DEMOGRAPHIC EFFECTS OF HABITAT FRAGMENTATION ON A TROPICAL HERB: LIFE-TABLE RESPONSE EXPERIMENTS

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Abstract. Habitat fragmentation is a leading cause of extinction, with effects that may be particularly pronounced in tropical ecosystems. However, little is known regarding the demographic mechanisms underlying changes in abundance in fragmented landscapes. Using six years of demographic data collected from >6600 individuals of the Amazonian understory herb *Heliconia acuminata*, we calculated population growth rate (λ) in experimentally isolated 10-ha forest fragments, 1-ha forest fragments, and continuous forest. We then used life-table response experiment analyses to elucidate the mechanisms responsible for observed differences in λ. On average, $\lambda \approx 1.05$ in continuous forest, while $\lambda \approx 1$ in both 1-ha and 10-ha fragments. However, while the differences in λ between 10-ha fragments and continuous forest were largely attributable to the negative contribution of stage-specific fertility rates, reduced λ in 1-ha fragments was due to both reductions in reproductive rates and changes in the rate of plant growth. Our results show that similar reductions in λ in fragments of different sizes can be driven by distinct demographic mechanisms. Without comprehensive demographic data, attempts to mitigate the decline of populations in fragmented landscapes could be unsuccessful because they might be focusing on inappropriate demographic targets.

Key words: Amazon; deforestation; Heliconia acuminata; *Heliconiaceae; life table response experiment, LTRE; matrix models; population growth rate, lambda; sensitivity analysis.*

INTRODUCTION

Understanding how the growth rate (λ) of populations responds to spatial and temporal environmental heterogeneity is a fundamental goal of ecological research. In recent decades, the fragmentation of once contiguous habitat has become a pervasive form of heterogeneity in most terrestrial ecosystems (Saunders et al. 1991, Harrison and Bruna 1999). Some of the most commonly observed consequences of fragmentation are changes in population size (reviewed in Harrison and Bruna 1999, Debinski and Holt 2000, Laurance et al. 2002), with some plant and animal species increasing in abundance while others suffer precipitous declines (e.g., Leach and Givnish 1996, Bierregaard and Stouffer 1997, Malcolm 1997, Davies and Margules 1998, Funk and Mills 2003). Surprisingly almost nothing is known regarding the demographic mechanisms responsible for these changes (Bruna 2003). Studies in which multiple aspects of life history are simultaneously evaluated for populations in both fragments and continuous habitat are exceedingly rare (e.g., Holt et al. 1995, Bruna 2003, Funk and Mills 2003).

One of the principal mechanisms hypothesized to drive population declines in habitat fragments, particularly for shade-tolerant or understory plants, is reduced reproduction and recruitment (Cardoso da Silva and Tabarelli 2000). Fruit production by individual plants is often low in fragmented areas, which can be the result of reductions in pollinator abundance, changes in pollinator visitation rates, or decreases in the efficacy of pollen transfer (Aizen and Feinsinger 1994, Jules and Rathcke 1999, Cunningham 2000*a*). These reductions can be exacerbated by limited seed dispersal (Santos and Telleria 1994, Andresen 2003, McEuen and Curran 2004), elevated seed predation (Santos and Telleria 1997, Curran and Webb 2000), reduced seed germination (Bruna 1999), or increased seedling damage and mortality in fragments (Scariot 2001). Despite the emphasis placed on reproduction, however, other vital rates are also altered in fragmented habitats. For instance, plant growth rates can be lower in fragments than in continuous habitat (Bruna et al. 2002), and the mortality rates of large trees have been shown to increase dramatically near forest edges (Laurance et al. 1998). Presumably these changes have detrimental demographic consequences (Young and Clarke 2000, Hobbs and Yates 2003).

When comprehensive demographic data are available, two approaches can be used to evaluate how demographic variables influence population growth rates:

PLATE 1.   Two of the experimentally isolated forest fragments near Manaus, Brazil, in which the demography of *Heliconia acuminata* was investigated. A 10-ha fragment is in the foreground, with a 1-ha fragment on the right. Photo credit: Rob Bierregaard.

prospective and retrospective analyses (reviewed in Horvitz et al. 1996, Caswell 2001). Prospective approaches, such as sensitivity and elasticity analyses, evaluate how *hypothetical* changes in vital rates would alter λ. In contrast, life-table response experiment analyses (LTRE) and other retrospective analyses decompose *observed* differences in λ into the actual contributions from individual demographic variables (Caswell 1989, 2000). They are therefore a powerful tool for investigating not only the effects of natural variation in environmental conditions on population growth rates, but also how experimental manipulations of ecological variables have influenced λ via their influences on demographic rates. Recent LTREs have evaluated the demographic basis for changes in population growth rate resulting from factors as diverse as population density (Oli et al. 2001), food abundance (Cooch et al. 2001, Dobson and Oli 2001), exposure to pollutants (Levin et al. 1996, Gotelli and Ellison 2002), and natural variation in demographic parameters over time or space (Oli and Armitage 2004).

We used LTRE analysis to elucidate the consequences of forest fragmentation for the demography of an Amazonian understory herb (*Heliconia acuminata*, Heliconiaceae), and evaluated the demographic mechanisms underlying differences in population growth rates. This analysis was based on a long-term study of *H. acuminata* population dynamics conducted at Brazil's Biological Dynamics of Forest Fragments Project (Bruna and Kress 2002, Bruna 2003), where 13 populations located in forest fragments and continuous forest have been studied annually since 1998. Using an-

nual transition matrices constructed for the time interval 1998–2003, we addressed the following questions: (1) What is the projected rate of population growth (λ) in each habitat type (i.e., 1-ha fragment, 10-ha fragment, continuous forest) in each year? (2) What is the contribution of different demographic rates to the differences in projected λ between habitat types? (3) Is there interannual variation in the contribution of different stage classes to differences in projected λ?

METHODS

Study system

This study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located 70 km north of Manaus, Brazil (2°30′ S, 60° W; see Plate 1). The BDFFP maintains several forest fragment reserves ranging in size from 1 to 100 ha. These reserves were originally isolated in the early 1980s by the creation of cattle pastures; since then the secondary growth surrounding them has been periodically cleared to maintain their isolation. In addition to these forest fragments, a number of continuous forest reserves were established in nearby tracts of primary forest. The habitat in all sites is nonflooded lowland rain forest with rugged topography. Mean annual temperature is 26°C (range 19–39°C), and annual rainfall ranges from 1900 to 3500 mm, with a pronounced dry season from June to November. A complete summary of the BDFFP and its history can be found in Bierregaard et al. (2002).

In January 1998, one of us (E. M. Bruna) initiated a long-term study at the BDFFP, investigating the de-

mographic consequences of fragmentation for tropical understory plants (see Bruna and Kress 2002, Bruna 2003 for a complete description). The focal species for this study was *Heliconia acuminata*, a perennial herb native to central Amazonia and the Guyanas (Berry and Kress 1991). Thirteen permanent 50×100 m plots in which to monitor *H. acuminata* populations were established in the BDFFP reserves; these plots were located in continuous forest ($n = 6$ plots), 10-ha fragments ($n = 3$ plots), and 1-ha fragments ($n = 4$ plots). Plots in 1-ha fragments were established on one randomly selected half of the fragment, plots in 10-ha fragments were established in the fragment center, and plots in continuous forest were placed in locations 500–4000 m from the primary forest borders. The distance between plots ranged from 500 m to 41 km.

Estimation of demographic parameters and matrix model construction

The demographic methods, including construction of matrix models for these populations, are described thoroughly in Bruna and Kress (2002) and Bruna (2003). Briefly, all *H. acuminata* in the plots were marked and mapped; we also recorded the number of vegetative shoots each plant had. The plots were then regularly surveyed during the reproductive season (January to May) to record the identity of flowering individuals. Since 1998, the plots have been censused annually to record plant growth, mortality, and the emergence of new seedlings (i.e., established plants less than one year old). The analyses presented here are based on data from the 1998–2003 surveys; during this time period we marked, measured, and recorded the fates of $N = 6646$ plants ($N = 3869$ in continuous forest, $N = 1705$ in 10-ha fragments, and $N = 1072$ in 1-ha fragments). *H. acuminata* density in 2003 ranged from 222 to 2038 plants/ha (E. M. Bruna, *unpublished data*). Additional details regarding the demographic structure of these populations can be found elsewhere (Bruna and Kress 2002, Bruna 2003).

Each *H. acuminata* was assigned to one of six stages: seedlings (all plants less than one year old, stage 1), and plants with 1, 2, 3, 4, or ≥ 5 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 nonseedling 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. The probability of transition from stage i to stage j during the interval t and $t + 1$ was estimated as the proportion of plants in stage i at time t that made the transition to stage j at time $t + 1$. Stage-specific fertility (F_i) of plants in each stage was calculated as follows:

$$F_i = p_i \times f_i \times s \times g \qquad (1)$$

where $p_i =$ the probability that an individual in size class i will flower, $f_i =$ the total number of fruits produced by individuals of size class i, $s =$ number of seeds per fruit, and $g =$ probability of successful seedling establishment (i.e., probability of seed germination and seedling survival to the next census). Values of f_i were based on annual phenological surveys, p_i and s were constants calculated with previous surveys conducted in nearby locations (see Bruna and Kress 2002 for details), and estimates of g were experimentally derived using field germination trials conducted in all three habitat types over the course of two years (described in Bruna 1999, Bruna et al. 2002). Dormant seeds were not placed in a separate stage because seeds produced in one flowering season germinate prior to the subsequent census, and experimental results indicate very few seeds germinate two or more years after dispersal (Bruna 2002). For further details regarding model construction, see Bruna (2003).

The life cycle of a species with stage-structured life histories (Fig. 1A) can be summarized in a stage-structured population projection matrix **A,** whose elements represent stage-specific transition probabilities or fertility rates (Lefkovitch 1965, Caswell 2001). The top row of matrix **A** contains the mean per-individual fertility (F_i) for plants in stage class i (Fig. 1B). The other entries of the matrix represent the probability of survival and growth from a given stage to a larger one (G_i), the probability of survival and regression to smaller stages (i.e., negative growth, R_i), or the probability of surviving and remaining in the same stage from one time interval to the next (i.e., stasis, S_i). The population can then be projected using the projection equation

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t \qquad (2)$$

where $\mathbf{n}_t$ is a vector with the abundance of individuals in each stage class at time t. The total population size in year t is the sum of the entries of $\mathbf{n}_t$.

Using estimates of transition probabilities and fertility rates, we constructed a summary population projection matrix **A** for each habitat type (i.e., 1-ha fragment, 10-ha fragment, continuous forest) for each of five transition years (i.e., 1998–1999, 1999–2000, 2000–2001, 2001–2002, 2002–2003). Summary matrices were constructed by pooling data from all plots of a given fragment size, and then estimating the transition probabilities and fertilities using the pooled data (Horvitz and Schemske 1995). A summary matrix is a better means of synthesizing the demography of multiple populations, as opposed to a matrix composed of the average of multiple projection matrices, because it accounts for the disproportionate weight that low plant numbers in some size classes in some locations can give to transition probabilities (Horvitz and Schemske 1995). We used these summary matrices to calculate the asymptotic population growth rate, λ, as well as
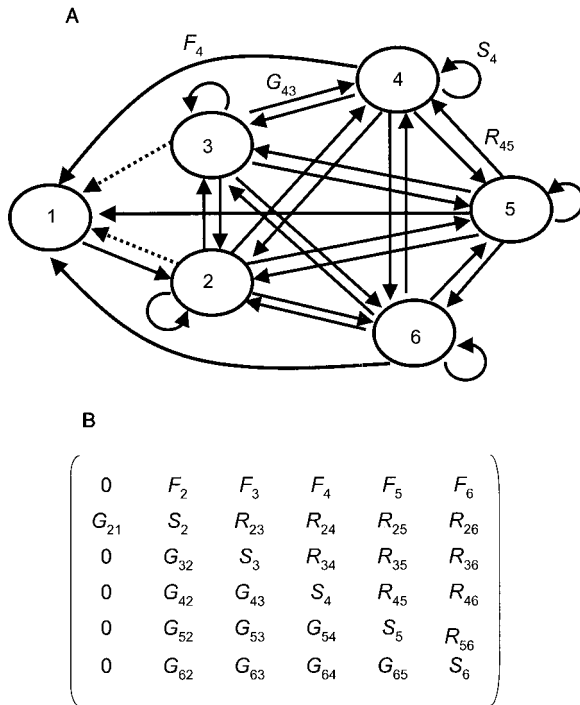
A

B

$$\begin{pmatrix} 0 & F_2 & F_3 & F_4 & F_5 & F_6 \\ G_{21} & S_2 & R_{23} & R_{24} & R_{25} & R_{26} \\ 0 & G_{32} & S_3 & R_{34} & R_{35} & R_{36} \\ 0 & G_{42} & G_{43} & S_4 & R_{45} & R_{46} \\ 0 & G_{52} & G_{53} & G_{54} & S_5 & R_{56} \\ 0 & G_{62} & G_{63} & G_{64} & G_{65} & S_6 \end{pmatrix}$$

FIG. 1. (A) Life-cycle graph for *Heliconia acuminata*. Arrows indicate potential transitions between six stage classes, including contribution to seedlings (stage class 1) via reproduction. Dashed lines indicate transitions that were rarely observed. Examples of the transition elements from matrix **A** that represent fertility, stasis, regression, and growth are included, with subscripts indicating the specific stage classes involved. (B) A population projection matrix corresponding to the life-cycle graph in Fig. 1A. The elements of the matrix represent mean fertility per individual (F_i) for plants in stage class *i*, the probability of survival and growth from a given stage to a larger one (G_{ij}), the probability of survival and regression to smaller stages (R_{ij}), or the probability of surviving and remaining in the same stage from one time interval to the next (i.e., stasis, S_i). Zero entries represent transitions that are never observed.

the sensitivity of λ to different demographic rates (Caswell 2001). It is worth noting that we are not attempting here to predict the future population dynamics of *H. acuminata* in this fragmented landscape. Instead, we focus on discerning the demographic factors that underlie differences in projected population growth rate, λ, among continuous forest and fragments of different sizes. Because λ quantifies how a population would grow in the long run if vital demographic rates remained constant, it does not necessarily reflect the current growth rate of the population (see Caswell 2001: 29–31, for a cogent discussion of "forecasting" vs. "projection").

Testing hypotheses about λ and other population-level demographic statistics is complicated by the fact that they are nonlinear functions of data collected on individuals, and their distributions under null hypotheses are usually unknown (Caswell 2001). As a result, classical statistical tests that assume the data are a ran-

dom sample of a certain distribution (e.g., normal) are generally not applicable (Caswell 2001). We therefore assessed whether estimates of λ were significantly different from each other using 95% confidence intervals, which we estimated by bootstrapping (Kalisz and McPeek 1992). The upper and lower 95% confidence intervals of 2000 bootstrap runs were estimated using bias-corrected percentile intervals (Manly 1997, Caswell 2001); values of λ were considered significantly different if their 95% confidence intervals were non-overlapping.

LTRE analysis

To quantify the contribution of each matrix element to the observed differences in λ between fragments of different sizes and continuous forest, we used a fixed-design LTRE (Horvitz et al. 1996, Caswell 2001). In this design the difference in λ between the control and experimental treatments in a given year, Δλ, is given by

$$\Delta\lambda = \lambda^t - \lambda^c$$

$$\approx \sum_{ij} (a_{ij}^t - a_{ij}^c) \times \left(\frac{\partial\lambda}{\partial a_{ij}}\right)\Bigg|_{(A^i + A^c)/2} \quad (3)$$

where $(a_{ij}^t - a_{ij}^c)$ is the difference in a_{ij} between the "treatment" matrix and the "control" matrix, and $\partial\lambda/\partial a_{ij}$ is the sensitivity of λ to changes in a_{ij} evaluated at the mean value (i.e., the matrix "midway" between the two matrices being compared [Caswell 2001]). We used the summary matrices for continuous forest as the control matrices, and those from 1-ha or 10-ha fragments as the "experimental treatment" matrices.

If the sensitivities of a_{ij} terms in the "mean" matrices are positive, a negative contribution of a matrix element (or group of matrix elements) to Δλ indicates the value of that variable in the experimental treatment matrix is lower than in the control matrix (and vice versa). In our LTRE, for instance, a negative contribution of "growth" terms to Δλ would mean that the values of those matrix elements are lower in the experimental matrix, i.e., the probability that a plant will grow from one time interval to the next is lower in forest fragments.

We conducted a total of 10 LTRE comparisons: 1-ha fragments vs. continuous forest and 10-ha fragments vs. continuous forest, each for five transition years. Close correspondence between values of Δλ and LTRE contributions would indicate the adequacy of the LTRE models.

RESULTS

The projected rates of population growth varied from 0.949 to 1.091 (Table 1), with λ < 1 in all habitat types in transition year 5 (Table 1). Values of λ for populations in continuous forest were significantly higher than those for populations in all forest fragments in four of five transition years; averaged across years the

TABLE 1. Projected population growth rate (λ) and 95% bootstrap confidence intervals (in parentheses) for populations in continuous forest (CF), 10-ha fragments, and 1-ha fragments for the mean matrices used for the life-table response experiment analyses.

Year	λ_{CF}	$\lambda_{10\text{-ha}}$	$\lambda_{1\text{-ha}}$	λ_{Mean}‡	λ_{Mean}§
1	1.091 (1.074–1.109)†	1.023 (1.014–1.034)	1.009 (0.993–1.028)	1.041	1.041
2	1.083 (1.070–1.096)†	1.008 (0.999–1.017)	0.995 (0.979–1.011)	1.034	1.024
3	1.033 (1.023–1.044)†	0.996 (0.989–1.002)	0.999 (0.976–1.010)	1.017	1.010
4	1.074 (1.060–1.087)†	1.007 (0.996–1.016)	1.008 (0.987–1.026)	1.039	1.029
5	0.949 (0.936–0.961)	0.958 (0.942–0.971)	0.951 (0.932–0.966)	0.951	0.955

Notes: For details on LTRE, see ''LTRE analysis'' in *Methods*). Projections of λ were made using summary matrices for each habitat type.

† λ for CF populations was significantly higher than for populations in 1-ha and 10-ha fragments, based on nonoverlapping 95% confidence intervals. There was no significant difference in λ between 1-ha and 10-ha fragments in any year, nor between any 1-ha fragments, 10-ha fragments, and CF in year 5.

‡ 1-ha and CF.

§ 10-ha and CF.

estimate of λ for continuous forest was 1.055 ± 0.018 ($\bar{X} \pm$ SE), with mean values in 10-ha fragments and 1-ha fragments that were very similar to each other ($\bar{X} \pm$ SE = 0.998 ± 0.011 and 0.992 ± 0.011, respectively). In none of the five transition years were projected values of λ significantly different for populations in 1-ha and 10-ha fragments (Table 1).

Our LTRE analysis revealed that the generally lower λ in 1-ha fragments was due primarily to reduced fertility and growth (Fig. 2A–D). However, there was substantial interyear variability in the contribution of demographic rates to Δλ (Fig. 2A–D). For instance, the contribution of growth terms (G_i) of plants with two shoots varied up to 10-fold, while the contributions of fertility rates (F_i) of the largest size class varied as much as 30-fold. Overall, however, LTRE contributions of F_i and G_i were consistently negative, and those of regression (R_i) were positive for most stages (Fig. 2A–D).

On average, growth and regression made the largest total contributions to Δλ, though the contributions of growth were negative, while those of regression were positive. However, not all stage classes contributed equally to Δλ. The total contributions of seedlings and older plants with 1 shoot were negligible, while the contributions of greatest magnitude came from plants with ≥5 shoots (Fig. 3A). Plants with 2–4 shoots made contributions to Δλ that were negative and intermediate in magnitude.

The LTRE comparing populations in 10-ha fragments with those in continuous forest revealed similar patterns of interannual variation in the contributions to Δλ. The contributions of greatest magnitude were again the negative contributions of F_i of large plants (Fig. 2E). However, the contributions of G_i, R_i, and S_i were more idiosyncratic (Fig. 2F–H), with contributions of different signs and magnitudes in different years.

In contrast to the results for 1-ha fragments, the average contributions of G_i, R_i, and S_i to Δλ in 10-ha fragments were relatively small (Fig. 3D). The contributions of F_i, however, were large and negative. On average, the contributions of greatest magnitude each year were again by the largest plants (Fig. 3B); contributions of demographic rates of smaller plants to Δλ were insubstantial.

DISCUSSION

Fragmented tropical forests are characterized by dramatically altered biotic and abiotic environments (Camargo and Kapos 1995, Didham and Lawton 1999), and it is thought that these changes could have a major influence on the dynamics of plant populations in fragments. Despite this, ecologists have yet to address several fundamental questions regarding the demography of populations in fragmented habitats, such as how fragmentation influences age- or stage-specific demographic parameters and population growth rates (but see Bruna 2003). Our study is the first to use life-table response experiments to explore the demographic mechanisms responsible for differences in the projected growth rates of populations in fragments. We discuss the mechanisms potentially responsible for the differences in projected values of λ, as well as the implications of our results for the conservation of plants in human-modified landscapes.

Do projected population growth rates differ in forest fragments and continuous forest?

Projections of λ for *Heliconia acuminata* populations in the fragments were significantly lower than those in continuous forest in four of the five transition years. With the exception of year 5, however, projected values of λ for populations in fragments were near equilibrium (i.e., λ ≈ 1). In contrast, populations in continuous forest were projected to grow by as much as 9% per year. These results suggest that populations in continuous forest may be able to recover rapidly from occasional years of negative population growth, while those in fragments are at elevated risk of population decline and extinction. Alternatively, isolated populations may be buffered from declines if there is dispersal of seeds into fragments from the secondary
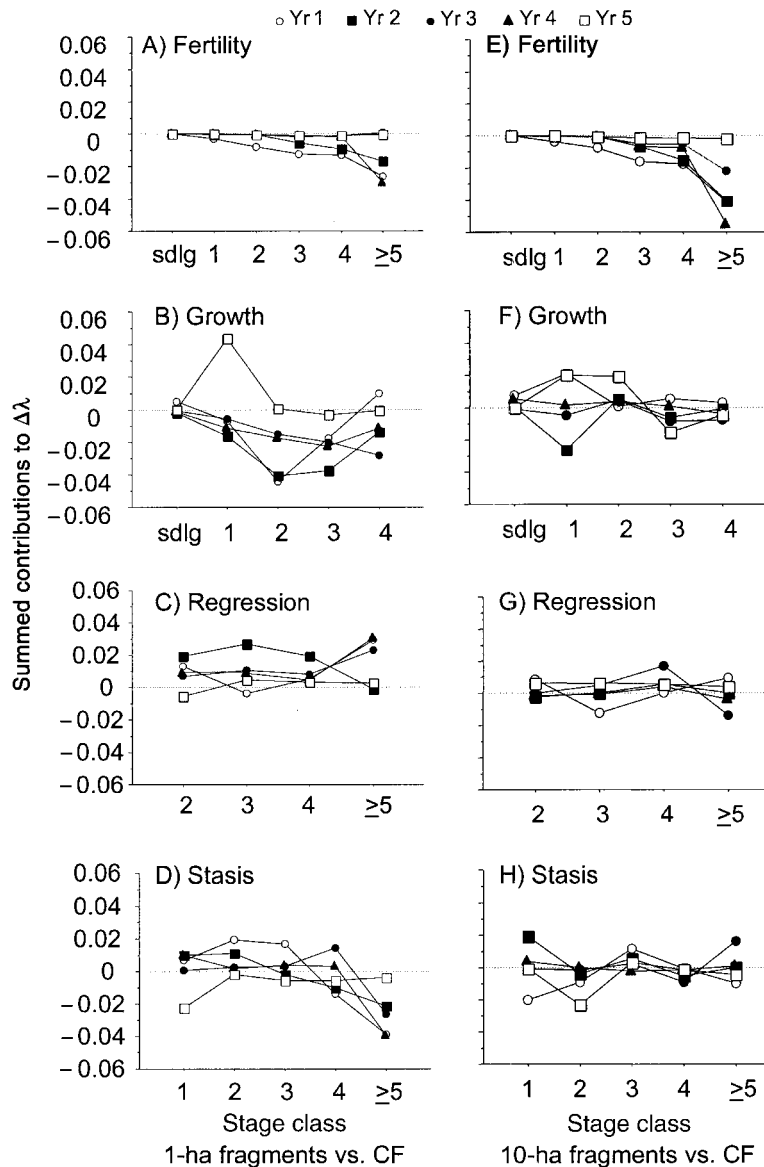
FIG. 2. Life-table response experiment (LTRE) contribution of matrix elements representing fertility, growth, regression, and stasis to annual differences in population growth rate (Δλ). Continuous forest (CF) was compared with 1-ha fragments (panels A–D) and with 10-ha fragments (panels E–H). One LTRE analysis was conducted for each transition year. Stage classes are seedling (sdlg), 1, 2, 3, 4, and ≥5.

growth that surrounds them or nearby areas of continuous forest. While the abundance of reproductive plants in secondary growth is extremely low (Bruna and Nogueira Ribeiro 2005), previous results suggest dispersal from continuous forest may be spatially and temporally idiosyncratic (Bruna 2003). Stochastic simulations to evaluate extinction risk, and the potential for it to be offset by seed dispersal, are currently underway.

What is the contribution of different demographic transitions and stage classes to Δλ?

Previous experimental and observational studies have demonstrated that *H. acuminata* seed germination and seedling establishment are lower in forest fragments than in continuous forest (Bruna 1999, 2002), as is the abundance of flowering individuals (Bruna and Kress 2002). As a result, it has been hypothesized that fragmentation-related changes in plant reproduction could lead to reductions in recruitment and population growth rates, and ultimately to population declines (Bruna 2002). The result of the LTREs comparing the demography of populations in 10-ha fragments and continuous forest is consistent with this hypothesis; we found the differences in λ were largely attributable to the negative contribution of stage-specific fertility rates. In addition, the contributions of individuals with
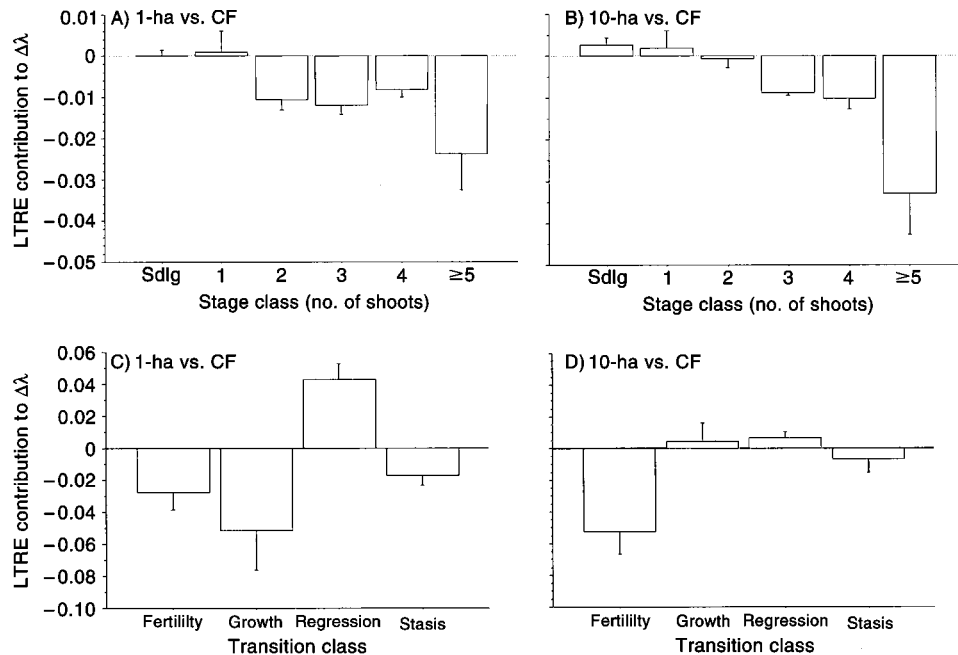
FIG. 3. Annual contribution to Δλ (mean and SE) by (A, B) demographic rate (i.e., fertility, growth, regression, or stasis) and (C, D) life history stage, averaged over five transition years. Comparisons are of 1-ha and 10-ha fragments with continuous forest (CF).

≥5 shoots, which are those most likely to flower and set seed, are consistently large and negative. Nevertheless the primacy of fertility may not be ubiquitous. The LTRE comparing populations in 1-ha fragments and continuous forest showed fertility terms contributed only half as much to Δλ, despite similarly low rates of seed germination and seedling establishment.

What, then, are the demographic mechanisms responsible for lower projected values of λ in 1-ha fragments? In the larger fragments, individuals of *H. acuminata* have reduced reproductive rates, but survival and growth do not appear to have been substantially altered. In contrast, the LTRE comparing 1-ha fragments and continuous forest showed that the bulk of the negative contributions to Δλ came from transitions describing growth to larger stage classes and lower probability of stasis in the same size class. In other words, reduced λ in 1-ha fragments is not only due to reductions in reproductive rates, but also reductions in the rate of plant growth. Interestingly, the contributions of regression terms were largely positive, which implies that regression into smaller stage classes can be demographically advantageous in forest fragments. We believe this counterintuitive result is an artifact of how these transition elements are calculated. Regression terms are conditional probabilities (i.e., the probability that a plant regresses to a smaller size class, given that it survives to be censused), and hence they include two vital rates with potentially contrasting effects. While there may be a demographic cost to regression (i.e., smaller plants are less likely to flower [Bruna and Kress

2002]), these costs are probably outweighed by the benefits of extremely high survivorship for postseedling individuals (Bruna 2003).

Although survival, fertility, and other vital rates in plants are often size dependent, studies comparing plant growth in fragments and continuous forest are virtually nonexistent (but see Bruna et al. 2002, McDonald and Urban 2004). Previous experimental work on *H. acuminata* has found that plant growth rates are frequently lower in 1-ha fragments than in continuous forest (Bruna et al. 2002) and that plants in the largest size classes can be very rare (Bruna and Kress 2002). This is almost certainly due to dramatically elevated air temperatures and lower relative humidity in fragments, which cause plants to shed shoots and leaves as a means of minimizing water loss (Bruna et al. 2002). However, while our LTRE suggests these environmental changes could have major demographic consequences via their effects on plant growth, it is worth emphasizing that this will not necessarily be the case in fragments of all sizes. For instance, our plots in 10-ha fragments were in the more protected fragment interiors, and as a result *H. acuminata* in these sites were probably less exposed to edge-dependent changes in abiotic conditions. This is probably why transitions related to plant growth made only small contributions to Δλ in the LTRE comparing continuous forest with 10-ha fragments. These results highlight the risk of focusing exclusively on λ as a metric of population status or the efficacy of conservation strategies, since

distinctly different demographic mechanisms can lead to comparable changes in λ in different populations.

Several caveats to these conclusions bear discussing. First, fruit production by *H. acuminata* is similar in 1-ha fragments and continuous forest (Bruna and Kress 2002). In systems where the fruit-set of plants in fragments is severely pollinator or resource limited (e.g., Jules and Rathcke 1999, Cunningham 2000*a, b*), the contributions of fertility terms to Δλ could potentially be much greater. Second, the BDFFP's fragments are protected from cattle, fires, plant harvesting, and other factors that can reduce plant growth and survivorship (e.g., Aizen and Feinsinger 1994, Ticktin 2004). The importance of these vital rates in other fragmented plant systems may therefore be even more notable.

Is there temporal variation in the pattern of contribution to Δλ?

Our LTRE analyses also revealed the presence of substantial interannual variation in the pattern of contribution to Δλ. For instance, the contributions of fertility terms varied as much as fivefold (Fig. 2A, E), which almost certainly reflects year-to-year variation in the abundance of flowering plants and seedling establishment. Even more notable was variation in the contributions related to plant growth; in some years the contributions of a particular size class were large and positive, while in other years they were similar in magnitude but in the opposite direction (Fig. 2B, F). The environmental causes of this demographic variability are unclear, but they may reflect temporal variation in gap formation and canopy closure, or changes in interannual variation in temperature and rainfall. Previous demographic work has concluded that tropical plant populations are more ''stable'' because they rarely exhibit the year-to-year variation in λ commonly observed in temperate plant populations (but see Horvitz and Schemske 1995); our results suggest that the underlying demographic structure may be much more dynamic than previously thought.

Conclusion

Identifying the specific demographic mechanisms underlying the responses of plant populations to habitat fragmentation is challenging but essential, as it is the first step toward defining appropriate strategies for conservation and management (Schemske et al. 1994). Our results clearly show that the same demographic rates can make contrasting contributions to λ in fragments of different sizes. Perhaps even more important, similar reductions of λ in fragments of different sizes can be driven by completely different demographic mechanisms. We hypothesize that this is probably the case in other species as well, and as a result, the responses of different populations to management practices that are applied at the landscape level could potentially vary widely. Unfortunately, a paucity of ''cradle-to-grave'' demographic studies for species found in human-mod-

ified landscapes makes tests of this hypothesis difficult. Our results suggest that without such comprehensive demographic data, attempts to mitigate the decline of populations inhabiting anthropogenically altered landscapes could be unsuccessful because they may inadvertently be focusing on incorrect demographic targets.

Literature Cited

Aizen, M. A., and P. Feinsinger. 1994. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. Ecology **75**:330–351.

Andresen, E. 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. Ecography **26**:87–97.

Berry, F., and W. J. Kress. 1991. *Heliconia*: an identification guide. Smithsonian Institution Press, Washington, D.C., USA.

Bierregaard, R. O., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. 2002. Lessons from Amazonia: the ecology and conservation of a fragmented forest. Yale University Press, New Haven, Connecticut, USA.

Bierregaard, R. O., and P. C. Stouffer. 1997. Understory birds and dynamic habitat mosaics in Amazonian rain forests. Pages 138–155 *in* W. F. Laurance and R. O. Bierregaard, editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, Illinois, USA.

Bruna, E. M. 1999. Seed germination in rainforest fragments. Nature **402**:139.

Bruna, E. M. 2002. Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. Oecologia **132**:235–243.

Bruna, E. M. 2003. Are plants in rain forest fragments recruitment limited? Tests with an Amazonian herb. Ecology **84**:932–947.

Bruna, E. M., and W. J. Kress. 2002. Habitat fragmentation and the demographic structure of an Amazonian understory herb (*Heliconia acuminata*). Conservation Biology **16**: 1256–1266.

Bruna, E. M., O. Nardy, S. Y. Strauss, and S. P. Harrison. 2002. Experimental assessment of *Heliconia acuminata* growth in a fragmented Amazonian landscape. Journal of Ecology **90**:639–649.

Bruna, E. M., and M. B. Nogueira Ribeiro. 2005. Regeneration and population structure of *Heliconia acuminata* in Amazonian secondary forests with contrasting land-use histories. Journal of Tropical Ecology **21**:127–131.

Camargo, J. L. C., and V. Kapos. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. Journal of Tropical Ecology **11**:205–221.

Cardoso da Silva, J. M., and M. Tabarelli. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature **404**:72–74.

Caswell, H. 1989. Analysis of life table response experiments 1. Decomposition of effects on population growth rate. Ecological Modelling **46**:221–237.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology **81**: 619–627.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.

Cooch, E., R. F. Rockwell, and S. Brault. 2001. Retrospective analysis of demographic responses to environmental change: a Lesser Snow Goose example. Ecological Monographs 71:377–400.

Cunningham, S. A. 2000a. Depressed pollination in habitat fragments causes low fruit set. Proceedings of the Royal Society Biological Sciences Series B 267:1149–1152.

Cunningham, S. A. 2000b. Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. Conservation Biology 14:758–768.

Curran, L. M., and C. O. Webb. 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. Ecological Monographs 70:129–148.

Davies, K. F., and C. R. Margules. 1998. Effects of habitat fragmentation on carabid beetles: experimental evidence. Journal of Animal Ecology 67:460–471.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14:342–355.

Didham, R. K., and J. H. Lawton. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31:17–30.

Dobson, F. S., and M. K. Oli. 2001. The demographic basis of population regulation in Columbian ground squirrels. American Naturalist 158:236–247.

Funk, W. C., and L. S. Mills. 2003. Potential causes of population declines in forest fragments of an Amazonian frog. Biological Conservation 111:205–214.

Gotelli, N. J., and A. M. Ellison. 2002. Nitrogen deposition and extinction risk in the northern pitcher plant, Sarracenia purpurea. Ecology 83:2758–2765.

Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22:225–232.

Hobbs, R. J., and C. J. Yates. 2003. Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. Australian Journal of Botany 51:471–488.

Holt, R. D., G. R. Robinson, and M. S. Gaines. 1995. Vegetation dynamics in an experimentally fragmented landscape. Ecology 76:1610–1624.

Horvitz, C., D. W. Schemske, and H. Caswell. 1996. The relative ''importance'' of life history stages to population growth: prospective and retrospective analyses. Pages 247–271 in S. Tuljapurkar and H. Caswell, editors. Structured population models in marine, terrestrial, and freshwater systems. Chapman and Hall, New York, New York, USA.

Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs 65:155–192.

Jules, E. S., and B. J. Rathcke. 1999. Mechanisms of reduced Trillium recruitment along edges of old-growth forest fragments. Conservation Biology 13:784–793.

Kalisz, S., and M. A. McPeek. 1992. Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. Ecology 73:1082–1093.

Laurance, W. F., L. V. Ferreira, J. M. Rankin de Merona, and S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79:2032–2040.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, Jr., S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments, a 22 year investigation. Conservation Biology 16:605–618.

Leach, M. K., and T. J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. Science 273:1555–1558.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1–18.

Levin, L. A., H. Caswell, T. Bridges, D. Cabera, G. Plaia, and C. DiBacco. 1996. Demographic responses of estuarine polychaetes to pollutants: life table response experiments. Ecological Applications 6:1295–1313.

Malcolm, J. R. 1997. Biomass and diversity of small mammals in Amazonian forest fragments. Pages 207–221 in W. F. Laurance and R. O. Bierregaard, Jr., editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, Illinois, USA.

Manly, B. F. J. 1997. Randomization, bootstrap, and Monte Carlo methods in biology. Chapman and Hall, New York, New York, USA.

McDonald, R. I., and D. L. Urban. 2004. Forest edges and tree growth rates in the North Carolina Piedmont. Ecology 85:2258–2266.

McEuen, A. B., and L. M. Curran. 2004. Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments. Ecology 85:507–518.

Oli, M. K., and K. B. Armitage. 2004. Yellow-bellied marmot population dynamics: demographic mechanisms of growth and decline. Ecology 85:2446–2455.

Oli, M. K., N. A. Slade, and F. S. Dobson. 2001. Effect of density reduction on Uinta ground squirrels: analysis of life table response experiments. Ecology 82:1921–1929.

Santos, T., and J. L. Telleria. 1994. Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper Juniperus thurifera. Biological Conservation 70:129–134.

Santos, T., and J. L. Telleria. 1997. Vertebrate predation on Holm Oak, Quercus ilex, acorns in a fragmented habitat: effects on seedling recruitment. Forest Ecology and Management 98:181–187.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18–32.

Scariot, A. 2001. Seedling mortality by litterfall in Amazonian forest fragments. Biotropica 32:662–669.

Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker, and J. G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584–606.

Ticktin, T. 2004. The ecological implications of harvesting non-timber forest products. Journal of Applied Ecology 41:11–21.

Young, A. G., and G. M. Clarke, editors. 2000. Genetics, demography, and viability of fragmented populations. Cambridge University Press, Cambridge, UK.