ARE PLANT POPULATIONS IN FRAGMENTED HABITATS RECRUITMENT LIMITED? TESTS WITH AN AMAZONIAN HERB

Emilio M. Bruna[1,2,3]

[1]*Center for Population Biology, University of California–Davis, 1 Shields Ave., Davis, California 95616 USA*
[2]*The Biological Dynamics of Forest Fragments Project, PDBFF-INPA, CP 478 Manaus, AM 69011-970 Brazil*

Abstract. Decreased recruitment is hypothesized to be a primary mechanism driving the local extinctions of plant species from fragmented landscapes. A critical but untested assumption of this claim is that reductions in fecundity by individual plants actually result in demographic vulnerability at the population level. I tested this ''recruitment limitation hypothesis'' using three years of census data from 13 populations of the Amazonian understory herb *Heliconia acuminata*, which I integrated with empirical estimates of seedling establishment into matrix demographic models. I asked: (1) How much recruitment is necessary for $\lambda > 1$? (2) What are the projected values of λ for *H. acuminata* populations in fragments and continuous forest, given empirical estimates of seedling emergence? (3) What are the actual values of λ for populations in fragments and continuous forest, and why might projected and estimated values of λ differ? (4) What other demographic stages contribute to λ, and how are these affected by fragmentation? Simulation models suggest that extreme reductions in recruitment are necessary for population declines, and empirical estimates of seedling establishment were frequently below these thresholds. As a result, *Heliconia acuminata* populations in fragments are projected to shrink at a rate of 1–1.5% per year, while those in continuous forest are projected to grow 2.3–4% per year. Annual censuses, however, indicated populations in both continuous forest and fragments grew at rates well in excess of those projected by matrix models. This discrepancy is due to higher-than-predicted seedling numbers. While elasticity analyses indicated transitions related to growth and survivorship actually made the greatest proportional contribution to λ, these results suggest that dispersal into fragments is common and helping populations overcome the negative demographic consequences of reduced seedling establishment. Additional demographic studies of plant populations in fragmented areas are urgently needed to identify other potential mechanisms responsible for population declines. Particular attention should be paid to appraising the effect of fragmentation on plant growth and survivorship, as altering these life-history stages may have the most serious consequences for population growth rates.

Key words: Amazon; elasticity analyses; Heliconia acuminata; *lambda; matrix models; plant demography; recruitment limitation; seed dispersal; source–sink.*

INTRODUCTION

Understanding the consequences of habitat fragmentation for plant and animal populations is a central area of research in ecology (Harrison and Bruna 1999, Debinski and Holt 2000). While changes population size have been widely documented for animal taxa found in fragmented landscapes (Stouffer and Bierregaard 1995, Didham et al. 1998, Crooks et al. 2001), most ecological studies investigating how fragmentation influences plants have focused on describing community-wide rather than population-level trends (Scariot 1999, Tabarelli et al. 1999). These studies have found that certain plant species are less likely to be found in frag-

[3] Present address: Department of Wildlife Ecology and Conservation, University of Florida, P.O. Box 110430, Gainesville, Florida 32611 USA.
E-mail: BrunaE@wec.ufl.edu

ments (Dzwonko and Loster 1988, Norton et al. 1995, Scariot 1999), often as a result of local extinctions (Turner et al. 1995). However, the precise mechanisms responsible for these extinctions are usually unknown, as are the consequences of habitat fragmentation long-term plant population dynamics (Bierregaard et al. 1997).

Decreased recruitment in fragments is hypothesized to be a primary mechanism driving the local extinctions of plant populations (Bond 1995, Cardoso da Silva and Tabarelli 2000). Numerous studies have shown that fruit production can be reduced in fragments due to lower pollinator abundance, altered pollinator visitation rates, or decreases in pollen transfer (Aizen and Feinsinger 1994, Jules and Rathcke 1999, Cunningham 2000*a, b*; but see Dick 2001, White et al. 2002). Both primary and secondary seed dispersal can also be reduced in and around fragments (Santos and Telleria 1994, Andresen 2002), and seed predation often increases due to an influx of predators from the habitat

surrounding isolates (Santos and Telleria 1997, Curran and Webb 2000). Finally, seedling establishment can be markedly lower in fragments, due in part to altered environmental conditions (Bruna 1999) or inbreeding depression (Menges 1991).

Fragmentation of tropical rain forests is pervasive (Whitmore 1997), and the recruitment of understory plants may be particularly sensitive to the changes associated with it. The recruitment of these plants is frequently dependent upon gap creation and forest regeneration cycles (Alvarez-Buylla and Garcia-Barrios 1991, Alvarez-Buylla 1994, Horvitz and Schemske 1995), both of which can be strongly altered in fragmented areas (Laurance et al. 1998, Didham and Lawton 1999). Furthermore, many of these plants have specialized plant–pollinator interactions (Bawa 1990) or are obligately animal dispersed (Loiselle and Blake 1999). While a seed bank could compensate for the temporary loss of dispersers or pollinators (Bond 1995), the intensity of predation and other agents of seed mortality in tropical forests make long-term seed banks rare (Vázquez-Yanes and Orozco-Segovia 1993, Chambers and MacMahon 1994). As a result, the seed-to-seedling transition is considered a critical bottleneck in the dynamics of many tropical plants (Alvarez-Buylla and Garcia-Barrios 1991, Horvitz and Schemske 1995). Rather than relying on seed banks, many rain forest plants have ''seedling banks,'' in which individuals are capable of surviving for years until conditions for growth become favorable (Lieberman et al. 1985, Clark and Clark 1987). These generalizations, coupled with empirical demonstrations of fragmentation-related declines in reproduction or recruitment, have led some to assert that fragmented forests ''are losing plant species through the disruption of key ecological processes such as pollination and seed dispersal'' (Cardosso da Silva and Tabarelli 2000:72).

A critical but overlooked assumption of this claim is that reductions in fecundity by individual plants are demographically costly at the population level. Surprisingly, the relationship between seed production, seedling establishment, and long-term population growth remains unclear (Andersen 1989, Crawley 1990), despite the obvious necessity of recruitment for population persistence. Considerable theoretical and empirical work has explored how reductions in seed abundance and the availability of sites suitable for seedling establishment influence the proportion of seeds becoming seedlings (Clark et al. 1999, Kiviniemi and Eriksson 1999, Maron and Gardner 2000). However, to link these changes in recruitment to changes in population dynamics it is necessary to assesses variation in other life-history stages as well, as they may have large and potentially opposing effects on population growth rates (Horvitz and Schemske 1995). Unfortunately, multiyear demographic data for multiple populations of a single species remain extremely limited (Crawley 1990, Horvitz and Schemske 1995, Husband and Barrett 1996). This is particularly true for fragmented systems—to date only one study examining the consequences of fragmentation for plant recruitment has simultaneously also evaluated other aspects of plant life history (Jules 1998). As a result, the hypothesis that reduced recruitment limits population growth in habitat fragments remains largely untested.

Matrix-based demographic models provide an excellent means by which to assess the consequences of altered recruitment for plant population dynamics. They have become increasingly common in ecology because of their application from life-history evolution to conservation (Alvarez-Buylla et al. 1996, Riessen 1999, Parker 2000), and there is a broad body of literature describing their construction, interpretation, assumptions, and limitations (e.g., Bierzychudek 1999, de Kroon et al. 2000, Wisdom et al. 2000, Caswell 2001). Matrix models are commonly used to project what the asymptotic growth rate of a population, or λ, would be if a set of environmental conditions were maintained indefinitely. However, they can also be used to calculate the proportional contribution of different demographic transitions to λ, known as the elasticity of transitions. This analysis may be useful for conservation, since it can indicate what demographic transitions, and therefore ecological processes, should be the focus of conservation and management strategies (Silvertown et al. 1996).

Here, I test the hypothesis that fragmentation-related reductions in recruitment lead to negative population growth rates for plants in fragmented tropical landscapes. I use as a model system the Amazonian understory herb *Heliconia acuminata* (Heliconiaceae), found in both the experimentally isolated forest fragments and continuous forest reserves of Brazil's Biological Dynamics of Forest Fragments Project (BDFFP). *Heliconia acuminata* populations in the BDFFP fragments have few flowering individuals, both in terms of absolute numbers of flowering plants and the proportion of the population flowering (Bruna and Kress 2002). In addition, while fruit production by *H. acuminata* is similar in continuous forest and forest fragments (Bruna and Kress 2002), *H. acuminata* seeds dispersed to fragments are less likely to germinate and establish as seedlings (Bruna 1999). Using matrix models parameterized with three years of census data from 13 populations in fragments and continuous forest, I investigate the demographic consequences of fragmentation-related differences in seedling establishment. Specifically, I address the following four questions: (1) How much seedling establishment is necessary for *H. acuminata* populations to attain positive population growth rates (i.e., $\lambda > 1$)? (2) What are the projected values of λ for *H. acuminata* populations in forest fragments and continuous forest, given empirical estimates of seedling establishment? (3) What are the actual values of λ for populations in forest fragments and continuous forest, and why might projected and observed

estimates of λ differ? (4) What other size classes and transitions contribute to λ, and how are these affected by fragmentation? The answers to these questions will then be used to assess the relative importance of recruitment limitation to the dynamics of plant populations in tropical forest fragments, with the goal of evaluating what life-history stages should be the focus of conservation action.

METHODS

Study site and organism

All fieldwork was conducted at the Biological Dynamics of Forest Fragments Project, located 80 km north of Manaus, Brazil (2°30′ S, 60° W). The BDFFP reserves are found in nonflooded tropical lowland rainforest with undulating topography ranging from 50 to 150 m in elevation. Soils are nutrient-poor xanthic ferralsols that drain well (Chauvel et al. 1987), and the density of flowering and fruiting plants is low (Gentry and Emmons 1987). Mean annual temperature is 26°C (range 19°–39°C) with annual rainfall ranging from 1900 to 2300 mm (BDFFP records). There is a pronounced dry season from June through November.

The fragments at the BDFFP were isolated from 1980 to 1984 by felling the trees surrounding the fragment and, in most cases, burning the downed trees once they had dried (Lovejoy et al. 1986). Fragments were fenced to prevent intrusion by the cattle initially kept in the surrounding pastures. Since their original isolation, the secondary growth surrounding the fragments has been cleared three or four times (BDFFP records).

Heliconia acuminata is a perennial, self-incompatible herb native to the nonflooded forests of central Amazonia (Berry and Kress 1991). Each plant is composed of vegetative shoots that emerge from a rhizome and, if reproductive, one or more flowering shoots. Clonal reproduction via underground runners, common in some species of *Heliconia* (Stiles 1975), is rare in *H. acuminata* (E. M. Bruna and W. J. Kress, *personal observation*). Instead, plants depend on seeds for recruitment. Each flowering shoot has a single inflorescence of 20–25 flowers; flowering begins in late January and continues through April (Bruna and Kress 2002). At our sites, *H. acuminata* is pollinated solely by the hermit hummingbirds *Phaethornis superciliosus* and *P. bourcieri* (E. M. Bruna, *personal observation*). Developing fruits ripen through June and are dispersed by birds (Kress 1985). Each fruit produces a maximum of three seeds that remain dormant until the onset of the following rainy season (Bruna 1999).

Demographic plots and annual censuses

Demographic censuses were conducted in 13 large (50 × 100 m) permanent plots established in the BDFFP reserves. Six of these plots were in continuous forest (CF 1–6), four were in 1-ha fragments (FF 1–4), and three were in 10-ha fragments (FF 5–7). Plots in 1-ha fragments were established in a randomly selected half of the fragment, plots in 10-ha fragments were established in the fragment center, and plots in continuous forest sites were haphazardly placed at locations 500–4000 m from any secondary forest/mature forest borders. The plots furthest apart from each other were separated by ~42 km. For a complete description of the study site and demographic plots see Bruna and Kress (2002).

In January 1998, I marked all *H. acuminata* plants in the seven demographic plots located in fragments and in three of the continuous forest plots (CF 1–3). Each plant was marked with a stake to which I attached an individually numbered aluminum tag. I measured all plants by counting (a) the number of vegetative shoots they had and (b) the height of the plant (measured as the distance from the base of the plant to its highest point above the ground). Throughout the 1998 reproductive season, I regularly surveyed the plots to record the identity of flowering individuals, how many flowers they produced, and the proportion of these flowers developing into fruits. In August 1998, I established plots in the final three continuous forest sites (CF 4–6), tagging and measuring plants as before.

I returned to survey the original 10 plots in January 1999 and 2000, when I recorded plant mortality, marked and measured all new seedlings, and measured all surviving plants. I again recorded reproduction throughout the flowering season. Plants in the three continuous forest plots established in August 1998 were censused in August 1999, however, reproduction in these plots was recorded during the flowering season along with all other plots. These censuses resulted in complete demographic data for two transition years: 1998–1999 and 1999–2000.

Stage classification and transition rules

The life cycle graph for *H. acuminata* is shown in Fig. 1. Plants were assigned to one of six size classes: seedlings and plants with one, two, three, four, and five or more vegetative shoots. I chose to delimit *H. acuminata* size classes on the basis of shoot number for three principal reasons. First, the probability an *H. acuminata* individual will flower increases with the number of vegetative shoots it has (Bruna and Kress 2002). Second, shoot number is a discrete character, therefore no arbitrary cutoffs are required to assign plants to different size categories. This also minimizes measurement error in the field. Finally, shoot number is highly correlated with leaf area and plant height (Bruna and Kress 2002, Bruna et al. 2002), two other measures of plant size that are demographically important in understory herbs (Horvitz and Schemske 1995).

Although *H. acuminata* seedlings have only one shoot, they were placed in a separate category because their survivorship often differs from that of nonseedling plants of the same shoot number (see *Results*). Note that there is no category for dormant seeds in the

Fig. 1. Life-cycle graph for *Heliconia acuminata*. Arrows indicate potential transitions between stage classes, including contribution to seedlings via reproduction. Dashed lines indicate transitions that were rarely observed.
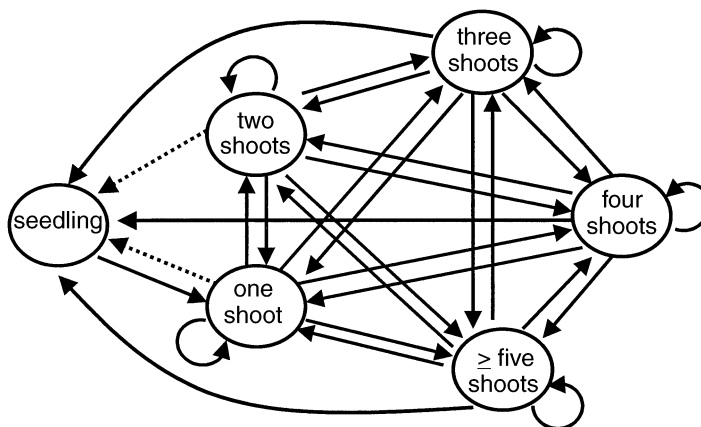
life-cycle diagram, since seeds produced in one flowering season germinate prior to the subsequent census. Although experimental results indicate some seeds are capable of surviving up to 24 months, this is usually when provided with artificial protection from burial under leaf-litter and other natural agents of seed mortality (Bruna 2002).

From one year to the next, plants can grow into larger size classes, remain the same size, shrink into smaller size classes, or die. The one exception to this rule is surviving seedlings, which become one-shoot plants in the second year.

Matrix model construction

The construction of Lefkovitch matrices (Lefkovitch 1965) and their analysis is described in detail elsewhere (Caswell 2001). Briefly, I calculated the probability of transition between stages using the annual censuses, and estimated the per-individual fecundity (F_i) of plants in each stage/size class i with the formula $F_i = p_i \times f_i \times s \times g$, where p_i is the probability that an individual in size class i flowered, f_i is the total number of fruits produced by individuals of size class i, s_i is the number of seeds per fruit, and g is the probability of successful seedling establishment (i.e., of seed germination and seedling survivorship to the next census). Note that no term for seed dispersal is included in this calculation—it is assumed that all developing seeds are successfully dispersed and that dispersal is entirely local (i.e., there is no immigration or emigration of seeds from the plot). Values of f_i, p_i, and s were based on the annual censuses, while estimates of g for each plot in each year were experimentally derived (see Appendix A for details).

A total of 23 projection matrices describing *H. acuminata* dynamics were constructed: 10 for the 1998–1999 transition year (seven forest fragments, three continuous forest sites) and 13 for the 1999–2000 transition year (seven forest fragments, six continuous forest sites; see Appendix B). In addition to matrices for individual plots, I also constructed matrices summarizing the dynamics in each habitat type. Summary matrices are constructed by pooling all individuals from plots

within a habitat class, then calculating the transition probabilities and fecundities. A summary matrix is a superior means of synthesizing the demography of multiple populations than one composed of the average of transition values from many different matrices; summary matrices correct for the disproportionate weight that low plant numbers in some size classes in some locations can give to some transition probabilities (Horvitz and Schemske 1995, Caswell 2001). I constructed two summary matrices for 1-ha fragments (1998–1999, 1999–2000), two for 10-ha fragments (1998–1999, 1999–2000), and two for continuous forest (1998–1999, 1999–2000; see Appendix C).

I monitored 5205 *H. acuminata* individuals over the course of this study, with density per plot in 1999 ranging from 112 to 753 plants (Table 1, Bruna and Kress 2002). Of the 2911 plants measured in 1998, 45 could not be found in the 1999 census (1.5%), while 110 of the 3871 measured in 1999 were not found in the 2000 census (2.86%). Missing plants, which were not included in the calculation of transition matrices, were usually in smaller size classes (number of shoots in 1998 of plants missing in 1999, 2.49 ± 0.18 [mean ± 1 SE], number of shoots in 1999 of plants missing in 2000, 2.70 ± 0.09). While this could have resulted in slight underestimates of mortality for some stage classes, considering these missing plants dead in the calculations had little effect on the stage-specific estimates of survivorship.

Question 1: How much recruitment is necessary to maintain λ > 1?

To determine the levels of recruitment necessary to maintain positive population growth rates (i.e., λ > 1), I used a computer simulation in which I evaluated how λ changed as g, the proportion of seeds that successfully established as seedlings, increased from 0 to 100%. I used the four summary matrices for 1-ha and 10-ha fragments to conduct these simulations, since preliminary analyses indicated there was no spatial variation among transition matrices from these size classes (Bruna 2001). However, the transition matrices from

TABLE 1. Asymptotic growth rates (λ) of the populations used in this study and characteristics of the plots where they are located.

Plot	Habitat type†	BDFFP reserve no.‡	Year isolated	*Heliconia acuminata* density in 1999§	1998–1999 λ (95% CI)	1999–2000 λ (95% CI)
FF-1	1-ha	2107	1984	214	0.983 (0.937–1.000)	0.997 (0.967–1.017)
FF-2	1-ha	2108	1984	161	0.978 (0.880–1.000)	0.988 (0.955–1.000)
FF-3	1-ha	1104	1980	206	0.987 (0.859–1.040)	0.989 (0.967–1.000)
FF-4	1-ha	3114	1983	250	0.988 (0.960–1.000)	0.978 (0.948–0.991)
FF-5	10-ha	2206	1984	162	0.988 (0.945–1.000)	0.978 (0.942–0.996)
FF-6	10-ha	1202	1980	402	0.991 (0.975–0.998)	0.994 (0.984–0.999)
FF-7	10-ha	3209	1983	577	0.999 (0.995–1.000)	0.996 (0.990–0.999)
CF-1	CF	1301	...	753	1.028 (1.001–1.054)	1.040 (1.028–1.058)
CF-2	CF	1501	...	555	1.079 (1.059–1.106)	1.022 (1.013–1.033)
CF-3	CF	1501	...	703	0.987 (0.967–1.003)	0.991 (0.979–0.997)
CF-4	CF	Porto Alegre	...	112	plot not established	1.014 (1.001–1.040)
CF-5	CF	Dimona	...	171	plot not established	1.018 (1.004–1.046)
CF-6	CF	3402	...	235	plot not established	1.016 (1.006–1.040)

Note: All fieldwork was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located 80 km north of Manaus, Brazil.
† Abbreviations: 1-ha, 1-ha fragments; 10-ha, 10-ha fragments; CF, continuous forest.
‡ CF-4 and 5 have no BDFFP numbers; therefore I used the name of the ranch in which they are located instead.
§ From Bruna and Kress (2002).

the continuous forest plots were significantly different from each other in both years (Bruna 2001). I therefore conducted the simulations for continuous forest using both the summary matrices and the matrices for individual plots. Results for simulations based on summary matrices were very similar to those based on matrices describing the demography of individual plots; for simplicity I present only the results based on the summary matrices.

To calculate λ, I used a corrected version of the MATLAB code in Caswell (2001). Confidence intervals for each estimate of λ were calculated using bootstrapping (Kalisz and McPeek 1992), since the assumptions of independence among matrix elements and minimal variance in matrix parameters that are necessary for analytical approximations are rarely met (Caswell 2001). The upper and lower 95% confidence intervals of 2000 bootstrap runs were estimated using bias-corrected percentile intervals (Manly 1997, Caswell 2001).

Question 2: What are the projected values of λ in fragments and continuous forest?

To project λ for each plot in each transition year, I used the empirically derived estimates of seedling establishment, *g*, for that plot (Bruna 1999, 2002, Appendix A). I again estimated 95% confidence intervals of λ using bootstrapping. Finally, I estimated λ and the 95% confidence intervals for each of the summary matrices using the overall average rates of experimental seedling establishment in the corresponding habitat type (Appendix A).

Question 3: Do the projected and observed estimates of λ differ? If so, why?

To determine the actual rate at which populations grew from one year to the next, I simply divided the

number of *H. acuminata* plants in each plot in year *t* + 1 by the number of plants there in year *t*. To determine if these growth rates were significantly different from projected ones, I compared the actual values of λ with the 95% confidence intervals for each plot's projected λ. The actual λs were considered significantly different from the projected ones if they exceeded these 95% confidence intervals. I also calculated the landscape-wide growth rates for each habitat type by pooling plots within a habitat type and dividing pooled abundance in year *t* + 1 by pooled abundance in year *t* as above. Actual growth rates were again compared with the 95% confidence intervals of projected λs calculated with summary matrices.

To investigate whether differences in projected and observed estimates of λ could be related to differences in seedling recruitment, I compared the projected number of seedlings expected to establish in plots of each habitat type with the number actually emerging. The projected number of seedlings in a demographic plot in year *t* + 1 was calculated using the transition matrices and vectors of population size in year *t*; the observed number of seedlings was based on the annual surveys. I also calculated the projected number of seedlings for each habitat class using summary matrices and summary population vectors, while the observed number of seedlings landscape-wide was calculated by summing the number of seedlings censused in all plots in that category. Observed and expected numbers of seedlings were compared for both transition years using *G* tests (after adding 0.5 to each cell [Zar 1999]).

To gain additional insight into differences between observed and projected estimates of λ, I calculated the stable-stage distribution (SSD) for each summary matrix. I then compared the SSD and the observed distribution in each habitat type in each year using *G* tests.

The SSD, which is the right eigenvector of the transition matrix, was scaled to 100 so that each element of the vector represents the percentage of the population in that stage class (Caswell 2001).

Question 4: What other size classes and transitions contribute to λ?

To assess the contribution of different transitions to λ I conducted elasticity analyses. I first calculated the sensitivity of λ to each matrix element a_{ij} using the formula

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}$$

where w and v are the dominant right and left eigenvectors and $\langle \mathbf{w}, \mathbf{v} \rangle = 1$ (Caswell 2001). The proportional contribution to λ of each element (i.e., elasticity) can then be calculated as

$$e_{ij} = \frac{a_{ij}}{\lambda} \times \frac{\partial \lambda}{\partial a_{ij}}$$

(Caswell 2001). I calculated elasticity matrices for all estimates of λ from both transition years, using individual plot matrices as well as summary matrices. Since analyses using log-linear models indicated no spatiotemporal variation in elasticity or sensitivity matrices from the different plots in each habitat class (Bruna 2001), I present the results of elasticity analyses for summary matrices only.

RESULTS

General patterns of Heliconia acuminata demography

Heliconia acuminata survivorship was high for all stage classes and exceeded 90% for postseedling stages in most locations (Fig. 2). The most variable survivorship was of seedlings, with survivorship as low as 50% in some locations and as high as 100% in others (Fig. 2). In part this is due to low numbers of seedlings in some plots, however, seedling survivorship still varied considerably among habitat types when compared using summary matrices (Fig. 2D and 2H). At the landscape level, survivorship of seedlings was highest in 10-ha fragments in both transition years (97.06% in 1998–1999; 84.55% in 1999–2000). However, while from 1998 to 1999 survivorship was higher for seedlings in 1-ha fragments than those in continuous forest (85.71% and 74.81%, respectively), this pattern was reversed in 1999–2000 (survivorship in CF = 81.5% vs. 73.85% in 1-ha fragments). Although individuals in some stage classes were capable of extremely rapid transitions among size classes, most plants stayed in the same size class, increased one size class, or decreased one size class from one census interval to the next. When accounting for the effects of limited plant numbers in some stage classes in some locations using summary matrices, post-seedling survivorship exceeded 95% for all stages (Fig. 2D and 2H).

Question 1: How much recruitment is necessary to maintain λ > 1?

Extremely low levels of seed germination and seedling establishment are sufficient to maintain positive population growth rates (i.e., λ > 1) in both continuous forest and 10-ha fragments. Only 1–2% of the *Heliconia acuminata* seeds produced by plants in continuous forest plots had to germinate and establish as seedlings for λ > 1, and the lower 95% confidence intervals were beyond the λ = 1 threshold with only 1–3% germination and establishment (Fig. 3). These results are almost identical to those for 10-ha fragment summary matrices, in which only 1% of seeds had to germinate for λ > 1 (Fig. 3). In 1-ha fragments, however, slightly higher levels of seedling establishment are necessary for population growth rates to remain positive. Estimates of λ based on 1-ha summary matrices cross the λ = 1 threshold with 5–6% seed germination success, and the lower 95% confidence intervals are not beyond λ = 1 until 12–15% of seeds germinate and are successfully established (Fig. 3).

With maximal seedling establishment (i.e., g = 100%), λ in 1-ha fragments reached a high of 1.13 and 1.17 (1998–1999 and 1999–2000, respectively). In 10-ha fragments and continuous forest, the maximal value of λ was considerably higher, with λ = 1.382 and 1.308 in 1998–1999 (10-ha fragments and CF, respectively) and λ = 1.234 and 1.267 in 1999–2000 (10-ha fragments and CF, respectively).

Question 2: What are the projected values of λ in fragments and continuous forest?

Based on summary matrices, *H. acuminata* populations in 1-ha fragments are projected to shrink at rates of 1 and 1.5% per year (1998–1999 λ = 0.985, 1999–2000 λ = 0.990), with 95% confidence intervals for these estimates failing to exceed one in both transition years (Table 2). Lambda in continuous forest is significantly greater, based on nonoverlapping 95% confidence intervals, with populations in continuous forest projected to grow at rates of 4% and 2.3% per year (1998–1999 and 1999–2000 transition years, respectively). Lambda for populations in 10-ha fragments is intermediate in both years. In 1998–1999, it is significantly lower than in continuous forest and higher, though not significantly higher, than in 1-ha fragments (10-ha λ = 1.012). In the 1999–2000 transition year, it is significantly higher than in 1-ha fragments but significantly lower than in continuous forest (10-ha λ = 1.000, Table 2).

These results are consistent with those for matrices based on individual plots (Table 1). For 1-ha fragments, λ was less than one in all locations in both transition years (range for 1998–1999, λ = 0.978–0.988; range for 1999–2000, λ = 0.978–0.997). Of the eight matrices constructed for 1-ha fragments, only two had upper 95% confidence intervals exceeding λ = 1 (FF-3 in
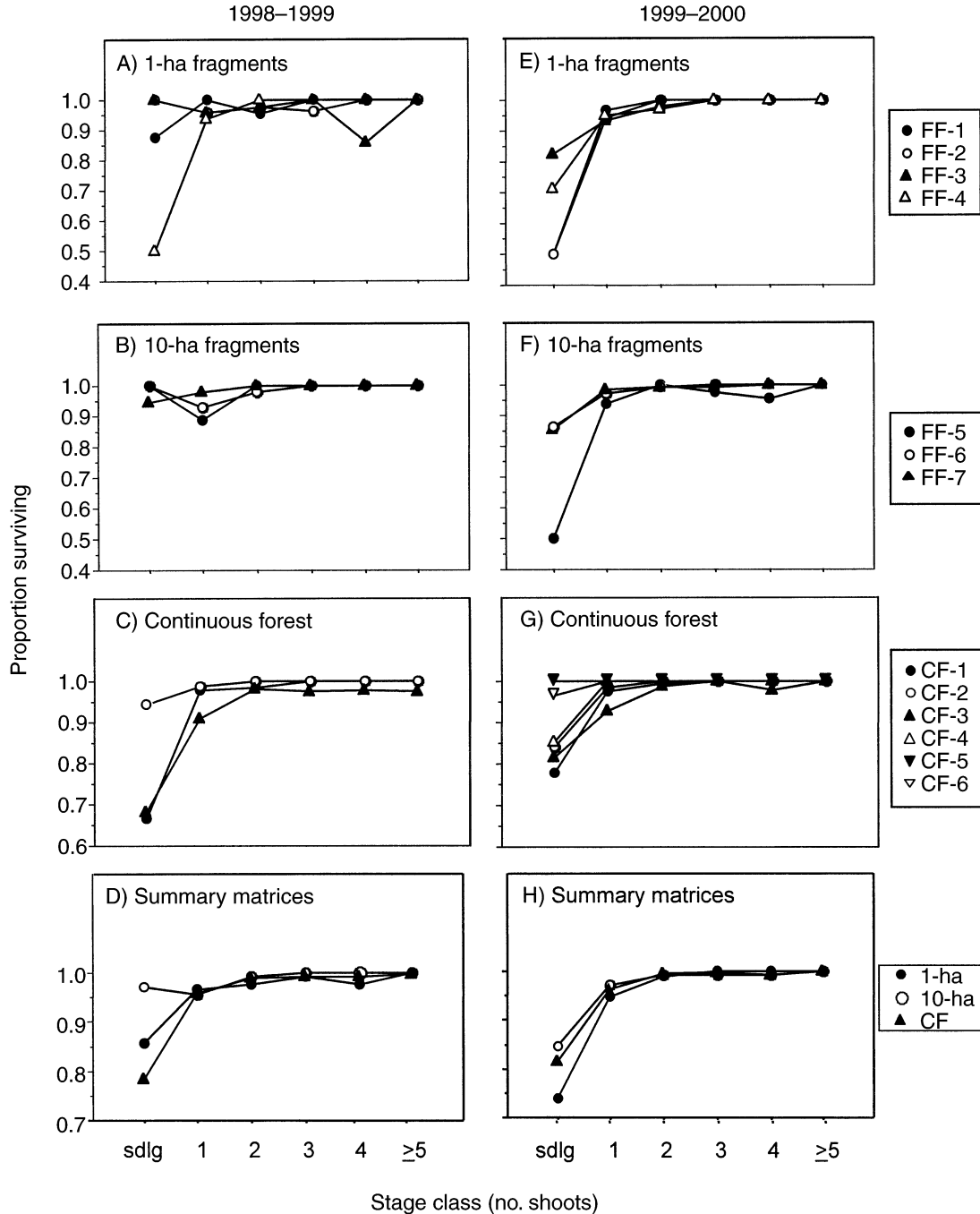
Fig. 2. Survivorship of plants in each stage class based on individual plot and summary matrices (sdlg = seedling): (A–D) 1998–1999 transition year; (E–H) 1999–2000 transition year. Abbreviations in keys are: FF, forest fragment; CF, continuous forest.

1998–1999, FF-1 in 1999–2000), and the overlap of 95% confidence intervals indicates values of λ for the individual 1-ha fragments do not differ significantly from one another (Table 1).

Lambda values for individual demographic plots in the 10-ha fragments were similar to those calculated with summary matrices, with the exception of the population in FF-5 (Table 1). This population is projected to decline at an annual rate of 1.2% and 2.2% (1998–1999 and 1999–2000, respectively), although the upper 95% confidence interval for these estimates is either one or extremely close to it (Table 1). Once again, the
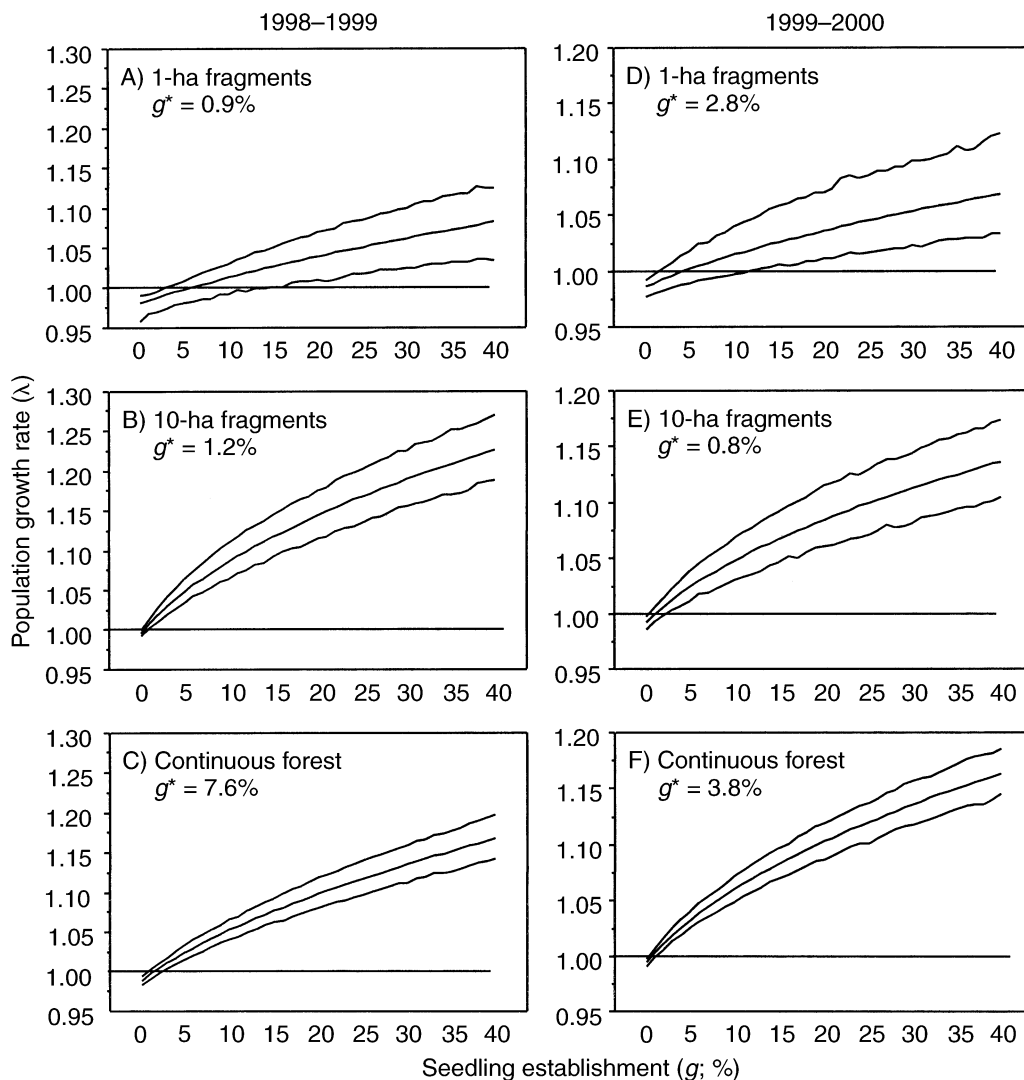
FIG. 3. Results of simulations describing changes in the population growth rate (λ) as a function of increasing seed germination and seedling establishment (g). The center line is the estimate of λ; the upper and lower lines represent the 95% confidence intervals. The solid horizontal line is the threshold value of λ at which population growth rate is constant ($\lambda = 1$). Panels A–C are based on summary matrices for the 1998–1999 transition year, panels D–F are based on summary matrices for the 1999–2000 transition year. The empirical value for seed germination and seedling establishment in each habitat type (from Bruna 1999, 2001) is given by g^*.

95% confidence intervals for λ from individual plots overlapped with each other, indicating the growth rates of populations in different 10-ha fragments did not vary significantly from one another (Table 1).

In contrast to the populations in fragments, the dynamics of *H. acuminata* populations in continuous forest are more variable. Estimates of λ for individual continuous forest plots ranged from 0.987 (CF-3 in

TABLE 2. Asymptotic growth rates (λ) of populations in 1-ha fragments, 10-ha fragments, and continuous forests, based on summary transition matrices.

Habitat type	1998–1999 λ	1999–2000 λ
1-ha fragments	0.985 (0.970–0.995)	0.990 (0.980–0.997)
10-ha fragments	1.012 (1.005–1.018)	1.000 (0.993–1.006)
Continuous forest	1.040 (1.029–1.051)	1.023 (1.018–1.028)

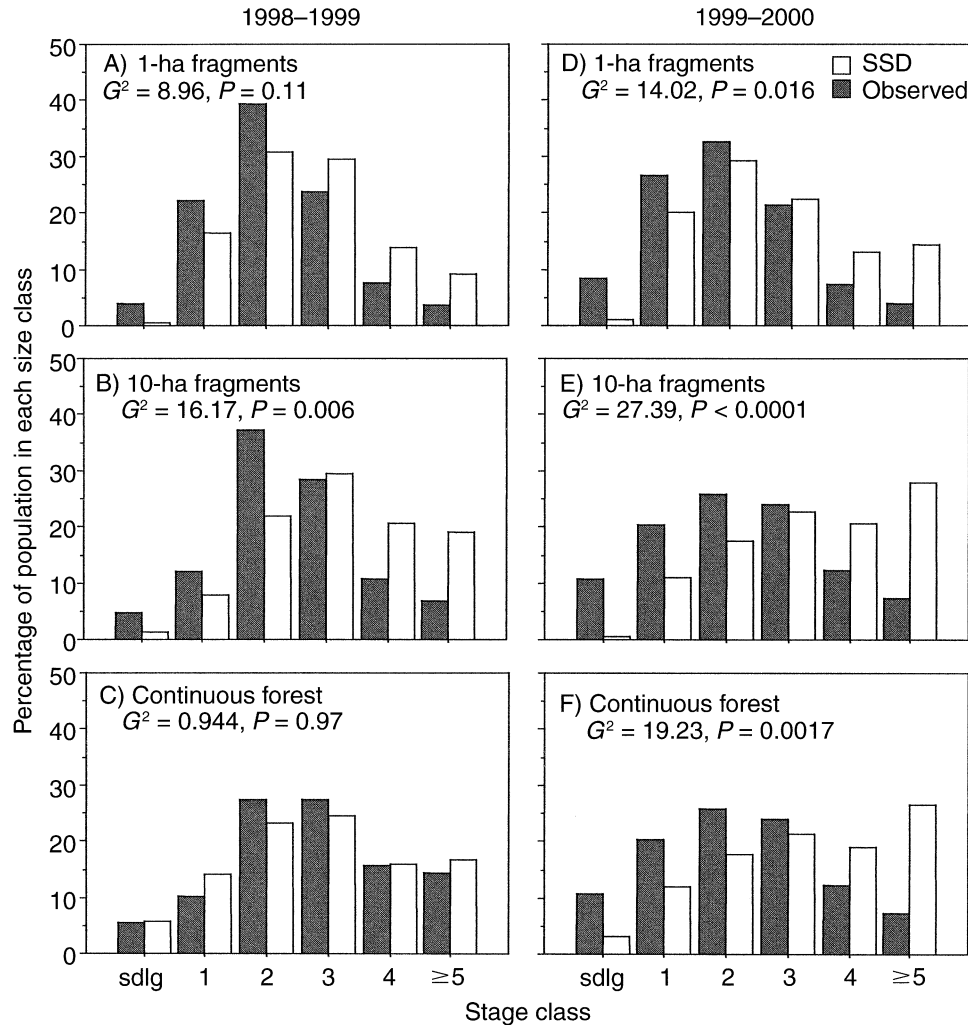*Note:* The 95% confidence intervals for each estimate are given in parentheses.

FIG. 4. The stable-stage distribution (open bars) for summary matrices and the observed distribution (shaded bars) for populations of *Heliconia acuminata* in each habitat type in each transition year (sdlg = seedling). The G^2 statistic indicates whether there is a significant difference between the observed and stable stage distribution.

1998–1999) to 1.079 (CF-2 in 1998–1999). While one continuous forest plot did have $\lambda < 1$ in both years of this study (CF-3: 1998–1999, $\lambda = 0.987$; 1999–2000, $\lambda = 0.991$), the lower 95% confidence intervals of the other five plots were always greater than one. While CF λ was usually significantly higher than 10-ha λ and 1-ha λ, plots in continuous forest usually had overlapping confidence limits and hence did not vary significantly from one another (Table 1).

The stable-stage distribution was significantly different from the observed distribution in four of the six habitat type × year combinations (Fig. 4). Seedlings were underrepresented when compared to the observed distributions in all cases but one (CF in the 1998–1999 transition year, Fig. 4C). In contrast, plants with four or more shoots were typically overrepresented in the SSD relative to the actual distribution.

Question 3: Do the projected and observed estimates of λ differ?

During this study period, *H. acuminata* populations grew at rates well in excess of those projected by matrix models. Comparisons of projected and observed values of λ indicate projected values are significantly lower than observed values for 19 of 23 combinations of location and transition year. Only for FF-1, CF-2, and CF-3 in 1998–1999 and CF-5 in 1999–2000 were the actual population growth rates within the confidence intervals of estimated values (Fig. 5). There is, however, considerable variation in the extent to which matrix models underestimate the observed value of λ. For instance, in the 1998–1999 transition year, models underestimated λ by 21.1% in FF-3, but only by 0.008% in FF-1 (Fig. 5A). While underestimates for some lo-
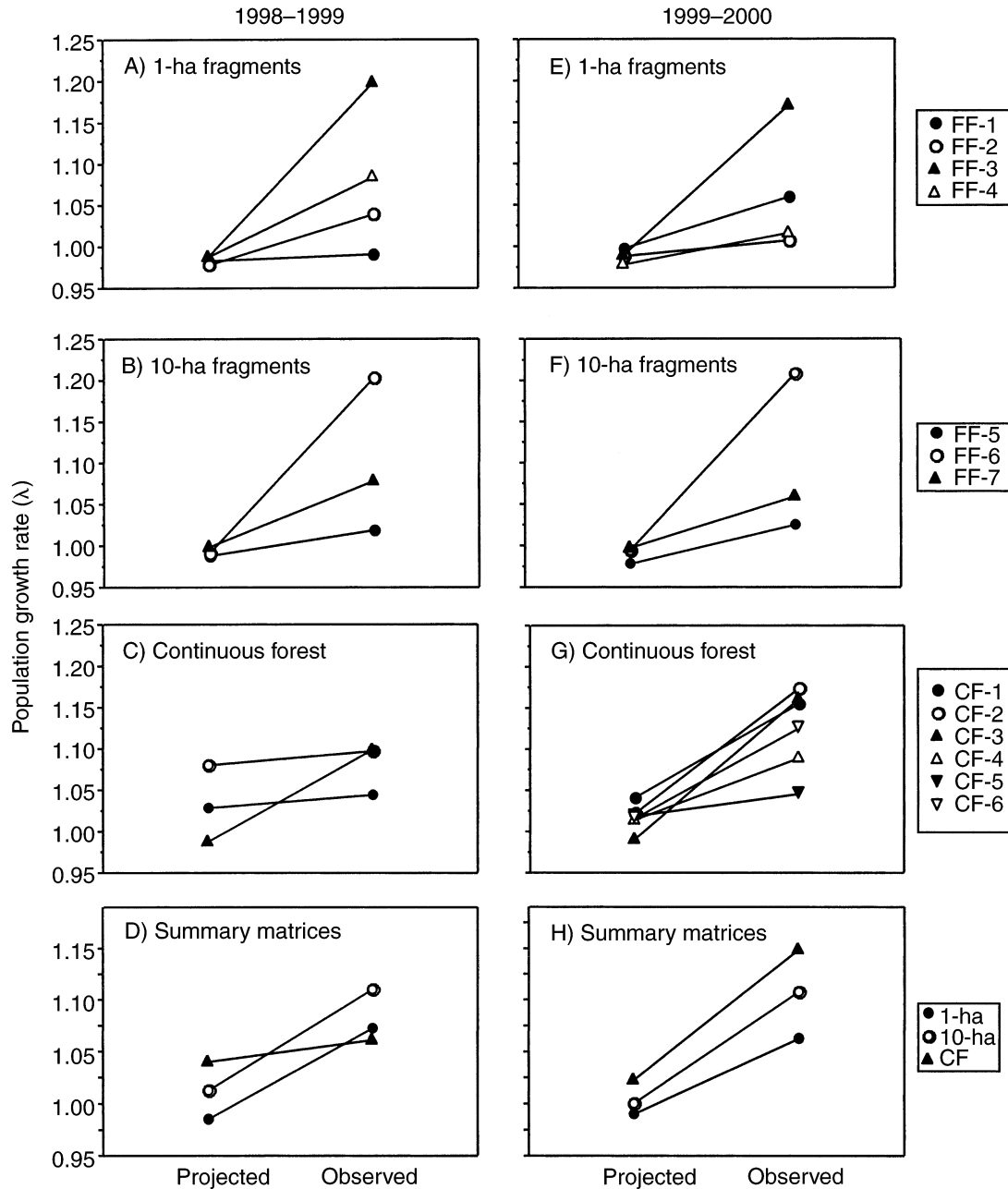
FIG. 5. Projected and actual population growth rates for individual plots and summary matrices: (A–D) 1998–1999 transition year; (E–H) 1999–2000 transition year. Note the different scales for individual plot and summary matrices.

cations were often consistent from year to year (e.g., in 10-ha fragments, Fig. 5B and 5F), in some locations the extent to which λ was underestimated varied between transition years (e.g., in 1-ha fragments, Fig. 5A vs. 5E).

Summary matrices also significantly underestimated λ in all three habitat types in both years. The summary matrices for 1-ha fragments underestimated λ by 8.8% and 7.3% (1998–1999 and 1999–2000, respectively), while the summary matrices for 10-ha fragments un-

derestimated λ by 9.8% and 10.8% (1998–1999 and 1999–2000, respectively). Summary matrices for continuous forest were mixed in their accuracy, underestimating λ by only 2% in 1998–1999 but by 12.6% in 1999–2000 (Fig. 5D and 5H). However, while the magnitude of λ was underestimated in both transition years, the relative rank order of the actual values of λ was the same as that of the estimates based on matrix models (1-ha λ < 10-ha λ < CF λ). The one exception was the observed value of λ in continuous forest in the
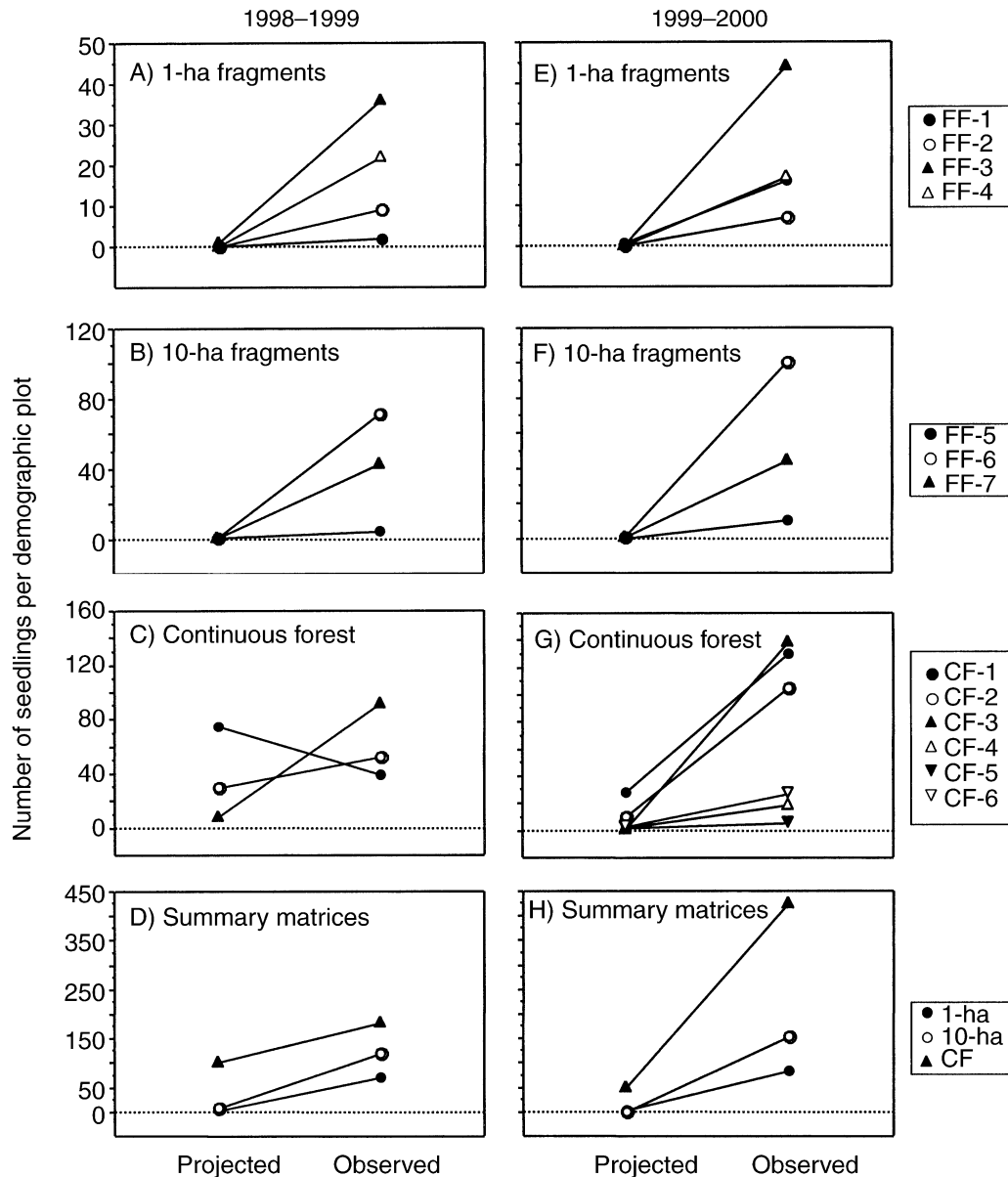
FIG. 6. Projected and observed number of established seedlings in each site, as well as landscape-level values based on summary matrices: (A–D) 1998–1999 transition year; (E–H) 1999–2000 transition year. Note the different scales for each habitat type.

1999–2000 transition year. While models projected λ for continuous forest would be greater than for fragments, the observed value of λ for continuous forest was actually lower than for either fragment size class.

Patterns of projected vs. observed seedling recruitment are similar to those for population growth rates. In both transition years, the number of seedlings projected to emerge in plots was significantly lower than the number actually counted during the census (1998–1999, $G^2 = 178.95$, $P < 0.0001$; 1999–2000, $G^2 = 52.36$, $P < 0.0001$; Fig. 6). Projections based on summary matrices were also underestimates (1998–1999,

$G^2 = 73.15$, $P < 0.0001$; 1999–2000, $G^2 = 23.12$, $P < 0.0001$), however, the projected pattern of abundance was in the same rank order as the observed pattern. Projected and observed seedling abundances were greatest in continuous forest, followed by 10-ha then 1-ha fragments. This trend was consistent for both survey years (Fig. 6D and 6H).

As with estimates of λ, there was considerable interplot variation in the extent to which seedling numbers were underestimated. Estimates of new seedling numbers were only slight underestimates for some plots (FF-1, FF-5, CF-4) while in some locations the number

of new seedlings was underestimated over 20-fold (CF-4, FF-6, FF-3, Fig. 6).

Question 4: What other size classes and transitions contribute to λ?

Elasticity patterns for summary matrices from the different habitat types were very similar to each other for both years analyzed, with the highest elasticities for transitions representing stasis within the same size class (38.77–46.41%, Appendix D). Values for transitions representing movement into subsequently larger or smaller stage classes were also relatively high, with total contributions to λ of 15.25–28.29% (Appendix D). Elasticity values for fecundity were extremely low in both transition years in all locations, contributing only 0.27–4.09% of λ (Appendix D).

DISCUSSION

This study is the first to use complete, multiyear census data of populations in both forest fragments and nearby continuous habitat to test the hypothesis that reduced recruitment leads to negative rates of population growth. My results suggest that fragmentation-related reductions in recruitment can lead to negative growth rates in fragments, however, only when recruitment is severely limited. Below, I discuss the implications of these results, as well as evidence suggesting recruitment in fragments is well above the threshold value necessary for population persistence due to immigration of seeds from nearby habitat.

How much recruitment is necessary for λ > 1?

Although direct evidence remains rare, populations of long-lived perennials are rarely thought to be recruitment-limited (Crawley 1990). This conclusion is borne out for *H. acuminata* populations in both continuous forest and 10-ha fragments, where simulation models indicate λ will be positive with only minimal establishment of seedlings. In fact, even when using highly conservative demographic models that do not allow for immigration of seeds from sources outside of the plots, the production of seeds by local flowering plants is sufficient to insure an average λ ≥ 1 in 10-ha fragments across the entire BDFFP landscape.

This was not the case with 1-ha fragments, however, where empirically estimated establishment of local seeds was below the threshold needed for positive population growth (Bruna 1999, 2002). If there is no seed dispersal, *H. acuminata* populations in 1-ha fragments are projected to decline at rates of 1–1.5% per year. Had these rates been maintained for the 20 yr since fragment isolation, populations would have declined by 18–25%. Occasional ''boom'' years might have negated these declines, however, tropical plants rarely appear to exhibit the year-to-year dynamism in λ that typifies many temperate plant species (Pinero et al. 1984, Alvarez-Buylla and Garcia-Barrios 1991, Olmsted and Alvarez-Buylla 1995). It is therefore conceivable that in the complete absence of any seed dispersal, fragmentation-related reductions in fruit production or seed germination could lead to extinctions of plant populations from smaller forest fragments. However, for long-lived species with high adult survivorship found at reasonable population densities, it appears decreases in recruitment must be exceptionally severe and persistent in order to be a major cause of extinction from fragments.

Several caveats to this generalization bear discussing. First, fruit production by *H. acuminata* is similar in fragments and continuous forest (Bruna and Kress 2002). Concluding reduced recruitment is unlikely to drive populations extinct may be optimistic if fruit set in fragments is severely pollinator- or resource-limited (Jules and Rathcke 1999, Cunningham 2000a, b). Second, per capita flowering rates are also similar in fragments and continuous forest (Bruna and Kress 2002). Had they been lower in fragments, more seedling establishment would have been necessary to maintain λ > 1. Finally, these fragments are protected from intrusion by cattle and other ''nonnative'' agents that can cause highly elevated mortality (Aizen and Feinsinger 1994). However, note that even with zero recruitment, the lower 95% confidence limits of λ in fragments were never below 0.965–0.975. Even moderate recruitment will increase λ above the threshold necessary for positive population growth.

Predicting the demographic consequences of altered reproduction in fragmented habitats will clearly require an increased understanding of how the different processes related to fecundity are modified by fragment isolation and edge creation (Jules and Rathcke 1999). To date, only one study has investigated how a suite of mechanisms influencing reproduction is altered by fragmentation. Jules and Rathcke (1999) found that for *Trillium* in fragments of North American conifer forest there were no fragmentation-related changes in seed dispersal, resource limitation of seed set, phenology, or germination. There were, however, increases in seed predation and decreases in seed production. Whether these changes are severe enough to drive demographic change is unclear, though it appears that they might be. Both are highly correlated with decreased *Trillium* recruitment along fragment edges (Jules and Rathcke 1999).

Why do projected and observed values of λ differ?

Contrary to projections based on matrix models, annual censuses indicate *H. acuminata* populations in 1-ha fragments are growing an average of 5–6% per year, with population size in one of the 1-ha fragments increasing by 17–20%. Underestimates of λ were also considerable in 10-ha fragments, where λ was an average of 10% higher than predicted by models. Mismatches between projected and observed estimates of λ are useful because they allow us to identify mechanisms not included in models that may influence pop-

ulation dynamics (Doak and Morris 1999, Mills et al. 1999). In this case, the disparity between projected and observed values of λ is due to increases in the observed number of *H. acuminata* seedlings relative to predicted numbers. While some 1-ha and 10-ha fragments had extremely low numbers of seedlings in them—numbers equivalent to those projected—several of them had seedling abundances comparable to those in continuous forest sites (e.g., FF-3, FF-6, FF-7).

Two potential mechanisms could explain this discrepancy. First, it could be that the empirically derived estimates of seedling establishment used in calculations of fecundity underestimate the true rates. However, this does not appear to be the case. Only by incorporating rates of seedling establishment three- to sixfold greater than those from experimental treatments offering artificial protection to seeds (Bruna 1999, 2002) did the estimated λ approach observed λ in fragments forest (E. M. Bruna, *unpublished data*). Instead, the discrepancy between estimated and observed values is probably the consequence of a key assumption of calculations of per-individual fecundity. I assumed that dispersal was highly localized, i.e., that the only source of seeds was flowering plants within a plot. This assumption is a common one in studies using matrix models to describe population dynamics, in large part because explicit details regarding dispersal are unknown (Alvarez-Buylla and Garcia-Barrios 1991), especially in tropical systems (but see Alvarez-Buylla [1994], Martinez-Ramos and Alvarez-Buylla [1995] for examples explicitly incorporating interpatch dispersal). However, the disparity between projected and observed seedling numbers suggests there is substantial immigration of *H. acuminata* seeds into all demographic plots. This conclusion is further supported by the comparison of observed and stable-stage distributions. While SSDs predict only a minimal fraction of the populations in the seedling class, seedlings actual comprise ~5–10% of the observed populations.

This result has important implications for the dynamics of plants at landscape scales. A number of prior studies, including several conducted in tropical systems, have demonstrated dispersal is a critical component of the dynamics of gap-dependent plants (e.g., Alvarez-Buylla 1994, Cipollini et al. 1994, Martinez-Ramos and Alvarez-Buylla 1995). In his comprehensive review of plant population dynamics, however, Eriksson (1996) states he found ''no example of a significant between-patch seed dispersal among established local populations where the populations are separated by inhospitable habitat, such as in . . . landscapes with isolated fragments'' (Eriksson 1996:251). In addition the few studies exploring source–sink dynamics (Pulliam 1988) in plants have found at most weak evidence they are important (Eriksson 1996, Kunin 1998, Kadmon and Tielborger 1999). If dispersal from outside fragments is causing *H. acuminata* population growth rates to shift from λ < 1 to λ > 1, this

suggests both between-fragment dispersal and source–sink dynamics may be important to the dynamics of at least some plant species found in fragmented tropical landscapes.

Ultimately, assessing the importance of recruitment limitation for *H. acuminata* and other plant species persisting in fragments depends on our ability to accurately quantify seed dispersal. However, at issue is not simply whether there is less dispersal per se, but what the amount of dispersal is relative to the underlying population structure, i.e., how much dispersal there is per capita. The implications for population dynamics of reduced dispersal will still be difficult to interpret without demographic information on the survivorship of established individuals.

Effect of other size classes and transitions on λ: elasticity analyses

As in other demographic studies of long-lived tropical plants, the greatest contribution to λ comes from transitions related to survivorship and growth and not those related to reproduction (Pinero et al. 1984, Horvitz and Schemske 1995, Olmsted and Alvarez-Buylla 1995). Stasis within larger size classes is especially important—*H. acuminata* that remained in the largest size class (five or more shoots) typically made the single greatest contribution to λ. Plants with three or more shoots also made up the greatest percentage of the stable-stage distribution (9.1–29.5%), especially in continuous forest. Given this elasticity structure and SSD one might predict that fragmentation-related changes in *H. acuminata* survivorship and growth (Bruna et al. 2002), and not those related to recruitment (Bruna 1999, 2002), would have the greatest impact on λ. However while simulated decreases in *H. acuminata* survivorship do cause λ to decrease precipitously (E. M. Bruna, *unpublished data*), increases in seedling establishment actually cause λ to increase by 13–38%.

These results underscore those of earlier studies advocating careful interpretation of elasticity analyses in conservation settings (e.g., Silvertown et al. 1996, Mills et al. 1999, de Kroon et al. 2000). The unexpected rise in population growth rate stems from the mathematical description of elasticities, which measure how λ changes with an infinitesimally small perturbation in a transition value (de Kroon et al. 2000, Caswell 2001). As transition elements change their elasticities may change as well, often in unanticipated ways (Mills et al. 1999, de Kroon et al. 2000). My results therefore support the conclusion that despite having low elasticity values, reproduction may nevertheless be a suitable target for plant conservation strategies as it can frequently be increased by human intervention (Silvertown et al. 1996). It appears the best strategy for the conservation of understory plants, such as *H. acuminata*, is one that both maintains high levels of adult survivorship and increases low seedling recruitment

rates (Santos and Telleria 1997, Jules 1998, Bruna 2002).

Implications for plant conservation

My results suggest that, for long-lived perennials in fragmented landscapes, only extreme reductions in recruitment will lead to extinctions. However, for most plant species, it is completely unknown what the critical threshold levels of recruitment actually are. This is because studies of plants in fragmented areas have focused almost entirely on reproduction and ignored other aspects of life history that also influence population dynamics (Jules 1998). Neglecting these other demographic stages and interactions could be a serious oversight.

In addition, my results support the hypothesis that dispersal into fragments from nearby habitat can ameliorate the negative demographic consequences of reduced reproduction. While theoretical work suggests this should be the case, empirical evidence to date has been limited (Harrison and Bruna 1999) and evidence that source–sink dynamics are operating in plant systems remains circumstantial (Eriksson 1996). Despite the inherent difficulties in doing so, an effort must be made to measure seed dispersal in fragmented habitats (e.g., Martinez-Garza and Gonzalez-Montagut 1999, Sizer and Tanner 1999). Many promising techniques for doing so are now available (reviewed in Wang and Smith 2002); for example, we are using paternity analyses based on microsatellites to determine if *H. acuminata* seedlings in fragments were sired by plants in those plots (W. J. Kress and E. M. Bruna, *unpublished data*). Coupled with investigations of *H. acuminata* density, population structure, and reproduction in the secondary growth surrounding fragments (M. B. Nogueira-Ribeiro and E. M. Bruna, *unpublished data*) and landscape-scale studies of seed disperser movements (e.g., Bierregaard and Stouffer 1997), these studies may help explain why recruitment is far greater in some fragments than others of similar size and age.

Finally, increasing seedling establishment in simulation models increased λ substantially, despite elasticity structure that suggested this would not be the case. This is reassuring from a management perspective, since increases in recruitment are often easier to implement than stimulated plant growth or survivorship (de Kroon et al. 2000). This result highlights one of the often-overlooked constraints of elasticity analyses, namely that they are local estimates around a particular value of λ. As λ changes—which is usually the hope in a conservation setting—the relative importance of different transition values and ecological interactions may change as well.

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APPENDIX A

A calculation of per-individual fecundity (F_i) for transition matrices is available in ESA's Electronic Data Archive: *Ecological Archives* E084-018-A1.

APPENDIX B

Transition probability matrices describing the dynamics of the 13 *Meliconia acuminata* populations used in this study are available in ESA's Electronic Data Archive: *Ecological Archives* E084-018-A2.

APPENDIX C

Summary transition matrices describing the average demography of *Heliconia acuminata* in 1-ha fragments, 10-ha fragments, and continuous forest are available in ESA's Electronic Data Archive: *Ecological Archives* E084-018-A3.

APPENDIX D

Elasticity matrices for 1-ha fragment, 10-ha fragment, and continuous forest summary matrices are available in ESA's Electronic Data Archive: *Ecological Archives* E084-018-A4.