, then seed limitation at the 1 m^2 scale is equal to the square of seed limitation at the 0.5 m^2 scale. From these estimates, we then calculated corresponding bounds upon establishment limitation.

Establishment limitation is strong in all four species; correspondingly, seedling limitation is always substantially higher than seed limitation (Fig. 3.2). Differences in establishment limitation across species parallel differences in shade tolerance. No seedlings of the very light-demanding *Terminalia* ever appear in any of the census plots, despite its abundant seed rain. Moderately light-demanding *Cordia* appears in some plots, but still exhibits high establishment limitation, which combines with moderate seed limitation to effect strong seedling limitation. *Trichilia* and *Beilschmiedia*, both shade-tolerant, show lower establishment limitation. Given *Trichilia*'s low seed limitation, establishment limitation is nevertheless the main factor contributing to significant seedling limitation at the 1 m^2 scale – although this limitation is still much lower than for any other species examined. For *Beilschmiedia*, with its very large seeds and high shade tolerance, seed limitation appears to be somewhat more important than establishment limitation at these scales, although better estimates of seed limitation at the 1 m^2 scale are needed to evaluate their relative magnitude with confidence.

Discussion

Interpreting limitation measures

The examples presented here illustrate how we can assess seed and seedling limitation and their components from data routinely collected in studies of seed dispersal. The results of such analyses can provide information about the success of a species in distributing its seeds and seedlings and on the relative importance of factors limiting its ability to do so. However, as is the case with any analysis, the insight that can be obtained is circumscribed by the amount and scale of data collection and the appropriateness of the underlying assumptions to the study system.

As our results illustrate, limitation measures change in both absolute and relative magnitude across scales. The spatial and temporal scales we examined in our case-studies are relevant for understanding seed and establishment limitation of seedling and small sapling abundances in this tropical forest, but they are not the only relevant scales. We anticipate that future research that examines how spatiotemporal correlations change across scales will provide a basis for extrapolation across scales within individual systems. Even then, however, it will be necessary to gather at least some data at all scales at which limitation measures are calculated or extrapolated.

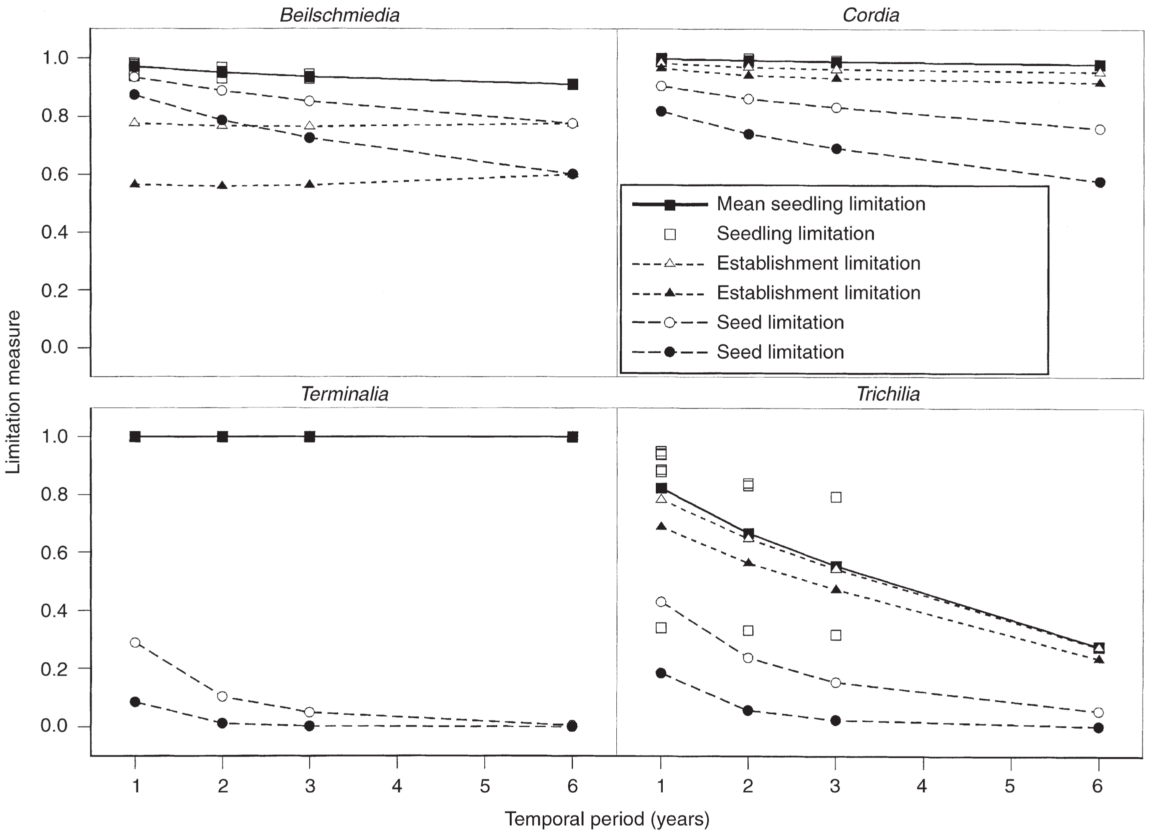


Fig. 3.2. Fundamental seedling limitation (the proportion of sites in which no new seedling recruits emerge in the given time period), establishment limitation (the proportion of sites receiving seeds in which no seedlings emerge) and seed limitation (the proportion of sites not receiving seeds) at the spatial scale of 1 m^2 and temporal scales of 1–6 years, as estimated from the seedling plot and seed-trap data. Values of seed limitation for individual years or non-overlapping blocks of years are shown with open squares; mean values across periods are shown with filled squares. Upper and lower bounds on seed and establishment limitation were estimated using two extreme assumptions on how seed arrival at the 1 m^2 spatial scale relates to seed arrival at the 0.5 m^2 spatial scale: perfect independence of seed rain into adjacent 0.5 m^2 plots (upper bound on seed limitation, lower bound on establishment limitation) and perfect positive correlation (lower bound on seed limitation, upper bound on establishment limitation).

One shortcoming of our study is that rare microhabitats, such as canopy gaps, were inadequately sampled. The 200 sets of seed traps and seedling plots we used provide a representative sample of microhabitats – which necessarily means very few fall within gaps, a rare but important habitat for establishment (Hubbell *et al.*, 1999). For species with restricted regeneration niches, larger samples of their rare but preferred habitats may be needed to reliably estimate establishment limitation. For example, we encountered not a single seedling of *Terminalia*, a large gap specialist, and thus calculated its seedling limitation and establishment limitation to be 1, both obviously overestimates. In contrast, in their 1996 censuses of all the canopy gaps in the plot, Dalling *et al.* (1998) found a total of 19 *Terminalia* seedlings of various sizes in 15 different 1 m × 1 m plots. If these are the only seedlings on the 50 ha plot, then the density of first-year seedlings is less than 0.38 ha^{-1}, seedling limitation at the 1 m^2 1-year scale is at least 0.99997 and establishment limitation is between 0.99996 and 0.99997.

While the examples presented involved only fundamental seed limitation, data such as these can potentially be combined with information on establishment to estimate realized seed limitation as well. Data on the proportions of sites with different establishment conditions and on establishment likelihood in each of these sets of conditions can be combined with information on seed rain to predict likely seedling numbers under current conditions and under conditions of seed augmentation. Density-dependent establishment could also be incorporated in such a framework; indeed, this can be expanded to a full-scale individual-based, spatially explicit model enabling simulations to test population limitation resulting from many different factors (as in Pacala *et al.*, 1996). However, care should be taken that model complexity does not outstrip the quality of the data available to estimate model components.

Ideally, observational studies of seed rain should be combined with experimental studies to develop a complete understanding of seed and establishment limitation. It will soon be possible to compare the results of the observational studies reported here with those of seed addition experiments currently being conducted on BCI by Jens-Christian Svenning. Preliminary results from these experiments with 32 species suggest strong realized seed limitation in this community (Jens-Christian Svenning, November 2000, personal communication), which accords with our results here.

Implications for understanding communities

To understand the importance of seed rain and regeneration niches for community structure and dynamics, we need to consider seed and establishment limitation of all species in a community. Our results suggest that seedling abundances of most tropical tree species are likely to be both strongly seed-limited and strongly establishment-limited, with considerable variation across species. Extrapolation from the species we examined is difficult because all are somewhat atypical for BCI; they have either high abundance (*Beilschmiedia*, *Trichilia*) or small seeds (*Cordia*, *Terminalia*). Not coincidentally, these properties ensure that seeds arrive in our seed traps in sufficient numbers to allow detailed analyses. In contrast, 67% of the 305 tree species present in the 50 ha plot are rare (< 1 adult ha^{-1}) and 81% have seeds larger than those of *Cordia* and *Terminalia* – that is, too large to allow production of millions per tree (Grubb, 1998). Thus, most species produce insufficient seeds to reach a majority of potential regeneration sites; they are source-limited at annual 1 m^2 scales. Further, even if we consider larger spatiotemporal scales at which population seed production is in theory sufficient to cover all sites, most sites will not be reached by seeds of any given species because virtually all species are strongly dispersal-limited. Most seeds remain near parent trees and those that do travel further are often deposited in clumps, reducing the number of sites that are colonized. Exceptions include a few pioneer species (e.g. *Terminalia*) that have very high seed production and long dispersal distances, allowing them to reach most sites in most years. To do so requires small seeds, which results in strong establishment limitation. Thus, most species in this forest are strongly seed-limited, with 88% reaching on average fewer than 5% of traps per year. The only species to largely escape both seed and establishment limitation are extremely abundant and widely distributed shade-tolerant species with moderate or large seeds, such as *Trichilia* in this forest and monodominants elsewhere (Hart *et al.*, 1989).

Our results provide some support for the hypothesis of a trade-off among species between colonization ability and establishment ability, mediated by seed size. The four species examined here exhibit a positive relationship between seed mass and establishment probability (the number of seedlings per seed) and a negative relationship between seed mass and seed production per unit basal area, as do species in the BCI assemblage as a whole (S. Joseph Wright, unpublished data) and in other systems (Westoby *et al.*, 1996; Grubb, 1998). Thus, in general, larger-seeded species are expected to suffer more seed limitation (due to more source limitation) and less establishment limitation than smaller-seeded species, consistent with results in temperate forests (Clark *et al.*, 1998) and grasslands (Kiviniemi and Telenius, 1998; Turnbull *et al.*, 1999). However, both seed and establishment limitation also depend upon abundance; higher abundance tends to reduce both types of limitation because it corresponds to increased seed sources (reproductive adults) and increased average seed number per site reached (providing more chances to establish at each site).

Pervasive seed limitation depresses local species diversity (alpha diversity) because not all potential species that might coexist in an area will reach it. At the same time, it enhances larger-scale diversity (beta diversity), because of stochastic variation in which species end up arriving and dominating in different areas (Horn, 1981). Essentially, seed limitation slows competitive dynamics and enhances opportunities for non-equilibrium coexistence on large scales (Hubbell, 1979; Hubbell and Foster, 1986). Experimental studies show that when seed limitation is decreased through addition of seeds of multiple species, local species diversity within seed addition plots increases (Tilman, 1997).

The negative relationship between seed limitation and establishment limitation across species also acts to increase local species diversity, enhancing coexistence of species according to a competition–colonization trade-off (Hastings, 1980; Tilman, 1994). This diversity enhancement is qualitatively different from that of pervasive seed limitation alone because it is equilibrium, rather than non-equilibrium: differences among species in competition–colonization strategies stabilize their coexistence, while pervasive seed limitation merely slows competitive exclusion. This effect has been demonstrated in large-scale, spatially explicit models: model communities in which species differ according to a competition–colonization trade-off have more species than those in which species are equivalent (Chave *et al.*, 2001). In real plant communities, this trade-off appears to be mediated by seed size, as discussed earlier. The best demonstration of the effects of seed size on seed and establishment limitation is a multispecies seed addition experiment by Turnbull *et al.* (1999). When no or few seeds of each species were added, small-seeded species were somewhat more abundant than large-seeded species. When many seeds of each species were added in equal numbers, seed limitation was essentially removed completely; thus, the large-seeded species dominated, nearly excluding the small-seeded species.

Conservation Implications

Consideration of seed and establishment limitation can help us understand the effects of human activity on tropical forests, and thus inform conservation. Anthropogenic habitat modification has a direct impact on establishment limitation and indirectly affects seed limitation. When a habitat is modified to become entirely unsuitable for regeneration (e.g. paved, built upon, farmed), total establishment limitation increases for all species, and seed limitation within the remaining suitable habitat may also increase, due to the loss of seed input from the modified area. Species with longer dispersal distances and those that rely on vectors that cross into the newly unsuitable habitat (wind, some small animals) will be disproportionately affected, because they will deposit more seeds in these areas. At the same time, the creation of an unsuitable habitat is usually accompanied by habitat modification to sites on the edge, which experience greater light availability, reducing the establishment limitation of light-demanding species and giving them an advantage relative to shade-tolerant species (Laurance *et al*., 1998).

Loss of frugivorous animals to hunting can lead tree species that depend on these animals for seed dispersal to suffer increased dispersal limitation and seed limitation in their absence (e.g. Wright *et al*., 2000). These tree species may also experience increased establishment limitation, since seeds in high concentrations near parents are more likely to suffer predation and less likely to successfully establish (Janzen, 1970; Connell, 1971; Wright *et al*., 2000). Large-seeded trees are disproportionately affected, because they are most likely to depend on large animals for dispersal and large animals are the most often hunted (Redford and Robinson, 1987).

The differential effects of these anthropogenic disturbances on different tree species upset the competitive balances that contribute to the equilibrium coexistence of tree species, changing community composition and diversity (Leigh *et al*., 1993; Laurance *et al*., 1998). The best hope for conserving and restoring tropical forests is to conserve and restore the processes that maintain these competitive balances, including differential seed and establishment limitation, which depend fundamentally on the disperser assemblage and the relative abundances of establishment conditions.

Conclusions and future directions

Much remains to be learned about the magnitude, causes and consequences of recruitment limitation in tropical forests and elsewhere. The available evidence suggests that most tropical tree species are likely to be strongly seed-limited, with seeds reaching only a small minority of potential regeneration sites because of low adult abundances and limited dispersal. Theoretical studies show that such limitation and observed trade-offs among species between seed and establishment limitation could strongly influence community dynamics and contribute to the maintenance of species diversity. More studies are needed on more species comprising a wider and more representative sample of abundances and life histories and at larger spatial and temporal scales. Integrated studies of seed dispersal and subsequent establishment, especially if they include seed-sowing experiments, will greatly contribute to our understanding of the population dynamics of individual species and, ultimately, of community structure and dynamics.

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