

# Habitat Fragmentation and the Demographic Structure of an Amazonian Understory Herb (*Heliconia acuminata*)

EMILIO M. BRUNA \*‡§ AND W. JOHN KRESS †‡

\*Department of Environmental Science and Policy & Center for Population Biology, University of California, Davis, One Shields Avenue, Davis, CA 95616, U.S.A.

†Department of Systematic Biology-Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0166, U.S.A.

‡Biological Dynamics of Forest Fragments Project, National Institute for Research in the Amazon (INPA), C.P. 478 Manaus, AM 69011-970, Brazil

**Abstract:** Little is known about the demographic consequences of fragmentation for plant populations. By assessing the population structure of a common herb (*Heliconia acuminata*) in an experimentally fragmented landscape in the central Amazon, we tested the predictions that fragmentation could reduce population density, alter population structure, and reduce reproductive effort. Population density in continuous forest varied six-fold, some areas having high density and others low density. Population density in small fragments and on the edges of large fragments was often low, but it was within the range of densities found in continuous forest, and the difference between locations was not significant. *Heliconia* populations in forest fragments were skewed toward smaller demographic size classes, however. Because reproduction in *H. acuminata* is positively correlated with plant size, these shifts were predicted to result in fewer flowering plants in forest fragments. The proportion of the population flowering in forest fragments and continuous forest was not significantly different, although there was a trend toward proportionately greater flowering in continuous forest. For plants that did flower, per-individual reproductive success (measured as developing fruit set) was the same in forest fragments and continuous forests. Our results suggest that per-individual and population-level reproduction by understory herbs in tropical forest fragments may be resistant to the detrimental consequences of fragment isolation. Our study also highlights the need to consider how fragmentation influences aspects of population structure and demography beyond abundance and fruit production, because these alternative measures of population structure can be modified in forest fragments in subtle, unexpected ways.

Fragmentación del Hábitat y la Estructura Demográfica de una Hierba (*Heliconia acuminata*) del Sotobosque Amazónico

**Resumen:** Se conoce poco de las consecuencias demográficas de la fragmentación sobre poblaciones vegetales. Probamos las predicciones de que la fragmentación puede reducir la densidad poblacional, alterar la estructura de la población y reducir el esfuerzo reproductivo, evaluamos la estructura poblacional de una hierba común (*Heliconia acuminata*) en un paisaje experimentalmente fragmentado en la Amazonía central. La densidad poblacional en bosque continuo varió hasta seis veces, con algunas áreas con alta densidad y otras con baja densidad. La densidad poblacional en fragmentos pequeños y en los bordes de fragmentos grandes a menudo fue baja, pero estaba en el rango de las densidades encontradas en el bosque continuo, y la diferencia entre localidades no fue significativa. Sin embargo, las poblaciones de *Heliconia* en los fragmentos de bosque estaban sesgadas hacia las clases de tamaño demográfico más pequeñas. Debido a que la re-

§Current address: Department of Wildlife Ecology and Conservation, University of Florida, PO Box 110430, Gainesville, FL, 32611, U.S.A., email [brunae@wec.ufl.edu](mailto:brunae@wec.ufl.edu)

Paper submitted October 28, 1999; revised manuscript accepted November 28, 2001.

*producción en H. acuminata esta positivamente correlacionada con el tamaño de la planta, se predijo que estos cambios resultarían en menos plantas florecientes en los fragmentos de bosque. La proporción de la población floreciente en los fragmentos de bosque y en el bosque continuo no fue significativamente diferente, aunque hubo una tendencia hacia una mayor proporción de plantas florecientes en el bosque continuo. Para plantas que florecieron, el éxito reproductivo por individuo (medido como el desarrollo de frutos) fue igual en fragmentos de bosque que en bosques continuos. Nuestros resultados sugieren que la reproducción, por individuo y al nivel poblacional, de hierbas del sotobosque en fragmentos de bosque tropical puede ser resistente a las consecuencias perjudiciales del aislamiento por fragmentación. Nuestro estudio también resalta la necesidad de considerar como la fragmentación influye sobre aspectos de la estructura poblacional y la demografía más allá de la abundancia y producción de frutos, debido a que estas medidas de estructura poblacional alternativas pueden ser modificadas de manera sutil e inesperada en los fragmentos de bosque.*

## Introduction

Deforestation and subsequent habitat fragmentation result in the extensive disturbance of Neotropical forests (reviewed by Schelhas & Greenberg 1996; Laurance & Bierregaard 1997). Obtaining information on the consequences of fragmentation for populations persisting in fragmented tropical landscapes is necessary to derive effective conservation strategies for these species-rich regions (Bierregaard et al. 1997). Although the effect of fragmentation on tropical or subtropical tree communities has received considerable attention (e.g., Aizen & Feinsinger 1994; Turner et al. 1995; Andersen et al. 1997; Laurance et al. 1998; Cunningham 2000a, 2000b), to our knowledge no studies have examined how fragmentation in the tropics influences herbaceous understory plants.

Several studies suggest that reductions in habitat area and proximity to forest edges can influence critical life-history stages in plants, particularly pollination and other stages related to recruitment (Rathcke & Jules 1993; Bond 1995; Jules 1998). As a result, it is frequently hypothesized that plant populations in forest fragments will be reduced in size, exhibit altered population structures, and show increased probability of extinction from demographic, environmental, and genetic stochasticity (Jules 1998; Gigord et al. 1999; Eisto et al. 2000). Despite this widespread assumption, however, few studies have explicitly quantified the population structure of understory plants in fragmented landscapes (but see Jules 1998), especially in the tropics.

The quantification of demographic structure is essential for assessing long-term population viability because it is required for many of the "cornerstone" approaches to species conservation, such as population viability analysis (Gilpin & Soulé 1986) and metapopulation theory (Hanski & Simberloff 1997). The current stage structure of a population reflects prior variation in recruitment and mortality (Harper 1977) and can be the result of factors as diverse as environmental variability (Casper 1996; Kephart & Paladino 1997), gap formation (Horvitz

& Schemske 1986; Alvarez-Buylla 1994), and herbivory (Doak 1992; Bullock et al. 1994). If fragmentation has influenced demographic processes, for instance by disrupting the interactions responsible for recruitment (Jules & Rathcke 1999) or by causing increased mortality near fragment edges (Laurance et al. 1998), then this disruption should also be reflected in current population stage structures (Jules 1998).

Because vital demographic rates in plants are usually stage-dependent (Harper 1977), the structure of a population can also be indicative of its demographic future. In a conservation setting, where long-term demographic monitoring may not be feasible, a population's stage structure can be the basis for immediate management decisions. In fact, Schemske et al. (1994) suggest that a good starting point for recovery of threatened plant species is an assessment of the current demographic structure of the populations of interest, with the goal of estimating limiting life-history stages and using this information to build demographic models (e.g., Olmsted & Alvarez-Buylla 1995; Ratsirarson et al. 1996). Once the life-history stages altered by fragmentation have been identified, one can begin to study how the physical and biological mechanisms that shape these stages have been modified by isolation (Schemske et al. 1994).

Much of the difficulty in assessing the effects of fragmentation results from limited information about fragment attributes such as age and isolation history (Jules 1998). Many of these issues have been addressed by the Biological Dynamics of Forest Fragments Project (BDFFP), a collaborative project administered by the Smithsonian Tropical Research Institute and Brazil's National Institute of Research in the Amazon. The BDFFP is a large-scale experimental project designed specifically to study the effects of fragmentation in the tropics (Lovejoy et al. 1986; Bierregaard et al. 1992). It includes 1-, 10-, and 100-ha fragments of rainforest isolated 16–20 years ago by cattle ranching and several reserves embedded in over 10,000 ha of continuous forest. Studies conducted by the BDFFP have revealed how fragmentation and

edge effects influence birds, invertebrates, amphibians, and other taxa (reviewed by Laurance et al. 2002).

We compared the demographic stage structure and reproductive success of the understory herb *Heliconia acuminata* L. C. Richard (Heliconiaceae) in the forest fragment and continuous-forest reserves of the BDFFP. Specifically, we tested the following three predictions: (1) densities of *H. acuminata* are reduced in habitat fragments relative to continuous forest, suggesting reductions in population sizes due to either episodic catastrophes or ongoing demographic decline; (2) the demographic structure of populations is altered in forest fragments, independent of any differences in population size; and (3) plant reproductive output, at both population and individual levels, is reduced in forest fragments. In testing these hypotheses, our goal is to determine which demographic size classes and interactions may be most susceptible to the effects of forest fragmentation, and to use this information as the basis for future experiments and matrix models of *Heliconia* population dynamics.

## Methods

### Study Site

All fieldwork was conducted at the BDFFP site, located 70 km north of Manaus, Brazil (lat. 2°30'S, long. 60°W; Fig. 1). The BDFFP reserves are located 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 (Food and Agriculture Organization & United Nations Educational, Scientific, and Cultural Organization 1971). The forests in the BDFFP reserves have a 30 to 37-m tall canopy, with emergents up to 55 m (Rankin-de Mérona et al. 1992), and are among the most floristically diverse in the world, with 1200–1300 species of trees in at least 64 families (Laurance 2001). Palms dominate the relatively depauperate understory (Scariot 1999). Mean annual temperature is 26° C (range 19–39° C), and mean annual rainfall ranges from 1900 to 2300 mm (BDFFP records). A pronounced dry season occurs from June to October.

The forest fragments at the BDFFP were all isolated between 1980 and 1984 by felling of all trees surrounding the fragment and, in most cases, burning of the downed trees once they dried. The exceptions to this treatment were reserves number 3209 and 3114 (Table 1), where felled trees were not burned because of early rains. Associated with each of these isolation treatments is a particular form of secondary growth: burned areas sprouted regrowth dominated by *Vismia* species (Clusiaceae), whereas the secondary growth in unburned areas was dominated by *Cecropia* species (Cecropiaceae). Since their original isolation, the secondary forest surrounding the fragments has been cleared one or two times.

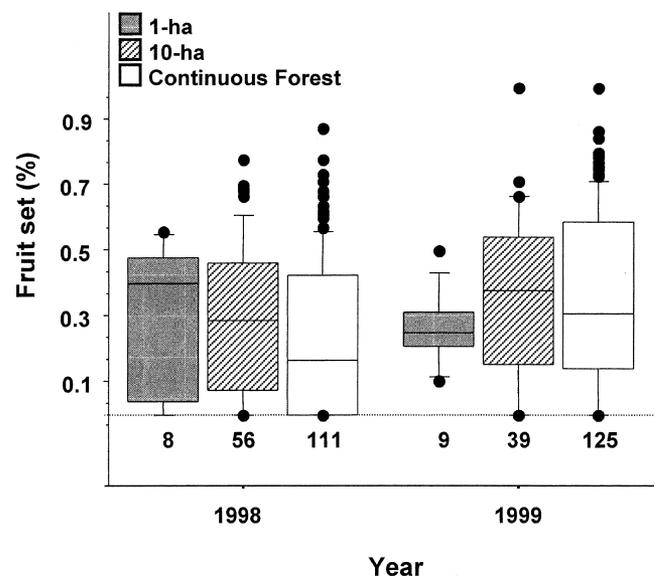


Figure 1. Proportion of flowers developing into fruits in forest, 1-ha fragments, and 10-ha fragments in 1998 and 1999. Plants from different plots within the same habitat type (i.e., 1-ha fragments, 10-ha fragments, and continuous forest) were pooled because of limited sample sizes in some fragments. The upper and lower limits of the box represent the seventy-fifth and twenty-fifth percentiles, respectively. The line through the box is the median value. Marks beyond the error bars represent outliers less than or greater than the tenth and ninetieth percentiles. Numbers below the boxes are the sample sizes of reproductive plants in each habitat type.

### Study System

A common element of the understory of these forests is *Heliconia acuminata*, a species native to the nonflooded forests of central Amazonia. The more than 200 species of *Heliconia* and the hummingbirds that pollinate them represent one of the most widely studied plant-pollinator associations in the Neotropics (Linhart 1973; Stiles 1975; Kress 1983, 1985). *Heliconia* are often divided into two groups based on the foraging strategy of the hummingbirds that pollinate them (Linhart 1973; Stiles 1975; Kress & Beach 1994). Some species of *Heliconia* grow in large, often monoclonal stands along forest edges or in disturbed habitats. These species produce copious amounts of nectar each day and are pollinated by hummingbirds that establish territories to defend this resource (Kress 1985). In contrast, forest understory species of *Heliconia* are found at lower density, produce fewer flowers and less nectar, and are generally visited by hermit hummingbirds that “trapline” from one *Heliconia* plant to the next (Kress 1985). *Heliconia acuminata* falls into the second category, with the Long-tailed Hermit (*Phaethornis superciliosus*) and the

**Table 1.** Biological Dynamics of Forest Fragments Project reserves in which *H. acuminata* demographic plots were established, their year of isolation, and attributes of plant populations measured.<sup>a</sup>

Plot location	Reserve	Year isolated	Plant density <sup>b</sup> (plants/0.5 ha)	No. flowering	
				1998	1999
1-ha fragments					
FF-1	2107	1984	214	2	3
FF-2	2108	1984	161	1	5
FF-3	1104	1980	206	6	6
FF-4	3114	1983	250	7	3
10-ha fragments					
FF-5	2206	1984	162	8	2
FF-6	1202	1980	402	10	9
FF-7	3209	1983	577	56	34
Continuous forest					
CF-1	1301	—	753	90	74
CF-2	1501	—	555	36	27
CF-3	1501	—	703	32	37
CF-4	none (Dimona)	—	112	NR	6
CF-5	none (Porto Alegre)	—	171	NR	4
CF-6	3402	—	235	NR	8
10-ha corners and edges					
edge, FF5	2206	1984	193	NR	NR
edge, FF6	1202	1980	198	NR	NR
edge, FF7	3209	1983	334	NR	NR
corner, FF5	2206	1984	167	NR	NR
corner, FF6	1202	1980	216	NR	NR
corner, FF7	3209	1983	257	NR	NR

<sup>a</sup> Reserve numbers and names follow Lovejoy et al. (1986); NR, not recorded.

<sup>b</sup> Densities in CF 1–6, FF 1–4, and the centers of FF 5–7 were recorded in January of 1999, and densities on the corners and edges of FF 5–7 were recorded in August 1998.

Straight-billed Hermit (*P. bourcierii*) as its primary pollinators in our study sites (Stouffer & Bierregaard 1995; Bruna 2001).

*Heliconia acuminata* is a self-incompatible hermaphroditic perennial with limited vegetative reproduction (E.M.B and W.J.K., unpublished data). Flowering begins in late January and continues through April. Most reproductive plants have one inflorescence with a total of 20–25 flowers (Bruna 2001). Each flower is open for 1 day, after which the perianth and the style abscise. Each fruit produces a maximum of three seeds (mean number of seeds/fruit =  $1.9 \pm .027$  SE,  $n = 873$  fruits), and mature fruits are dispersed by birds (Kress 1983).

*Heliconia acuminata* can be long-lived (>20 years; W.J.K., personal observation), as is the case for many other tropical understory herbs (Horvitz & Schemske 1995). As a result, it is probable that many of the individuals currently found in forest fragments were alive when fragments were initially isolated. This assumption is supported by ongoing demographic censuses that indicate high survivorship of established plants (Bruna 2001).

### Demographic Plots and Censuses

As part of a long-term study of the population dynamics of *H. acuminata*, we established 13 permanently

marked demographic plots 50 × 100 m in size. Six 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) (Table 1). Demographic plots in 1-ha fragments were established at random on either side 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 borders of secondary and mature forest.

In January 1998, we marked all the *H. acuminata* plants in the seven demographic plots in forest fragments and three of the continuous-forest plots (CF 1–3). Each plant was marked with a stake to which we attached an individually numbered aluminum tag. For each plant we counted the number of vegetative shoots and measured the height by the distance from the base to its highest point above the ground. During the 1998 reproductive season, we regularly surveyed the 10 established plots and recorded which individuals were flowering, how many flowers each produced, and the number of flowers developing into fruits.

In August 1998, we established plots in three additional continuous-forest sites (CF 4–6) and measured plants as before. Because previous research at the BD-FFP has demonstrated the importance of edge effects for plants in medium-size fragments (Benitez-Malvido 1998;

Laurance et al. 1998), we also surveyed (but did not mark or measure) all the plants in identical  $50 \times 100$  m plots on a randomly selected edge and corner of the 10-ha fragments in which demographic plots were located. In 1999 we returned to survey all 13 demographic plots and recorded reproduction as in the previous year.

### Analyses of Plant Density

To test the hypothesis that plant density is reduced in forest fragments, we compared the total number of plants found in demographic plots located in continuous forest, 1-ha fragments, 10-ha fragment corners, 10-ha fragment edges, and 10-ha fragment centers. To conduct this analysis, we used the August 1998 surveys of plant density conducted in 10-ha fragment edges and corners and the January 1999 survey results from plots in the remaining locations. Because the number of plots located in the different habitat types was limited, we could not examine the distributional assumptions of parametric tests. We therefore used the nonparametric Kruskal-Wallis test for this analysis.

### Analyses of Vegetative Characteristics and Demographic Structure

To compare the demographic structure of *Heliconia* populations in continuous forests and forest fragments, we used log-linear modeling. We first placed plants into six size classes based on height (0–15, 15–30, 30–45, 45–60, 60–75, and >75 cm). We used height because age is usually impossible to determine in tropical herbaceous taxa; furthermore, size is usually a better predictor of reproductive potential and plant fate (Horvitz & Schemske 1995). Height and shoot number were strongly positively correlated in this system ( $n = 4326$ ,  $\rho = 0.716$ ,  $p < 0.0001$ ), and results were similar for analyses based on shoot number. We therefore present comparisons of population structure based on height only.

Our null hypothesis was that the number of plants in each demographic size class was independent of both habitat type (i.e., 1-ha fragment, 10-ha fragment, and continuous forest) and plot identity (i.e., FF 1–7, CF1–6). To determine the importance of habitat type for predicting the number of plants in each size class, we compared the goodness of fit to the observed data of the null model with that of models including habitat type. Two models testing the importance of habitat type were used, one that included and one that excluded plot identity. Similarly, the importance of plot identity was tested with models that both included and excluded habitat type. Finally, the goodness of fit of a saturated model was used to test the importance of the interaction between habitat type and plot location.

### Analyses of Reproductive Characteristics

To determine if the proportion of the population that was reproductive differed among fragments and continuous forest, we used Kruskal-Wallis tests. These analyses were conducted on both the 1998 and 1999 survey results. We also plotted the proportion of individuals flowering in each demographic size classes for populations in each habitat type. To calculate female reproductive success for individuals that did flower, we divided the total number of developing fruits on each plant by the number of flowers it produced. The fruit-set percentages in forest plots were then compared to the values from 1-ha and 10-ha fragments with Kruskal-Wallis tests. Plants from different plots within the same habitat type (i.e., 1-ha and 10-ha fragments and continuous forest) were pooled because of limited sample sizes in some fragments. This analysis was done for both the 1998 and 1999 flowering seasons.

## Results

### Plant Density

*Heliconia acuminata* density ranged from 112 to 753 individuals per plot (Table 1). Although the rank order

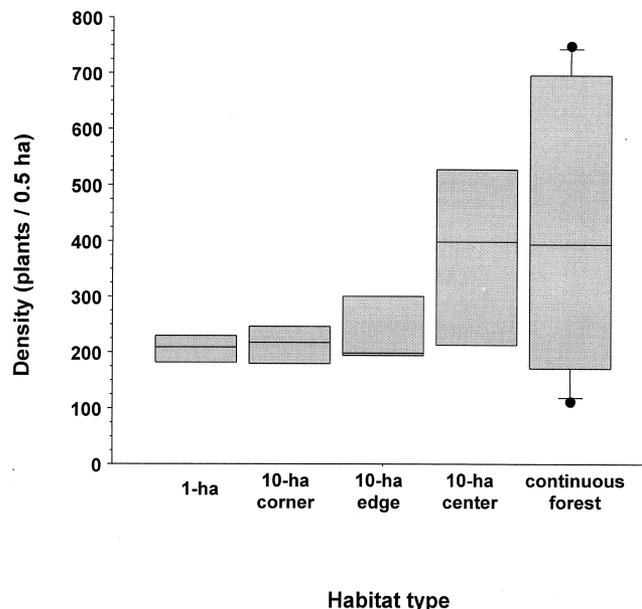


Figure 2. Density of plants per demographic plot in each habitat type: 1-ha fragments, 10-ha fragment edges, 10-ha fragment corners, 10-ha fragment centers, and continuous forest. The upper and lower limits of the box represent the seventy-fifth and twenty-fifth percentiles, respectively. The line through the box is the median value. Marks beyond the error bars represent outliers less than or greater than the tenth and ninetieth percentiles.

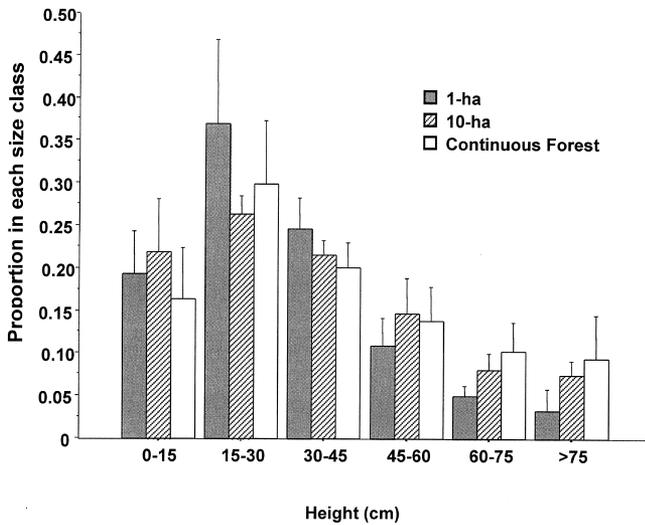


Figure 3. Proportion of plants (mean  $\pm$  1 SD) found in each of six height-based size classes in continuous forest, 1-ha fragments, and 10-ha fragments.

of median *Heliconia* density in the different habitat types was consistent with the hypothesis of reduced abundance in fragments (Fig. 2), the difference between locations was not significant ( $H = 1.389, p = 0.85$ ). Both the highest and lowest values for population density were in continuous forest (CF-1 and CF-4, respectively).

**Vegetative Characteristics and Demographic Structure of Plant Populations**

The null model that the number of plants in each size class is independent of plot location and habitat type was rejected ( $G^2 = 365.57, 60 \text{ df}, p < 0.001$ ). Both habitat type (e.g., 1-ha fragment) and plot identity had a significant effect on the number of plants in each demographic stage class when each factor was evaluated independently and when for the other factor was controlled for (Fig. 3). There was also significant interaction between plot and habitat type (Table 2).

**Reproductive Characteristics**

Differences in the proportion of the population that flowered in 1-ha fragments, 10-ha fragments, and continuous forests were only marginally significant in 1998 ( $H = 5.0, p = 0.08$ ) and not significant in 1999 ( $H = 4.34, p = 0.11$ ), although in both years there was a trend toward a greater proportion of the population flowering in continuous forest sites (Fig. 4).

As might be expected, the probability that an *H. acuminata* individual would flower increased with plant size (Fig. 5). Although the proportion of individuals that flowered in each demographic size class often varied substantially from plot to plot, the proportion flowering in each size class was similar for populations in 1-ha fragments, 10-ha fragments, and continuous forest (Fig. 5).

Median fruit set was not significantly different in forests and fragments in either year (1998:  $H = 2.103, p = 0.3411$ ; 1999:  $H = 0.842, p = 0.6558$ ). In 1998, however, plants in 1- and 10-ha fragments produced slightly more fruit than those in forests (29.3% and 29.0% developing fruit set vs. 23.5%, respectively, Fig. 6).

**Discussion**

We examined the relationship between forest fragmentation and three attributes of *H. acuminata* population structure: population size, the distribution of individuals in different demographic size classes, and reproduction at the population and individual levels. Contrary to our predictions, neither *H. acuminata* population size nor reproductive output was significantly lower in the BD-FFP’s forest fragments. However, the third attribute we examined—demographic size structure—does appear to have been altered, particularly in 1-ha fragments. This result suggests that although certain important population-level attributes may be resistant to the detrimental effects of forest fragmentation, the demography of plant populations surviving in forest fragments may be subtly altered in ways previously unexplored but the consequences of which could be significant.

Table 2. Results of log-linear analysis comparing the effects of habitat type (H), (i.e., 1-ha or 10-ha fragment or continuous forest), plot (P), (i.e., FF 1–7 and CF 1–6), and their interaction for predicting the number of *H. acuminata* individuals in each demographic size class (S).<sup>a</sup>

Effect	Contrast <sup>b</sup>	$\Delta G^2$	$\Delta df$	p
Habitat	HP, S vs. HP, HS	141.25	10	<0.001
Plot	HP, S vs. HP, PS	212.78	25	<0.001
Habitat, given plot	HP, PS vs. HP, PS, HS	72.01	10	<0.001
Plot, given habitat	HP, HS vs. HP, PS, HS	143.53	25	<0.001
Plot $\times$ habitat $\times$ size class	PS, HS, HP vs. PSH	95.61	25	<0.001

<sup>a</sup> Analyses were conducted for densities recorded in the 1999 survey.

<sup>b</sup> Notation follows Caswell (2001) and Horvitz and Schemske (1995) for denoting hierarchical models, such that all terms containing that interaction or lower-order interactions are included. The significance of each factor is determined by examining the change in  $G^2$  (i.e.,  $\Delta G^2$ ) when a factor is removed from a model that includes it. A constant of 0.5 was added to all cells prior to analysis (Caswell 2001).

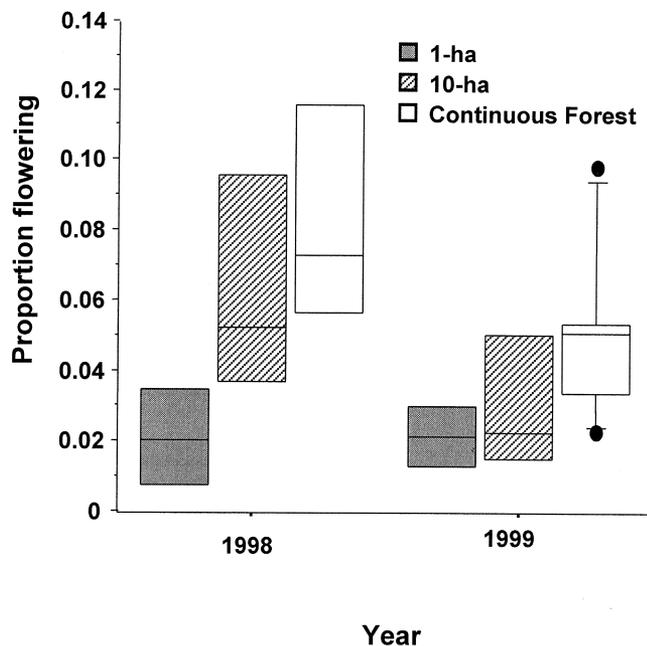


Figure 4. Proportion of plants flowering (per 0.5-ha plot) in continuous forest, 1-ha fragments, and 10-ha fragments in 1998 and 1999. The upper and lower limits of the box represent the seventy-fifth and twenty-fifth percentiles, respectively. The line through the box is the median value. Marks beyond the error bars represent outliers less than or greater than the tenth and ninetieth percentiles.

#### *Heliconia acuminata* Density in Forest Fragments

Given the broad range of densities in continuous forest and the lack of prefragmentation data, it is impossible to exclude the possibility that the densities observed in forest fragments reflect preexisting spatial variation. This result contrasts with the findings of several other studies, conducted at the BDFFP and in other systems, demonstrating that populations of plants on fragment edges are those most at risk from environmental perturbations (e.g., Didham 1997; Jules 1998; Laurance et al. 1998; Gehlhausen et al. 2000). For example, in a study conducted in several of the same reserves, Benitez-Malvido (1998) found that the density of seedlings of canopy trees was lower in fragments than in continuous forest. She also found that the density of seedlings on edges of large fragments was lower than in fragment interiors, although the pattern was not consistent across all fragments. Interestingly, *H. acuminata* density in two of three 10-ha fragments was lower on the edges or corners than in fragment centers (FF-6 and FF-7), whereas in the other 10-ha fragment density was similar in all locations (FF-5; Table 1; Fig. 2).

The density of *Heliconia acuminata* plants in the BDFFP's continuous-forest reserves was highly variable, with some populations at low density (112–235 plants

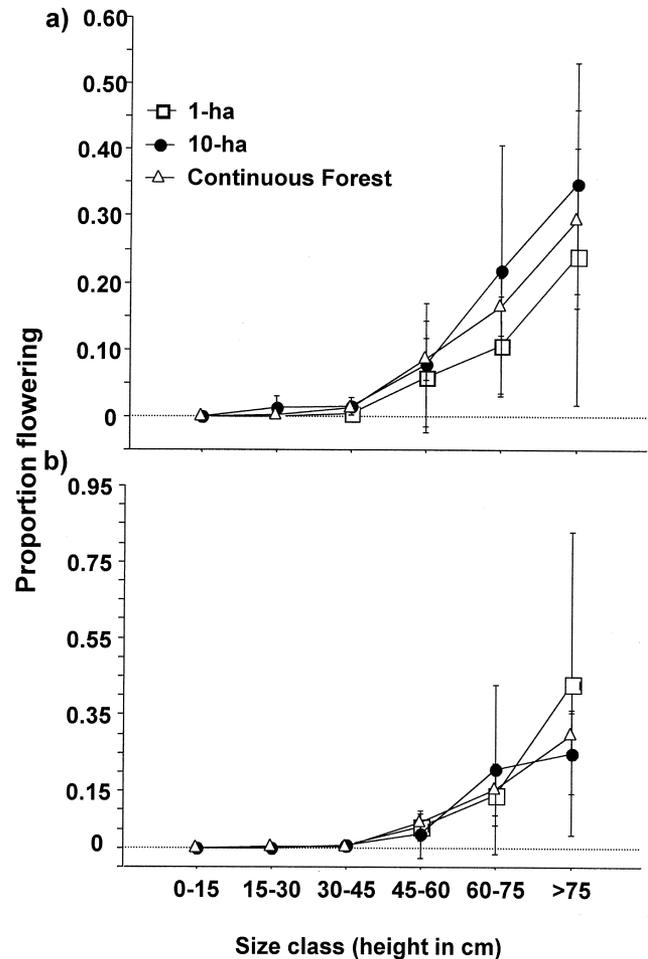


Figure 5. Proportion of plants (mean  $\pm 1$  SD) that were reproductive in each demographic size class in (a) 1998 and (b) 1999.

in CF plots 4–6) and others at much higher density (551–749 in CF plots 1–3). Interpopulation differences in abundance are not necessarily unexpected, because they are the natural result of changes in demographic and environmental conditions across sites (Horvitz & Schemske 1995). The factors responsible for the six-fold range in abundance observed in our study are unclear, however. Although none of the continuous-forest sites were noticeably different in forest structure or disturbance history, variation in both of these factors could be partly responsible for the observed differences. Variation in soil chemistry or texture may also influence *Heliconia* density. Plots with reduced abundance may be located in areas with sandy soils, a lower concentration of nitrogen, less organic matter, or higher aluminum saturation, all of which might influence *Heliconia* growth and abundance. In continuous-forest sites nearby, these chemical and textural parameters explain over 30% of the variation in the biomass of living trees (Laurance et al. 1999), indicating that even in the universally weathered

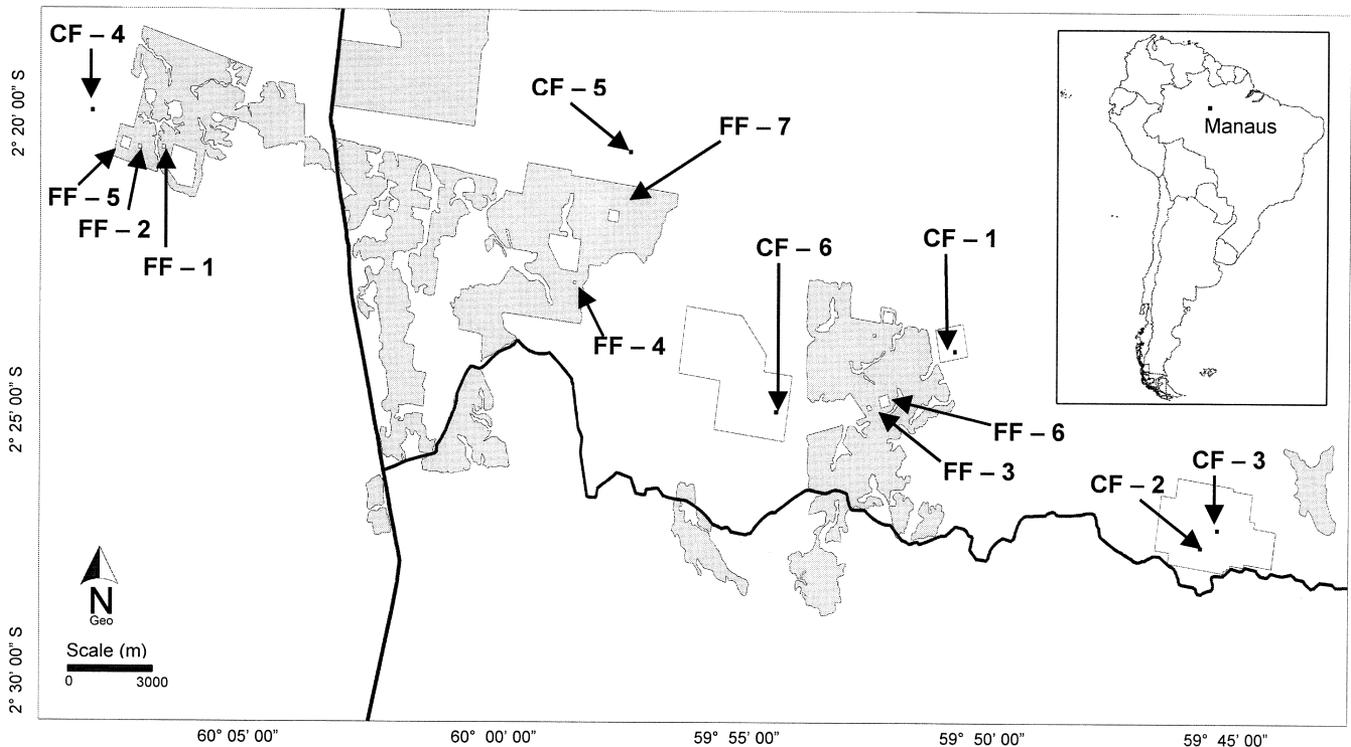


Figure 6. Map of the Biological Dynamics of Forest Fragments Project and location of demographic plots. White areas are continuous forest, shaded areas represent pasture and clearings surrounding fragments, and dark lines represent roads. See Table 1 for plot descriptions. Abbreviations: CF, continuous-forest plot; FF, forest-fragment plot.

and acidic soils characterizing our study sites, the consequences for plant populations of small-scale variation in soil chemistry can be significant.

#### Demographic Structure of *Heliconia acuminata* Populations

Although the isolation of fragments does not appear to have acted consistently to reduce density in the BDFFP fragments, there appears to have been a shift in the demographic structure of *Heliconia acuminata* populations found there. Log-linear modeling indicated that the proportion of individuals in each demographic size class was not independent of habitat type, despite the significant variation among plots. Populations in the fragments studied were skewed more toward smaller size classes, with proportionately more small individuals and fewer large ones than in continuous-forest plots. Individuals in the two largest size classes (60–75 cm and >75 cm tall) made up approximately 20% of the populations in continuous forest, whereas in 1-ha fragments these individuals comprised only about 8% of populations. *Heliconia* populations found in the interiors of 10-ha fragments also appeared to have been affected, although not to the extent of those in small fragments. In the larger isolates, the two largest size classes represented 15% of the total population (Fig. 3).

Several nonmutually exclusive mechanisms could be responsible for the observed pattern. First, large plants in fragments could have been susceptible to increased mortality following fragment isolation, causing the proportion of the population made up of the largest individuals to decrease. Second, there could be a flush of post-isolation recruitment in forest fragments, resulting in overrepresentation of the smallest size classes. This recruitment could be from either rhizomes that have lost all aboveground tissue following fragment isolation or newly germinating seeds. Finally, individuals could have survived in forest fragments but shifted from larger size classes to smaller ones following isolation.

Elevated mortality of large plants and proportionately greater recruitment in fragments are almost certainly not the mechanisms responsible for the observed demographic shift. Current mortality rates of plants with three or more shoots are extremely low in all locations, and they are almost identical in forest fragments and continuous forest (Bruna 2001). Furthermore, *Heliconia* seed germination and seedling survival are three to seven times lower in 1- and 10-ha fragments than they are in continuous forest (Bruna 1999, 2002), and the absolute number of seedlings recruited into fragments was considerably lower than in continuous forest ( $17.25 \pm 15.0$  SD vs.  $38.33 \pm 30.21$  SD). The per capita rate of recruitment, which would include both new seedlings and re-

cruits growing back from rhizomes, was similar in all habitat types in 1999 (Bruna 2001).

Instead, the observed shift is probably due to past and ongoing reductions in the number of plants in larger size classes. Plants that survived the slash-and-burn techniques used to isolate these fragments may have done so by shedding shoots and leaves, a pattern seen in other long-lived perennials exposed to harsh conditions such as drought and water stress (Hsaio 1973; Wright 1996). Recent experimental evidence supports this hypothesis. One year after *Heliconia* plants were reciprocally transplanted between 1-ha fragments and continuous forest, plants in continuous forest grew into larger size classes, whereas plants in fragments shrank into smaller ones (Bruna et al. 2002). If these reductions in size continue over multiple seasons, then the size distribution of populations in fragments could be shifted toward smaller size classes. The strength of these effects would probably be ameliorated by the structure and species composition of the surrounding forest (Mesquita et al. 1999), which can buffer plants from adverse environmental conditions. This may explain why size structures for plots in 10-ha fragments, which were more protected from edge effects as a result of their location in the fragment's core, were similar to those in continuous-forest locations.

Although no comparable studies have been conducted in tropical systems, at least one analysis of plant population structure has been conducted in temperate-forest fragments. By taking advantage of the ability to age plant rhizomes, Jules (1998) was able to estimate the pre- and post-isolation recruitment and mortality of *Trillium ovatum* found in fragments of old-growth forest in the northwestern United States. In contrast to our results, Jules found that populations that were close to clearcuts and edges had substantially fewer seedlings and juvenile plants, whereas older age classes of *Trillium* were not as strongly affected by edge creation.

### *H. acuminata* Reproduction in Forest Fragments

*Heliconia* reproduction does not appear to have been compromised in the forest fragments we studied, either at the population or the individual level. Although there was a trend toward a greater proportion of the population flowering in continuous forest than in forest fragments in both years, this difference was only marginally significant in 1998 and not significant in 1999 (when low-density continuous-forest sites were included in the analysis). The proportion of the population flowering was low in all locations, ranging in 1998 from 0.7% in FF-1 to 13.0% in CF-1. This is consistent with previous studies conducted in the region in which the density of flowering and fruiting plants was found to be extremely low (Gentry & Emmons 1987).

*Heliconia* of a given size are as likely to flower in forest fragments as they are in continuous forest (Fig. 5), suggesting that environmental cues used to initiate flowering are not altered in forest fragments. In addition, fruit production by plants that did flower was not significantly different in the different habitat types. Although several studies have shown that fruit production by plants can decrease in forest fragments as a result of reduced pollen deposition or decreased pollinator visitation rates (Aizen & Feinsinger 1994; Cunningham 2000a, 2000b; Parra-Tabla et al. 2000), our results are similar to those from other studies which found that fruit production remained constant or actually increased in fragmented areas (e.g., Aizen & Feinsinger 1994; Dick 2001). This is because both species of hummingbird that pollinate *H. acuminata* at our sites appear to be resistant to the effects of fragmentation. Results from a 12-year study documenting the abundance of *Phaethornis superciliosus* and *P. bourcieri* in the BDFFP reserves suggest that they move easily through the secondary growth surrounding these fragments (Stouffer & Bierregaard 1995, 1996), and the more common of the two species (*P. superciliosus*) actually increases dramatically in abundance in fragments during the rainy season (Stouffer & Bierregaard 1996), when *H. acuminata* is flowering. Although hummingbirds are rarely species-specific (Feinsinger 1987), other flowering plants in the understory of these fragments are rare during the rainy season (Gentry & Emmons 1987; E.M.B. & J.W.K., personal observation). *Heliconia acuminata* is therefore the primary source of nectar for hummingbirds moving through fragments, and flowering plants in fragments probably receive frequent visits.

Despite proportionately similar levels of reproduction in fragments and continuous forest, however, populations in 1-ha fragments could still be vulnerable to reproductive failure in some years because the absolute number of plants reproducing in them was extremely low (Table 1). Demographic plots 0.5 ha in size located in 1-ha fragments had as few as one or two flowering plants in them (1998: mean =  $4.00 \pm 2.94$  SD; 1999: mean =  $4.25 \pm 1.50$  SD), whereas flowering plants in analogous continuous-forest plots were 5–10 times more abundant (1998 mean =  $52.67 \pm 32.39$  SD; 1999 mean =  $26.00 \pm 26.96$  SD).

As a result of lower absolute numbers of flowering plants in fragments and low developing fruit sets (Fig. 6), the total number of seeds produced in fragments is probably very limited. Populations in fragments may therefore depend primarily on nearby continuous-forest areas for seed dispersal. Although low-density populations in continuous-forest also had low flowering-plant abundances, and hence produced few seeds, they were not isolated from source populations by matrix habitat through which frugivores may not easily disperse (Renjifo 1999; Tabarelli et al. 1999). In addition to reductions in

seed availability, the lower numbers of reproductive plants in fragments could also cause a substantial increase in inbreeding in these locations if pollen flow from outside the fragments is limited (Young et al. 1996).

Our results suggest that populations of *Heliconia* and other tropical understory herbs may be resistant to reductions in population density and the disruptions of reproduction predicted to follow fragment isolation. As a result, even small- to medium-sized fragments of tropical rainforest such as the ones we studied here could be important for plant conservation efforts, and their presence in a landscape could have considerable ecological value. Our results also indicate, however, that fragmentation can affect plant demographic structure in subtle ways and that testing for the effects of fragmentation at the individual level can overlook potentially critical population-level variation. Furthermore, the extensive variation in *Heliconia* density in areas of continuous forest also underscores the fact that not all areas of "continuous forest" can be considered equivalent in terms of the abundance of this, and probably other, common and geographically widespread plants. Therefore the creation of protected areas, agricultural clearing, or other forms of sampling within this single habitat type may be as likely to isolate small populations as large ones.

## Acknowledgments

We thank O. Nardy, F. Marques, O. Ferreira da Silva, A. Cardoso, and P. Aldrich for assistance in the field, the staff of the Biological Dynamics of Forest Fragmentation Project (BDFFP) for logistical help, and T. Fernandes for the map. Permission to conduct the research was granted by the Manaus Free Trade Zone Authority (SUFRAMA). E.M.B. was supported by fellowships from the National Science Foundation, the Ford Foundation, University of California-Davis Graduate Studies, and grants from the Smithsonian Institution, the Center for Population Biology at UC Davis, and the National Science Foundation (dissertation improvement grant INT 98-06351). W.J.K. was supported by the National Museum of Natural History (Neotropical Lowland Research Program) and the Smithsonian Institution (Scholarly Studies Program). S. Strauss, S. Harrison, M. Stanton, K. Rice, D. Marsh, P. Delamônica, H. Vasconcelos, R. Sharitz, B. Inouye, and three anonymous reviewers made comments on the manuscript and provided statistical help. This is publication number 363 in the BDFFP technical series.

## 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.

- Alvarez-Buylla, E. R. 1994. Density dependence and patch dynamics in tropical rain forests: matrix models and applications to a tree species. *The American Naturalist* **143**:155-191.
- Andersen, M., A. Thornhill, and H. Koopwitz. 1997. Tropical forest disruption and stochastic biodiversity losses. Pages 281-291 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.
- Benitez-Malvido, J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* **12**:380-389.
- Bierregaard, R. O., Jr., T. E. Lovejoy, V. Kapos, A. A. D. Santos, and R. W. Hutchings. 1992. The biological dynamics of tropical rain forest fragments: a prospective comparison of fragments and continuous forest. *Bioscience* **42**:859-866.
- Bierregaard, R. O., et al. 1997. Key priorities for the study of fragmented tropical ecosystems. Pages 515-525 in W. F. Laurance and R. O. Bierregaard, editors. *Tropical forest remnants: ecology, management and conservation of fragmented communities*. University of Chicago Press, Chicago.
- Bond, W. J. 1995. Assessing the risk of plant extinction due to pollinator and disperser failure. Pages 131-146 in J. H. Lawton and R. M. May, editors. *Extinction rates*. Oxford University Press, New York.
- Bruna, E. M. 1999. Seed germination in rain forest fragments. *Nature* **402**:139.
- Bruna, E. M. 2001. Effect of habitat fragmentation on the growth, reproduction, and population dynamics of an Amazonian understory herb (*Heliconia acuminata*, Heliconiaceae). Ph. D. Dissertation. University of California, Davis.
- Bruna, E. M. 2002. Effect of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. *Oecologia* **132**:235-243.
- Bruna, E. M., O. Nardy, S. Y. Strauss, and S. Harrison. 2002. Experimental assessment of *Heliconia acuminata* growth in a fragmented Amazonian landscape. *Journal of Ecology* **90**:639-649.
- Bullock, J. M., B. C. Hill, and J. Silvertown. 1994. Demography of *Cirsium vulgare* in a grazing experiment. *Journal of Ecology* **82**:101-111.
- Casper, B. B. 1996. Demographic consequences of drought in the herbaceous perennial *Cryptantha flava*: effects of density, associations with shrubs, and plant size. *Oecologia* **106**:144-152.
- Caswell, H. 2001. *Matrix population models: construction, analysis and interpretation*. Sinauer Associates, Sunderland, Massachusetts.
- 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.
- Dick, C. 2001. Habitat change, African honeybees, and fecundity in the Amazonian tree *Dinizia excelsa* (Fabaceae). Pages 146-157 in R. O. Bierregaard, C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. *Lessons from Amazonia: ecology and conservation of a fragmented forest*. Yale University Press, New Haven, Connecticut.
- Didham, R. K. 1997. The influence of edge effects and forest fragmentation on leaf litter invertebrates in Central Amazonia. Pages 55-70 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.
- Doak, D. F. 1992. Lifetime impacts of herbivory for a perennial plant. *Ecology* **73**:2086-2099.
- Eisto, A. K., M. Kuitunen, A. Lammi, V. Saari, J. Suhonen, S. Syrjasuo, and P. M. Tikka. 2000. Population persistence and offspring fitness in the rare bellflower *Campanula cervicaria* in relation to population size and habitat quality. *Conservation Biology* **14**:1413-1421.
- Feinsinger, P. 1987. Approaches to nectarivore-plant interactions in the New World. *Revista Chilena de Historia Natural* **60**:258-319.
- Food and Agriculture Organization (FAO) and United Nations Educa-

- tional, Scientific, and Cultural Organization. 1971. Soil map of the world at 1:5,000,000. FAO, Paris.
- Gehlhausen, S. M., M. W. Schwartz, and C. K. Augspurger. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* **147**:21–35.
- Gentry, A. H., and L. H. Emmons. 1987. Geographical variation in fertility, phenology and composition of the understory of Neotropical forests. *Biotropica* **19**:216–217.
- Gigord, L., F. Picot, and J. A. Shykoff. 1999. Effects of habitat fragmentation on *Dombeya acutangula* (Sterculiaceae), a native tree on La Reunion (Indian Ocean). *Biological Conservation* **88**:43–51.
- Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinctions. Pages 19–34 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in I. A. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, New York.
- Horvitz, C., and D. Schemske. 1986. Seed dispersal and environmental heterogeneity in a Neotropical herb: a model of population and patch dynamics. Pages 169–186 in A. Estrada and T. H. Fleming, editors. *Frugivores and seed dispersal*. W. Junk, Dordrecht, The Netherlands.
- 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.
- Hsiao, T. C. 1973. Plant responses to water stress. *Annual Review of Plant Physiology* **24**:519–570.
- Jules, E. S. 1998. Habitat fragmentation and demographic change for a common plant: *Trillium* in old-growth forest. *Ecology* **79**:1645–1656.
- 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.
- Kephart, S. R., and C. Paladino. 1997. Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae). *American Journal of Botany* **84**:179–189.
- Kress, W. J. 1983. Self-incompatibility systems in Central American *Heliconia*. *Evolution* **37**:735–744.
- Kress, W. J. 1985. Pollination and reproductive biology of *Heliconia*. Pages 267–271 in W. G. D'Arcy and M. D. Correa, editors. *The botany and natural history of Panama*. Missouri Botanical Garden, St. Louis.
- Kress, W. J., and J. H. Beach. 1994. Flowering plant reproductive systems at La Selva Biological Station. Pages 161–182 in L. A. McDade, K. S. Bawa, H. Hespeneide, and G. Hartshorn, editors. *La Selva: ecology and natural history of a Neotropical rain forest*. University of Chicago Press, Chicago.
- Laurance, W. F. 2001. The hyper-diverse flora of the central Amazon: an overview. Pages 47–53 in R. O. Bierregaard, C. Gascon, and R. Mesquita, editors. *Lessons from Amazonia*. Yale University Press, New Haven, Connecticut.
- Laurance, W. F., and R. O. Bierregaard. 1997. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago.
- 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., P. M. Fearnside, S. G. Laurance, P. Delamônica, T. E. Lovejoy, J. M. Rankin-de Merona, J. Q. Chambers, and C. Gascon. 1999. Relationship between soils and Amazon forest biomass: A landscape-scale study. *Forest Ecology and Management* **118**:127–138.
- Laurance, W. F., et al. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* **16**:605–618.
- Linhart, Y. B. 1973. Ecological and behavioral determinants of pollen dispersal in hummingbird pollinated *Heliconia*. *The American Naturalist* **107**:511–523.
- Lovejoy, T. E., et al. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in M. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer and Associates, Sunderland, Massachusetts.
- Mesquita, R., P. Delamonica, and W. F. Laurance. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation* **91**:129–134.
- Olmsted, I., and E. R. Alvarez-Buylla. 1995. Sustainable harvesting of tropical trees: demography and matrix models of two palm species in Mexico. *Ecological Applications* **5**:484–500.
- Parra-Tabla, V., C. F. Vargas, S. Magana-Rueda, and J. Navarro. 2000. Female and male pollination success of *Oncidium ascendens* Lindley (Orchidaceae) in two contrasting habitat patches: forest vs. agricultural field. *Biological Conservation* **94**:335–340.
- Rankin-de Mérona, J. M., G. T. Prance, R. W. Hutchings, F. M. Silva, W. A. Rodrigues, and M. E. Uehling. 1992. Preliminary results of large-scale tree inventory of upland rain forest in the central Amazon. *Acta Amazonica* **22**:493–534.
- Rathcke, B. J., and E. S. Jules. 1993. Habitat fragmentation and plant-pollinator interactions. *BioScience* **65**:273–277.
- Ratsirarson, J., J. A. Silander Jr., and A. F. Richard. 1996. Conservation and management of a threatened Madagascar palm species, *Neodypsis decaryi*, Jumelle. *Conservation Biology* **10**:40–52.
- Renjifo, L. M. 1999. Composition changes in a subandean avifauna after long-term forest fragmentation. *Conservation Biology* **13**:1124–1139.
- Scariot, A. 1999. Forest fragmentation effects on palm diversity in central Amazonia. *Journal of Ecology* **87**:66–76.
- Schelhas, J., and R. Greenberg. 1996. *Forest patches in tropical landscapes*. Island Press, Washington, D.C.
- 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.
- Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* **56**:285–301.
- Stouffer, P. C., and R. O. Bierregaard Jr. 1995. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conservation Biology* **9**:1085–1094.
- Stouffer, P. C., and R. O. Bierregaard Jr. 1996. Forest fragmentation and seasonal patterns of hummingbird abundance in Amazonian Brazil. *Ararajuba* **4**:9–14.
- Tabarelli, M., W. Mantovani, and C. A. Peres. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* **91**:119–127.
- Turner, I. M., K. S. Chua, J. S. Y. Ong, B. C. Soong, and H. T. W. Tan. 1995. A century of plant species loss from an isolated fragment of lowland tropical rain forest. *Conservation Biology* **10**:1229–1244.
- Wright, S. J. 1996. Phenological responses to seasonality in tropical forest plants. Pages 440–460 in S. S. Mulkey, R. L. Chazdon, and A. P. Smith, editors. *Tropical forest plant ecophysiology*. Chapman and Hall, New York.
- Young, A., T. Boyle, and T. Brown. 1996. The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology & Evolution* **11**:413–418.

