

Alternative spatial sampling in studies of plant demography: consequences for estimates of population growth rate

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Received: 25 July 2008 / Accepted: 9 September 2009 / Published online: 19 September 2009
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Abstract Ecologists commonly use matrix models to study the population dynamics of plants. Most studies of plant demography use plot-based methods to collect data, in part, because mapped individuals are easier to relocate in subsequent surveys and survey methods can be standardized among sites. However, there is tremendous variation among studies, both in terms of plot arrangement and the total area sampled. In addition, there has been little discussion of how alternative sampling arrangements influence estimates of population growth rates (λ)

calculated with matrix models. We surveyed the literature to determine what sampling designs are most used in studies of plant demography using matrix models. We then used simulations of three common sampling techniques—using a single randomly placed plot, multiple randomly placed plots, and systematically distributed plots—to evaluate how these alternative strategies influenced the precision of estimates of λ . These simulations were based on long-term demographic data collected on 13 populations of the Amazonian understory herb *Heliconia acuminata* (Heliconiaceae). We found that the method used to collect data did not affect the bias or precision of estimates in our system—a surprising result, since the advantage in efficiency that is gained from systematic sampling is a well-known result from sampling theory. Because the statistical advantage of systematic sampling is most evident when there is spatial structure in demographic vital rates, we attribute this result to the lack of spatially structured vital rates in our focal populations. Given the likelihood of spatial autocorrelation in most ecological systems, we advocate sampling with a systematic grid of plots in each study site, as well as that researchers ensure that enough area is sampled—both within and across sites—to encompass the range of spatial variation in plant survival, growth, and reproduction.

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Keywords Lambda · Matrix models · Plot · Population dynamics · Sampling · Vital rates

Introduction

Matrix models (Lefkovich 1965; Leslie 1945) are a powerful tool with which to study the dynamics and demography of structured populations, and they are increasingly applied in disciplines ranging from conservation biology to evolutionary ecology. While these models have often been used to project the asymptotic growth rate of a population (i.e., λ), increasingly sophisticated analytical and computational techniques also allow one to evaluate the effects of demographic and environmental stochasticity on λ , as well as explore the underlying mechanisms affecting the rate of population growth (reviewed in Caswell 2001; Morris and Doak 2002). This has made them increasingly useful in attempts to understand how environmental variability, including global change phenomena, influences the dynamics and demography of populations (reviewed in Boyce et al. 2006).

The increasing popularity of matrix models has resulted in an extensive literature describing their construction, interpretation, assumptions, and limitations (e.g., Bierzychudek 1999; de Kroon et al. 2000; Wisdom et al. 2000). However, there is a surprising dearth of information on how to properly design sampling efforts with which to collect demographic data (Doak et al. 2005), and previous efforts have focused primarily on the sample sizes needed to adequately estimate the vital rates of different stage classes. For instance, Gross (2002) suggested using prior information about the relative demographic importance of stage classes to increase sampling of the more “important” ones, thereby minimizing the variance of estimates of λ . In contrast, Münzbergová and Ehrlén (2005) advocated sampling equal numbers of individuals across all stage classes, which they argue provides equally accurate and more precise measures of λ and elasticities.

In addition to the number of individuals to be sampled, an important factor to consider when establishing demographic studies is the spatial arrangement of the sampling units. The data used for parameterizing matrix models of plants and other sessile organisms are often collected in permanent plots (e.g., Bierzychudek 1999; Gotelli 1991; Parker 2000; Silvertown et al. 1993). Although there are many scientific reasons for using plot-based methods (e.g., relating seedling recruitment to reproductive plants), the advantages of plot-based methods are often logistical—mapped individuals are easier to relocate in subsequent surveys,

survey methods can be standardized among sites, and surveys can be completed more quickly because individuals are often in close proximity to each other. However, there is tremendous variation among studies using plot-based sampling to collect demographic data, both in terms of plot arrangement and the total area sampled. For instance, Batista et al. (1998) mapped and tagged all *Fagus grandifolia* ≥ 2 cm dbh in a 4.5 ha plot. In contrast, Silva Matos et al. (1999) studied the demography of the understory palm *Euterpe edulis* by sampling 100 randomly placed plots (5 m \times 5 m each) within a 1-ha area. Finally, Valverde and Silvertown (1998) sampled the perennial herb *Primula vulgaris* in 1 m² quadrats located at regular intervals along a transect. These studies illustrate the three common types of plot-based sampling used in demographic studies: (1) identifying all individuals within a single plot; (2) measuring individuals within multiple, randomly placed subplots located within a larger area; and (3) systematically arranging plots at regular intervals along transects within the study area. Understanding how these alternative sampling schemes influences estimates of λ and other demographic parameters is essential, particularly in light of the potential effects of spatial variation and spatial autocorrelation in vital rates (Horvitz and Schemske 1995; Legendre 1993; Moloney 1988) and the large investment of time and capital required to establish demographic studies (Condit 1998).

In order to evaluate how alternative methods of data collection influence estimates of λ , we reviewed the ecological literature and conducted data-based simulations of three commonly used sampling techniques—a single randomly placed plot, multiple randomly placed plots, and systematically arranged plots. Our study addressed the following questions: (1) What sampling strategies are used in studies of plant demography? (2) How does the accuracy and precision of estimates of the population growth rate vary among the three principal sampling methods used?

Materials and methods

What sampling strategies are used in studies of plant demography?

In order to quantify the frequency of different sampling designs in demographic studies of plants,

we conducted a Web of Science search on March 15, 2006 using combinations of the search terms “matrix model,” “plant,” “demography,” and “population.” From each resulting paper, we extracted the total area sampled and number of plots sampled for each matrix model parameterized. We also assigned each study to one of the following five sampling methods: completely surveying a single plot (S), sampling randomly dispersed quadrats (RM), sampling systematically distributed quadrats (SM), completely surveying “populations” (P), and the sampling of individuals without using delineating plots or populations (I). We also recorded the number of species studied in each of the following categories: shrubs, trees, perennial herbs, and other (e.g., geophytes, grasses, and sedges). If a study used the same sampling process to study multiple species, we counted these studies as a single study. However, when a study examined a single species using multiple sampling strategies, we counted these separately. When different methods were used to sample for different stage classes, we recorded the design used to sample the largest individuals.

Do different sampling methods affect the precision of population growth estimates?

In order to address this question, we conducted simulations using data collected during a long-term and large-scale study of plant demography conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located ca. 60 km north of Manaus, Brazil (2°30'S, 60°W). The focal species for this study was *Heliconia acuminata* (Heliconiaceae), a perennial herb native to central Amazonia and the Guyanas (Berry and Kress 1991). Descriptions of the study site and *Heliconia* Demography Project can be found elsewhere (Bierregaard et al. 2002; Bruna 2003; Bruna and Kress 2002). Briefly, one 5,000 m² plot (50 m × 100 m) was established in each of 13 BDFFP sites: seven forest fragments and six continuous forest sites (Table 1). Each of these 50 m × 100 m plots was subdivided into 50 contiguous subplots (10 m × 10 m), making these data ideal for simulating alternative sampling methods that require sampling plots of different sizes or subsampling from a larger population.

Table 1 Results of simulations determining the minimum sampling area necessary for λ_s to be within 1% of the whole-plot estimate of λ

Plot	BDFFP Reserve No. ^a	Habitat type ^b	<i>Heliconia acuminata</i> density in 2003 ^c	Years surveyed	Sampling (m ²) necessary for 1% precision		
					RS	RM	SM
FF-1	2107	1 ha	214	7	3,000	3,600	2,400
FF-2	2108	1 ha	161	7	4,500	3,600	1,200
FF-3	5753	1 ha	206	7	2,500	4,000	2,800
FF-4	5751	1 ha	250	7	2,500	2,800	2,100
FF-5	2206	10 ha	162	7	2,500	3,200	2,800
FF-6	5754	10 ha	402	7	2,500	1,600	1,000
FF-7	5752	10 ha	577	7	2,500	2,800	2,100
CF-1	1301	CF	753	7	2,500	2,400	1,200
CF-2	1501	CF	555	7	1,600	2,000	1,200
CF-3	1501	CF	703	7	1,600	2,400	1,000
CF-4	Porto Alegre	CF	112	5	4,500	4,500	4,500
CF-5	Dimona	CF	171	5	4,500	3,800	4,000
CF-6	Cabo Frio	CF	235	3	4,500	5,000	4,500

Three alternative sampling methods were compared: a single quadrat randomly located within a plot (RS), multiple quadrats randomly located within a plot (RM), and a grid of systematically arranged quadrats (SM). The method requiring the least for 1% precision is indicated in *bold*

^a CF-4–6 have no official BDFFP numbers. We therefore indicate the name of the ranch in which they are located instead

^b Abbreviations: *1 ha* 1 ha fragments, *10 ha* 10 ha fragments, *CF* Continuous forest

^c From Bruna (2003)

Since 1998, the 13 plots have been surveyed annually to record the survivorship of individual plants, the emergence of new seedlings (i.e., newly established plants less than 1-year-old), and the identity of individuals flowering. We also measured each plant's size by recording the number of vegetative shoots it had; previous study has shown that shoot number is highly correlated with demographic parameters such as the probability of flowering and survivorship (Bruna 2003; Bruna and Kress 2002). The analysis presented here is based on data from the 1998–2005 surveys; we marked, measured, and recorded the fates of $N = 6,591$ plants during this time interval ($N = 3,842$ in continuous forest, $N = 1,688$ in 10 ha fragments, and $N = 1,061$ in 1 ha fragments). In 2003, the density of *Heliconia acuminata* in the plots ranged from 256 to 2,248 plants ha^{-1} .

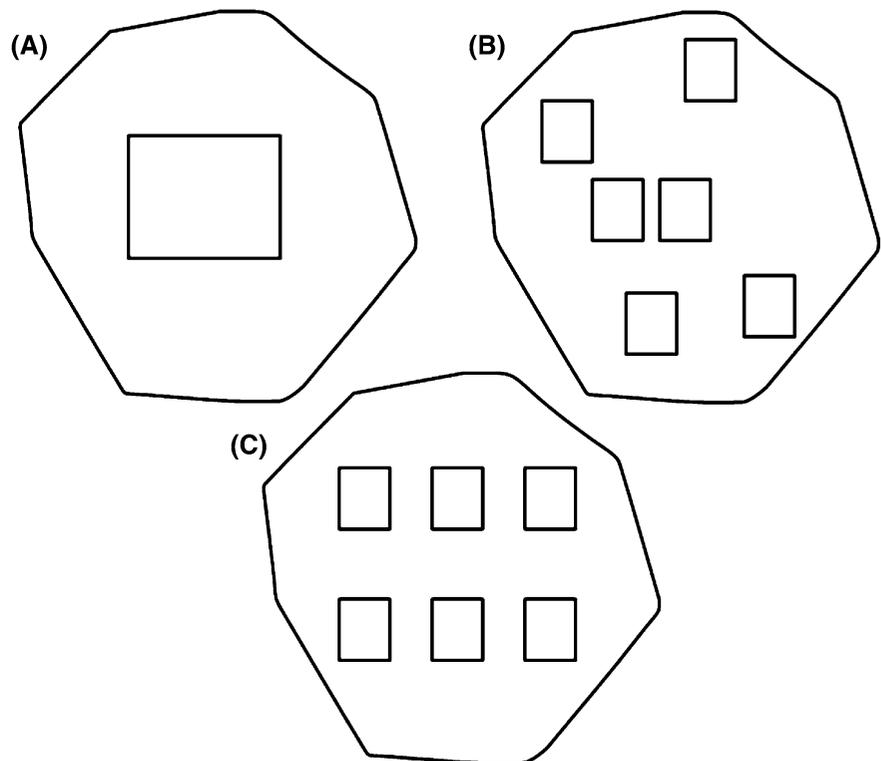
Simulations of alternative sampling methods

We simulated sampling in each of our 50 m \times 100 m plots using the three most commonly used sampling methods: a single quadrat that was randomly located in each plot (RS), multiple quadrats randomly located in the plot (RM), and a grid of systematically

arranged quadrats (SM; see Fig. 1). The dimensions of the plots used in simulations of RS sampling ranged from 20 m \times 20 m to 50 m \times 100 m, while RM sampling consisted of randomly selecting 4–50 of each plot's 10 \times 10 m quadrats. An SM sample consisted of a grid of 4–50 systematically arranged quadrats chosen by the *sp* package for R (Pebesma and Bivand 2005). Therefore, while the three methods were tested over the same range of sampling intensities, the resolution of sampling intensities differed among the methods. This difference in resolution did not affect conclusions emerging from our analyses (see “Results”).

Simulations were conducted as follows: for each site, sampling method and sampling intensity, we began by selecting 50 random arrangements of the appropriate number of quadrats. For each of these 50 samples, we calculated transition matrices based on lower-level vital rates (sensu Morris and Doak 2002) for each year of demographic data available using the plants found in those quadrats. The demographic models and their construction are described elsewhere (Fiske et al. 2008). Briefly, each *H. acuminata* was assigned to one of six stages: seedlings (all plants <1-year-old; stage 1) and plants with 1, 2, 3, 4, or ≥ 5

Fig. 1 Illustration of the three alternative sampling methods commonly used in demographic studies and used in our simulations **a** single randomly located plot (RS), **b** multiple randomly located plots (RM), and **c** a grid of systematically arranged plots (SM). Note that in this example the area sampled by each of the three methods is the same



vegetative shoots (stages 2–6). Although *H. acuminata* seedlings have only one shoot, they were placed in a separate category because their survival rate differs from that of non-seedling plants with one shoot (Bruna 2003). From one year to the next, plants can grow into larger size classes, remain in the size class, regress into smaller size classes, or die. The one exception to this rule is surviving seedlings, all of which were reclassified as one-shoot plants in the second year.

We then used the transition matrices to estimate the stochastic population growth rate (hereafter, λ_s) with the random transition matrix method (Caswell 2001) for each combination of site \times sampling method \times sampling intensity. An initial population vector with one individual in each stage class was multiplied by a transition matrix selected with equal probability and with replacement from the set of annual matrices. Because some sites were not surveyed in some years, the number of possible transition matrices for each site varied: 7 matrices for 10 of the sites, 5 for two of the sites and 3 for one site (Table 1). The resulting population vector was then multiplied by another randomly selected transition matrix; this process was repeated 30,000 times and the population growth rate was then calculated as:

$$\prod_{i=1}^{30,000} \frac{N_{i+1}}{N_i} \tag{1}$$

where N_i was the population size at time i summed across all stage classes. Samples that lacked individuals in at least one size class for a year or more (i.e., incomplete matrices) were common when the total area sampled in simulations was small. Although these samples make it impossible to correctly calculate the annual transition matrix, eliminating them and drawing alternatives ones would have biased estimates of λ_s and artificially reduced their variance. Therefore, we used the following rules to determine if a sampling intensity—defined here as total area sampled—was sufficient to estimate λ_s using a particular method at a particular site. First, if an annual sample lacked individuals in any of the size classes, then we did not estimate a deterministic matrix for that year. Second, we did not estimate λ_s for a sample if it was insufficient to estimate at least 50% of the possible annual transition matrices (based on Rule 1). Third, if fewer than 90% of samples for a given sample size could estimate λ_s after applying

Rule 2, we did not include that sample size for that plot and method in further analyses.

In order to compare how accurately each sampling method estimated the actual growth rate of the population in that plot, we used a linear mixed model (Bates and Maechler 2007) that estimated how the bias changed as a function of area sampled, where bias is defined as the average difference between λ_s and the growth rate of the entire population found in the 100 m \times 50 m plot (hereafter, λ or the “whole-plot value”). Because bias approaches zero as the area sampled in simulations approaches the total area of the demographic plots (e.g., “finite population sampling”; sensu Thompson 2002), we excluded simulations of total area $>4,000$ m² from the analysis. These excluded samples tell us little about the performance of the sampling methods, and would have violated the linearity assumption of our model. The model used was:

$$\left(\hat{\lambda}_i - \lambda_{\text{site}[i]}\right) = \left(\beta_{\text{method}[i]} + B_{\text{site}[i]}\right)a_i + S_{\text{site}[i]} + \varepsilon_i \tag{2}$$

where a_i is the area of the i th sample, $\beta_{\text{method}[i]}$ is the rate at which the bias varies with the area sampled for method of sample i , $B_{\text{site}[i]}$ is the random contribution to slope for site i , and $S_{\text{site}[i]}$ is the random intercept for the i th site. Note also that the notation above uses λ instead of λ_s to simplify the equation. ε_i is an independent deviation from the mean for sample i , and is normally distributed with mean 0 and variance proportional to the inverse of the area sampled. This weighted analysis accounts for the decreasing variance of estimates as the area sampled approaches the size of the original demographic plot. Thus, this is a weighted general linear model with a random intercept and slope for each site to account for the longitudinal nature of the data. In order to compare the precision of the three methods (i.e., how variation in estimates of λ_s changed as the area sampled increased), we used a generalized linear mixed model, with a gamma-distributed response and a log link for the mean (Bates and Maechler 2007):

$$\log(E[\text{SD}(\lambda_i)]) = S_{\text{site}[i]} + \left(\beta_{\text{method}[i]} + B_{\text{method}[i]}\right)a_i \tag{3}$$

where parameters $S_{\text{site}[i]}$, $\beta_{\text{method}[i]}$, $B_{\text{site}[i]}$, and a_i represent quantities similar to those in the bias model (Eq. 2). We chose the gamma distribution and log

link because standard deviation is a continuous measurement restricted to be positive.

Finally, we wanted to ensure that any difference between the methods that we observed was not an artifact of the number of individuals being sampled with a given area. To do so, we used simple linear regression to estimate the number of individuals sampled as a function of area for each method. All analyses were conducted in the R statistical computing environment (R Development Core Team 2007), using the lme4 package for mixed models (Bates and Maechler 2007).

Results

What sampling strategies are used in studies of plant demography?

Our literature search resulted in 63 studies of plant demography (Appendix). Almost half of the studies were on perennial herbs ($N = 30$), followed by trees ($N = 13$ studies), “other life-forms” (e.g., grasses, geophytes etc.; $N = 13$) and shrubs ($N = 7$ studies). Nine of 14 studies on trees used a single, large plot, while 13 of the 20 studies conducted on perennial herbs used randomly located subplots (RM). Most studies of the “other life forms” category also used RM (i.e., 9 of 13), while there was little consistency in studies of shrubs. The “population” method, in which populations were delineated and completely surveyed, was used in 8 studies and 4 studies sampled plants without delineating plots or populations. The total area used to parameterize matrix models ranged from 0.09 to 175,000 m² (median = 113.8 m²); not surprisingly studies of trees used the largest total areas (range = 1,500–175,000 m², median = 8,100 m², mean = 31,250 m² ± 488,14.3 SD), while those of perennial herbs used the smallest (range = 0.6–8,018.2 m², median = 10 m², mean = 574.6 ± 1,843.3 SD). Studies of shrubs sampled 375–1,500 m² (median = 612.5 m², mean = 775 m² ± 496.2 SD), while those of “other” life forms sampled areas ranging from 0.1 to 5,550 (median = 5 m², mean = 1,673.1 m² ± 2,259.9 SD).

Do different sampling methods affect the quality of population growth estimates?

For all sampling methods, the variance of λ_s decreased as total area sampled increased (Fig. 2).

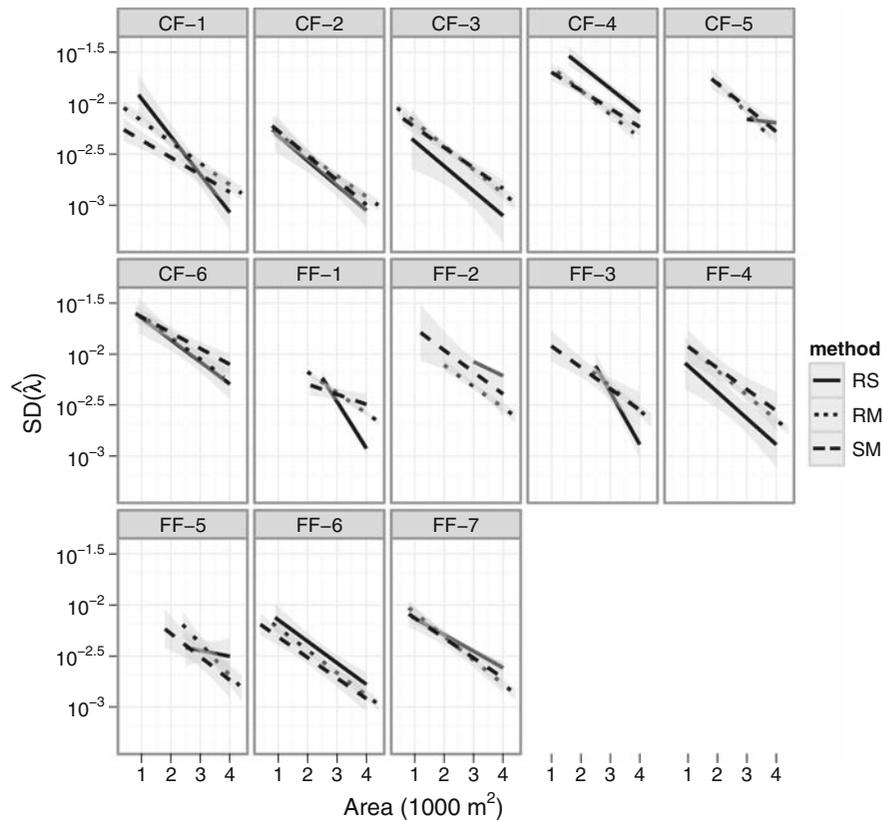
However, systematic sampling required the lowest sampling effort (i.e., area sampled) for λ_s to be within 1% of the whole-plot value in 8 of the 13 sites. Single plots were best for two of the locations, multiple random plots were best for one site, and in two of the sites single plots and systematic sampling were equivalent (Table 1). Nevertheless, a comparison of the bias model (Eq. 1) with a reduced model of equal β 's for all methods revealed no best method for bias reduction per unit sampling area ($\Delta\text{AIC} = 3.0$, $P = 0.569$). This conclusion was supported by plots of regression curves (Fig. 3). The precision analysis also found no significant effect of sampling method on the improvement in precision of estimates of λ_s per unit area ($\Delta\text{AIC} = 3.5$, $P = 0.759$). In summary, our analyses suggest that the method used to collect data does not affect the bias or precision of estimates in our system. The linear model fit between area and number of individuals was nearly identical among all methods, indicating that the methods sampled equal numbers of individuals for a given area.

Discussion

While there is a substantial literature evaluating how plot size and shape influence estimates of such ecological parameters as species diversity (e.g., Jalonen et al. 1998; Kenkel and Podani 1991; Laurance et al. 1998), population size (e.g., Gray 2003; Picard et al. 2004), and the strength of intraspecific competition (e.g., Hynynen and Ojansuu 2003), little is known regarding how the type and arrangement of sampling units influences demographic studies. Our simulations with 13 populations of *Heliconia acuminata* suggest that three prevalent sampling methods—a single, large plot, systematically arranged subplots, and randomly arranged subplots—all yield similarly precise estimates of vital rates and the stochastic population growth rate. This result is reassuring, as there is very little consistency among studies in the sampling methods used to collect demographic data. However, it is also somewhat surprising, since the advantage in efficiency that is gained from systematic sampling is a well-known result from sampling theory (Bellhouse 1977; Yates 1948).

This apparent contradiction can be explained by the fact that the statistical advantage of systematic sampling—an increase in precision that results from

Fig. 2 Weighted regression lines fit to the standard deviation of estimates of λ_s [i.e., SD ($\hat{\lambda}_s$)] as a function of the total area sampled at each of 13 sites and for each sampling method. Standard deviation is plotted on the log scale. Single randomly located plots (RS), multiple randomly located plots (RM), and systematically arranged plots (SM) are indicated with *solid*, *dashed*, and *dotted lines*, respectively. A description of each continuous forest (CF 1–6) or forest fragment (FF 1–7) site can be found in Table 1



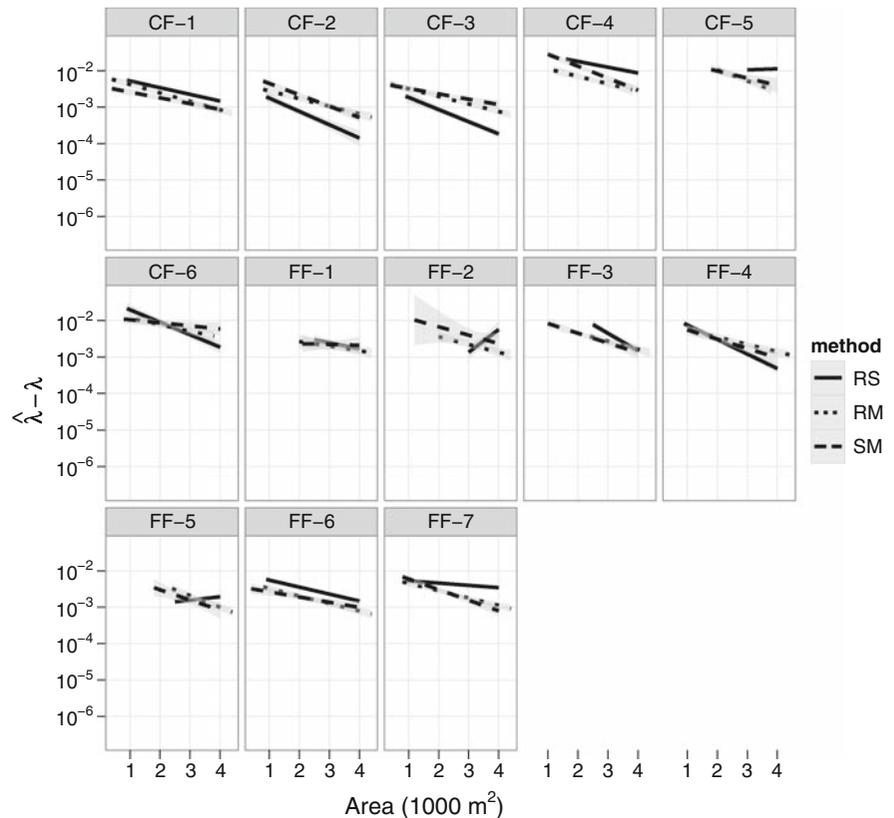
maximizing the distance between samples—is most evident when there is spatial structure in demographic vital rates, and there is no evidence for spatially structured vital rates in our *H. acuminata* populations (Fiske and Bruna, unpubl. data). Nevertheless, there are a host of reasons to suspect that vital rates in other systems may be spatially autocorrelated (Legendre 1993). Autocorrelation could result from ecological processes such as local variation in herbivore movement and abundance (e.g., Schnurr et al. 2004), competition with or facilitation by neighbors (e.g., Escudero et al. 2005), or the effects of local density on pollinator behavior (e.g., Kunin 1993). It could also result from spatially restricted dispersal, which can lead to increased relatedness among neighbors (Chung et al. 2005; Delesalle and Blum 1994). Finally, gradients in ecological variables, such as soil chemistry, microclimate, or microtopography (Legendre 1993), could drive subtle but important gradients in vital rates. Although, autocorrelation and gradients in vital rates could strongly influence the efficacy of demographic sampling methods. To the best of our knowledge, no studies have explicitly

tested for it prior to establishing demographic studies or once data collection efforts have concluded. We believe that the inherent difficulty in determining if there is spatial structure a priori and its prevalence in ecological systems suggest it would be prudent to use systematic sampling rather than the two more common alternatives when establishing demographic studies.

Are we sampling enough?

Regardless of the source of spatial variation, computing precise estimates of vital rates when they are positively autocorrelated also requires sampling larger areas (Legendre 1993), something well documented in agricultural field trials (Bhatti 2004; Fagroud and Van Meirvenne 2002; Poultney et al. 1997). Furthermore, larger plots are also critical for more accurately describing temporal variation in population dynamics, as noted by Crawley (1990) in his comprehensive and insightful review of plant demography. Indeed, he suggested that “quadrat size...is not just an issue for considerations of spatial variance, but is central in any discussion of plant

Fig. 3 Weighted least squares regression lines fit to the bias of λ_s (i.e., $\hat{\lambda}_s - \lambda_s$) as a function of the total area sampled for each of the three sampling methods at each of the 13 sites. Area sampled was truncated at 4,000 m² to avoid erroneously modeling small sampling variances as area approached the actual size of the demographic plot (i.e., 5,000 m²). Randomly located plots (RS), multiple randomly located plots (RM), and systematically arranged plots (SM) are indicated with *solid*, *dashed*, and *dotted lines*, respectively. A description of each continuous forest (CF 1–6) or forest fragment (FF 1–7) site can be found in Table 1



population dynamics” (Crawley 1990, p. 134). In light of our simulations and literature review, we believe that precisely estimating λ_s may require sampling areas much larger than those commonly used in studies of plant demography. It is notable that 48% of the studies conducted with perennial plants sampled a total area of less than 10 m², and that the largest total area sampled in a study of shrubs was equivalent to a 40 × 40 m plot. Clearly, there will be differences in the effort required for sampling species that vary in life history, density, and aggregation. However, it is unlikely that even studies focusing on a single population—except perhaps one investigating the importance of microsite variation—could encompass that population in only 10 m²; furthermore, plant demography includes many processes that operate at landscape scales (e.g., seed dispersal and pollinator movements). Even if the sampling requirements for *Heliconia acuminata* are orders of magnitude higher than other systems, our results suggest that the limited sampling effort used in many studies could influence the precision of estimates of some critical vital rates (Crawley 1990).

It is important to note that as area sampled increases, the number of plants sampled will also increase. This increased sample size could also influence the estimates of vital rates (e.g., Fiske et al. 2008). Our survey and simulations addressed area sampled because we were interested in the critical relationship between area sampled, habitat heterogeneity, and estimates of vital rates. We suggest further studies are needed in which the influence of density, area sampled, and habitat heterogeneity on estimates of population growth rate are evaluated. Unfortunately, we found that many published demographic studies fail to include the number of plants used to parameterize matrix models. As such, simulations using model populations (e.g., Doak et al. 2005) may provide the best approach for addressing this question.

Implications for the study of plant demography

The results of our and other studies (Doak et al. 2005; Gross 2002; Münzbergová and Ehrlén 2005) highlight several issues that must be considered when

designing a demographic study. With these results in mind, we end with the following four suggestions for researchers interested in establishing demographic studies. First, we propose that researchers should more explicitly consider the domain, extent, and grain of their study system (sensu Legendre and Legendre 1998) during the design phase, consider how these factors will potentially influence their estimates of vital rates, and design their sampling accordingly. Second, we advocate sampling with a systematic grid of plots in each study site, which statistical sampling theory (Bellhouse 1977; Cochran 1946; Yates 1948) suggests will result in the most precise estimates of vital rates for the least area sampled. Doing so will also ensure the inclusion of empty, but potentially colonizable areas, eliminating an important but often overlooked bias in studies of plant demography (Crawley 1990). Third, we urge researchers to ensure that enough area is sampled—both within and across sites—to encompass the range of spatial variation in plant density, survival, growth, and reproduction. The importance of this point cannot be overstated using plots that are too small within a site may inflate estimates of extinction (Fig. 1 in Crawley 1990), while sampling across a limited range of habitats will fail to quantify the true heterogeneity in population dynamics and demography. We recognize that this suggestion brings with it additional logistical and financial burdens. However, we feel that the potential consequences of failing to do so (e.g., poorly parameterized models, no estimates of the effects of spatial variation) are serious enough to warrant the effort, particularly when the analyses are to be applied to conservation problems. Fourth, we recognize an important caveat to our study that conclusions are based on the results of simulations conducted with one species, albeit a model species for studies with tropical herbs. Therefore, we suggest that it would be fruitful for other researchers with suitable datasets to conduct similar simulations with an eye toward testing our hypothesis that demographic studies have failed to sample the area necessary to adequately parameterize models. Finally, in reviewing the demographic literature, we were surprised to find that it was occasionally impossible to ascertain such critical details as the total number of plants on which each year's matrix models were based. We therefore implore researchers to better describe and justify their choice of sampling

design and effort, something common in most ecological subdisciplines, but notably absent in studies of plant demography.

Acknowledgments We thank M. Oli, B. Bolker, and three anonymous reviewers for helpful discussions and comments on the manuscript. We would also like to thank the many technicians and students who helped conduct the censuses and the logistical support of the BDFFP and its staff. Financial support was provided by the US National Science Foundation (award numbers DEB-0614149 and DEB-0614339) and the University of Florida. This is publication number 547 in the BDFFP Technical Series. Code used to conduct simulations is available from IJF upon request.

Appendix: studies of plant demography using matrix models reviewed to determine the sample sizes used to parameterize models

Allphin L and Harper KT (1997) Demography and life history characteristics of the rare Kachina daisy (*Erigeron kachinensis*, Asteraceae). *American Midland Naturalist* 138:109–120.

Alvarez-Buylla ER (1994) Density dependence and patch dynamics in tropical rain forests: matrix models and applications to a tree species. *American Naturalist* 143:155–191.

Barot S, Gignoux J, Vuattoux R et al. (2000) Demography of a savanna palm tree in Ivory Coast (Lamto): population persistence and life-history. *Journal of Tropical Ecology* 16:637–655.

Batista WB, Platt WJ and Macchiavelli RE (1998) Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. *Ecology* 79:38–53.

Berg H (2002) Population dynamics in *Oxalis acetosella*: the significance of sexual reproduction in a clonal, cleistogamous forest herb. *Ecography* 25:233–243.

Bierzychudek P (1982) The demography of Jack-in-the-Pulpit, a forest perennial that changes sex. *Ecological Monographs* 52:335–351.

Brewer JS (2001) A demographic analysis of fire-stimulated seedling establishment of *Sarracenia alata* (Sarraceniaceae). *American Journal of Botany* 88:1250–1257.

Bruna EM (2003) Are plant populations in fragmented habitats recruitment limited? Tests with an Amazonian herb. *Ecology* 84: 932–947.

- Brys R, Jacquemyn H, Endels P et al. (2004) The effects of grassland management on plant performance and demography in the perennial herb *Primula veris*. *Journal of Applied Ecology* 41: 1080–1091.
- Bullock SH (1980) Demography of an undergrowth palm in littoral Cameroon. *Biotropica* 12:247–255.
- Byers DL and Meagher TR (1997) A comparison of demographic characteristics in a rare and a common species of *Eupatorium*. *Ecological Applications* 7:519–530.
- Calvo RN (1993) Evolutionary demography of orchids: intensity and frequency of pollination and the cost of fruiting. *Ecology* 74:1033–1042.
- Charron D and Gagnon D (1991) The demography of northern populations of *Panax quinquefolium* (American Ginseng). *Journal of Ecology* 79:431–445.
- Cipollini ML, Wallacesent DA and Whigham DF (1994) A model of patch dynamics, seed dispersal, and sex-ratio in the dioecious shrub *Lindera benzoin* (Lauraceae). *Journal of Ecology* 82:621–633.
- Cipollini ML, Whigham DF and O’Neill J (1993) Population growth, structure, and seed dispersal in the understory herb *Cynoglossum virginianum*: a population and patch dynamics model. *Plant Species Biology* 8:117–129.
- Ehrlen J (1995) Demography of the perennial herb *Lathyrus vernus*: II. Herbivory and population dynamics. *Journal of Ecology* 83:297–308.
- Endress BA, Gorchoff DL and Noble RB (2004) Non-timber forest product extraction: effects of harvest and browsing on an understory palm. *Ecological Applications* 14:1139–1153.
- Enright N and Ogden J (1979) Applications of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. *Australian Journal of Ecology* 4:3–24.
- Enright NJ and Watson AD (1992) Population dynamics of the Nikau Palm *Rhopalostylis sapida* (Wendl. et. Drude) in a temperate forest remnant near Auckland, New Zealand. *New Zealand Journal of Botany* 30:29–43.
- Eriksson O (1988) Ramet behavior and population growth in the clonal herb *Potentilla anserina*. *Journal of Ecology* 76:522–536.
- Fiedler PL (1987) Life history and population dynamics of rare and common Mariposa Lilies (*Calochortus purshii*: Liliaceae). *Journal of Ecology* 75:977–996.
- Forbis TA and Doak DE (2004) Seedling establishment and life history trade-offs in alpine plants. *American Journal of Botany* 91:1147–1153.
- Garcia MB (2003) Demographic viability of a relict population of the critically endangered plant *Borderea chouardii*. *Conservation Biology* 17:1672–1680.
- Guardia R, Raventos J and Caswell H (2000) Spatial growth and population dynamics of a perennial tussock grass (*Achnatherum calamagrostis*) in a badland area. *Journal of Ecology* 88:950–963.
- Guedje NM, Lejoly J, Nkongmeneck BA et al. (2003) Population dynamics of *Garcinia lucida* (Clusiaceae) in Cameroonian Atlantic forests. *Forest Ecology and Management* 177:231–241.
- Hara M, Kanno H, Hirabuki Y et al. (2004) Population dynamics of four understory shrub species in beech forest. *Journal of Vegetation Science* 15:475–484.
- Hoffmann WA (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* 80:1354–1369.
- Horvitz CC and Schemske DW (1995) Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecological Monographs* 65:155–192.
- Huenneke LF and Marks PL (1987) Stem dynamics of the shrub *Alnus incana* ssp. *Rugosa*: transition matrix models. *Ecology* 68:1234–1242.
- Kiviniemi K (2002) Population dynamics of *Agri- monia eupatoria* and *Geum rivale*, two perennial grassland species. *Plant Ecology* 159:153–169.
- Lefebvre C and Chandler-Mortimer A (1984) Demographic characteristics of the perennial herb *Armeria maritima* on zinc lead mine wastes. *Journal of Applied Ecology* 21:255–264.
- Lesica P (1995) Demography of *Astragalus scaphoides* and effects of herbivory on population growth. *Great Basin Naturalist* 55:142–150.
- Matos JF, Trevisan MC, Estrada CA et al. (2000) Comparative demography of two giant caulescent rosettes (*Espeletia timotensis* and *E. spicata*) from the high tropical Andes. *Global Ecology and Biogeography* 9:403–413.
- McCauley RA and Ungar IA (2002) Demographic analysis of a disjunct population of *Froelichia*

- floridana* in the mid-Ohio River Valley. *Restoration Ecology* 10:348–361.
- Meagher TR (1982) The population biology of *Chamaelirium luteum*, a dioecious member of the lily family 2. Sex population projections and stable population structure. *Ecology* 63:1701–1711.
- Menges ES and Quintana-Ascencio PF (2004) Population viability with fire in *Eryngium cuneifolium*: Deciphering a decade of demographic data. *Ecological Monographs* 74:79–99.
- Moloney KA (1988) Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. *Ecology* 69:1588–1598.
- Morris WF and Doak DF (2005) How general are the determinants of the stochastic population growth rate across nearby sites? *Ecological Monographs* 75:119–137.
- Nakashizuka T (1991) Population dynamics of coniferous and broad-leaved trees in a Japanese temperate mixed forest. *Journal of Vegetation Science* 2:413–418.
- Nordbakken JF, Rydgren K and Okland RH (2004) Demography and population dynamics of *Drosera anglica* and *D. rotundifolia*. *Journal of Ecology* 92:110–121.
- Olmsted I and Alvarez-Buylla ER (1995) Sustainable harvesting of tropical trees: demography and matrix models of two palm species in Mexico. *Ecological Applications* 5:484–500.
- Oostermeijer JGB, Brugman ML, deBoer ER et al. (1996) Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology* 84:153–166.
- Parker IM (2000) Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecological Applications* 10:726–743.
- Pico FX and Riba M (2002) Regional-scale demography of *Ramonda myconi*: remnant population dynamics in a preglacial relict species. *Plant Ecology* 161:1–13.
- Pinard M (1993) Impacts of stem harvesting on populations of *Iriartea deltoidea* (Palmae) in an extractive reserve in Acre, Brazil. *Biotropica* 25: 2–14.
- Pinero D, Martinezramos M and Sarukhan J (1984) A Population model of *Astrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. *Journal of Ecology* 72:977–991.
- Platt WJ, Evans GW and Rathbun SL (1988) The population dynamics of a long-lived conifer (*Pinus palustris*). *American Naturalist* 131:491–525.
- Rae JG and Ebert TA (2002) Demography of the endangered fragrant prickly apple cactus, *Harrisia fragrans*. *International Journal of Plant Sciences* 163:631–640.
- Silva Matos DMS, Freckleton RP and Watkinson AR (1999) The role of density dependence in the population dynamics of a tropical palm. *Ecology* 80:2635–2650.
- Stokes KE, Allchin AE, Bullock JM et al. (2004) Population responses of *Ulex* shrubs to fire in a lowland heath community. *Journal of Vegetation Science* 15:505–514.
- Svensson BM, Carlsson BA, Karlsson PS et al. (1993) Comparative long-term demography of 3 species of *Pinguicula*. *Journal of Ecology* 81:635–645.
- Tolvanen A, Schroderus J and Henry GHR (2001a) Age- and stage-based bud demography of *Salix arctica* under contrasting muskox grazing pressure in the High Arctic. *Evolutionary Ecology* 15:443–462.
- Tolvanen A, Schroderus J and Henry GHR (2001b) Demography of three dominant sedges under contrasting grazing regimes in the High Arctic. *Journal of Vegetation Science* 12:659–670.
- Valverde T and Silvertown J (1998) Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. *Journal of Ecology* 86:545–562.
- Vavrek MC, mcgraw JB and Yang HS (1997) Within-population variation in demography of *Taraxacum officinale*: season- and size-dependent survival, growth and reproduction. *Journal of Ecology* 85:277–287.

References

- Bates D, Maechler M (2007) lme4: linear mixed-effects models using S4 classes. R package. <http://CRAN.R-project.org/package=lme4>
- Batista WB, Platt WJ, Macchiavelli RE (1998) Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. *Ecology* 79:38–53
- Bellhouse DR (1977) Some optimal designs for sampling in two dimensions. *Biometrika* 64:605–611

- Berry F, Kress WJ (1991) *Heliconia*: an identification guide. Smithsonian Institution Press, Washington, DC, USA
- Bhatti AU (2004) Using geostatistics to find optimum plot size for field research experiments. *Commun Soil Sci Plant Anal* 35:2299–2310
- Bierregaard RO, Gascon C, Lovejoy TE, Mesquita R (eds) (2002) Lessons from Amazonia: the ecology and conservation of a fragmented forest. Yale University Press, New Haven
- Bierzychudek P (1999) Looking backwards: assessing the projections of a transition matrix model. *Ecol Appl* 9:1278–1287
- Boyce MS, Haridas CV, Lee CT, Demography NS (2006) Demography in an increasingly variable world. *Trends Ecol Evol* 21:141–148
- Bruna EM (2003) Are plants in rain forest fragments recruitment limited? Tests with an Amazonian herb. *Ecology* 84:932–947
- Bruna EM, Kress WJ (2002) Habitat fragmentation and the demographic structure of an Amazonian understory herb (*Heliconia acuminata*). *Conserv Biol* 16:1256–1266
- Caswell H (2001) Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland
- Chung MY, Nason JD, Chung MG (2005) Spatial genetic structure in populations of the terrestrial orchid *Orchis cyclochila* (Orchidaceae). *Plant Syst Evol* 254:209–219
- Cochran WG (1946) Relative accuracy of systematic and stratified random samples for a certain class of populations. *Annals of Mathematical Statistics* 17:164–177
- Condit R (1998) Tropical forest census plots. Springer-Verlag, Berlin
- Crawley MJ (1990) The population dynamics of plants. *Phil Trans R Soc Lond B* 330:125–140
- de Kroon H, van Groenendael J, Ehrlén J (2000) Elasticities: a review of methods and model limitations. *Ecology* 81:607–618
- Delesalle VA, Blum S (1994) Variation in germination and survival among families of *Sagittaria latifolia* in response to salinity and temperature. *Int J Plant Sci* 155:187–195
- Doak DF, Gross K, Morris WF (2005) Understanding and predicting the effects of sparse data on demographic analyses. *Ecology* 86:1154–1163
- Escudero A, Romao RL, de la Cruz M, Maestre FT (2005) Spatial pattern and neighbour effects on *Helianthemum squamatum* seedlings in a Mediterranean gypsum community. *J Veg Sci* 16:383–390
- Fagroud M, Van Meirvenne M (2002) Accounting for soil spatial autocorrelation in the design of experimental trials. *Soil Sci Soc Am J* 66:1134–1142
- Fiske IJ, Bruna EM, Bolker BM (2008) Effects of sample size on estimates of population growth rates calculated with matrix models. *PLoS ONE* 3:e3080
- Gotelli NJ (1991) Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. *Ecology* 72:457–467
- Gray A (2003) Monitoring stand structure in mature coastal Douglas-fir forests: effect of plot size. *For Ecol Manag* 175:1–16
- Gross K (2002) Efficient data collection for estimating growth rates of structured populations. *Ecology* 83:1762–1767
- Horvitz CC, Schemske DW (1995) Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecol Monogr* 65:155–192
- Hynynen J, Ojansuu R (2003) Impact of plot size on individual-tree competition measures for growth and yield simulators. *Can J For Res (Revue Canadienne De Recherche Forestiere)* 33:455–465
- Jalonen J, Vanha-Majamaa I, Tonteri T (1998) Optimal sample and plot size for inventory of field and ground layer vegetation in a mature Myrtillus-type boreal spruce forest. *Ann Bot Fennici* 35:191–196
- Kenkel NC, Podani J (1991) Plot size and estimation efficiency in plant community studies. *J Veg Sci* 2:539–544
- Kunin WE (1993) Sex and the single mustard: population density and pollinator behavior effects on seed set. *Ecology* 74:2145–2160
- Laurance WF, Ferreira LV, Rankin-De Merona JM, Hutchings RW (1998) Influence of plot shape on estimates of tree diversity and community composition in central Amazonia. *Biotropica* 30:662–665
- Lefkovich LP (1965) The study of population growth in organisms grouped by stages. *Biometrics* 21:1–18
- Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier, New York
- Leslie PH (1945) On the use of matrices in certain population mathematics. *Biometrika* 33:183–212
- Moloney KA (1988) Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. *Ecology* 69:1588–1598
- Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland
- Münzbergová Z, Ehrlén J (2005) How best to collect demographic data for population viability analysis models. *J Appl Ecol* 42:1115–1120
- Parker IM (2000) Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecol Appl* 10:726–743
- Pebesma EJ, Bivand RS (2005) Classes and methods for spatial data in R. *R News* 5:9–13
- Picard N, Nouvellet Y, Sylla ML (2004) Relationship between plot size and the variance of the density estimator in West African savannas. *Can J For Res (Revue Canadienne De Recherche Forestiere)* 34:2018–2026
- Poultney R, Riley J, Webster R (1997) Optimizing plot size and shape for field experiments on terraces. *Exp Agric* 33:51–64
- R Development Core Team (2007) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Schnurr JL, Canham CD, Ostfeld RS, Inouye RS (2004) Neighborhood analyses of small-mammal dynamics: Impacts on seed predation and seedling establishment. *Ecology* 85:741–755
- Silva Matos DM, Freckelton RP, Watkinson AR (1999) The role of density dependence in the population dynamics of a tropical. *Ecology* 80:2635–2650
- Silvertown J, Franco M, Pisanty I, Mendoza A (1993) Comparative plant demography: relative importance of life-

- cycle components to the finite rate of increase in woody and herbaceous perennials. *J Ecol* 81:465–476
- Thompson SK (2002) *Sampling*. Wiley, New York
- Valverde T, Silvertown J (1998) Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: Projection matrix analysis. *J Ecol* 86:545–562
- Wisdom MJ, Mills LS, Doak DF (2000) Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* 81:628–641
- Yates F (1948) Systematic sampling. *Phil Trans R Soc Lond Ser A* 241:345–377