POPULATION ECOLOGY

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Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia

Abstract I present the results of a 2-year experiment comparing seed predation, seed germination, and seedling survivorship patterns of the Amazonian understory herb *Heliconia acuminata* in forest fragments and continuous forest. These empirical results were compared with natural patterns of recruitment in permanent 5,000 m² demographic plots adjacent to experimental areas. The number of naturally occurring seedlings established in demographic plots was 1.5–6 times greater in continuous forest than it was in 1-ha or 10-ha fragments. This result mirrors the pattern of seedling establishment in experimental transects, in which seeds in fragments were 3–7 times less likely to become established than those in continuous forest. Predation of experimentally sown seeds was extremely low at all sites, and is therefore not responsible for the observed pattern. Instead, reductions in seedling abundance in forest fragments are probably due to lower levels of seed germination. Forest fragments have higher air and soil temperatures, lower relative humidity, and increased leaf-litter accumulation, all of which can alter the cues used to initiate germination. While the growth of seedlings was similar in forest fragments and continuous forest, seedling survivorship in fragments was highly variable. These results suggest that altered environmental conditions may exacerbate reductions in plant recruitment resulting from modified plant-animal interactions. Strategies aimed at reducing the intensity of abiotic edge effects should therefore be incorporated into plant conservation efforts.

Keywords Habitat fragmentation · Heliconiaceae · Seed germination · Seed dispersal · Seed predation

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Introduction

The local extinction of plant populations from habitat fragments is common (Turner et al. 1994, 1995; Tabarelli et al. 1999; Cardoso da Silva and Tabarelli 2000), and it is frequently hypothesized that these extinctions result from reduced plant reproduction and recruitment (Janzen 1987; Bond 1995; Tabarelli et al. 1999). Although reduction in pollination and subsequent seed production are thought to be particularly important (Janzen 1987; Rathcke and Jules 1993; Bond 1995; Kearns et al. 1998), the modification of several post-pollination processes can also lead to reduction in seedling abundance (Jules and Rathcke 1999; Cunningham 2000). For example, the quantity and composition of seed rain into fragments could be altered by changes in the diversity, density, diet, or behavior of dispersers (Klein 1989; Martinez-Garza and Gonzalez-Montagut 1999; Restrepo et al. 1999; Santos et al. 1999; Ortiz-Pulido et al. 2000). Alternatively, seeds could be dispersed but fail to germinate if reductions in population size have led to inbreeding depression (Menges 1991; Young et al. 1996) or if abiotic conditions in fragments are unsuitable (Bruna 1999). Finally, increases in seed predation (Curran and Leighton 2000), seedling herbivory (Benitez-Malvido et al. 1999; Cadenasso and Pickett 2000; Benitez-Malvido 2002), structural damage (Scariot 2001), or competition (Luken and Goessling 1995; Sizer and Tanner 1999) could also depress seedling densities. Distinguishing among these mechanisms is difficult but essential, since management and conservation strategies for plant populations in fragmented landscapes will differ based on the mechanisms responsible for reductions in fecundity (Schemske et al. 1994).

The use of experiments to evaluate fragmentation-related changes in seed germination, predation, or dispersal is becoming increasingly common (Burkey 1993; Wong et al. 1998; Bruna 1999; Jules and Rathcke 1999; Morgan 1999; Restrepo and Vargas 1999; Curran and Leighton 2000). Only a limited number of studies, however, have compared the results of manipulations with natural patterns of seedling establishment in the frag-

ments where the experiments were conducted (Santos and Telleria 1997; Jules and Rathcke 1999; Curran and Webb 2000). While data are limited, these comparisons suggest low seedling density in fragments is most often correlated with reduced seed dispersal and increased seed predation (Santos and Telleria 1997; Jules and Rathcke 1999; Curran and Webb 2000). As a result, Restrepo and Vargas (1999) suggested that dispersal, predation, and other animal-mediated processes related to seedling establishment might be more strongly affected by fragment isolation and edge creation than physiological processes such as germination and growth.

Heliconia acuminata (Heliconiaceae) is an understory herb commonly found in the rain forests of central Amazonia. In a previous study, I found that *H. acuminata* seeds were significantly less likely to germinate and become established as seedlings in forest fragments than at continuous forest sites (Bruna 1999). Here I present the results of a 2-year study in which I compare the natural patterns of seedling establishment in forest fragments and continuous forest with two experimentally manipulated cohorts of seeds. I use these experimental and observational data to address the following four questions: (1) Does the abundance of naturally established seedlings differ in forest fragments and continuous forest? (2) Do these patterns of establishment mirror those of experimentally planted cohorts of seeds? (3) Is the growth and survivorship of seedlings lower in forest fragments than in continuous forest? (4) What do these patterns suggest regarding the relative importance of different mechanisms that influence seedling establishment?

Materials and methods

Study site and system

This study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located 70 km north of Manaus, Brazil (2°30′ S, 60° W). The habitat at the sites is non-flooded tropical lowland rainforest with undulating topography ranging from 50 to 150 m in elevation. The soils are nutrient-poor, well-draining xanthic ferralsols (Chauvel et al. 1987; Laurance et al. 1999), and palms dominate the forest's relatively depauperate understory (Scariot 1999). Mean annual temperature is 26°C (range 19–39°C), and rainfall ranges from 1,900 to 2,300 mm annually (BDFFP Records). There is a pronounced dry season from June to October.

In addition to expanses of continuous forest, the BDFFP reserve network includes several forest fragments. These were isolated from 1980 to 1984 by felling all trees surrounding the fragment and, in most cases, burning the downed trees once they had dried (Lovejoy et al. 1986). The secondary growth surrounding fragments has been cleared 3–4 times (BDFFP Records).

H. acuminata is a perennial herb native to the non-flooded forests of central Amazonia (Berry and Kress 1991). It is hermaphroditic and self-incompatible (W.J. Kress and E.M. Bruna, unpublished data), and although some *Heliconia* species reproduce vegetatively clonal reproduction in *H. acuminata* is extremely limited (E.M. Bruna and W.J. Kress, personal observation); *H. acuminata* therefore depends entirely on seeds for recruitment. At our study sites flowering begins in late January and continues through April, with most reproductive plants having a single inflorescence subtending 20–25 hummingbird pollinated flowers (Bruna and Kress

2002). Developing fruits ripen through June and mature fruits are bird-dispersed (Kress 1983). Each fruit produces a maximum of three seeds (mean $=1.9\pm0.02$ SE, $n=873$ fruits) approximately 7×5 mm in size and weighing 0.07–0.085 grams. Dispersed seeds remain dormant until the onset of the following rainy season (Bruna 1999).

As part of a long-term study of *H. acuminata* demography, a series of permanently marked 5,000 m² demographic plots have been established in the BDFFP reserves (see Bruna and Kress 2002 for details). Ten of these plots were used to conduct this study: three in continuous forest (CF: one in Reserve 1301, two in Reserve 1501), three in 10-ha fragments (Reserves 2206, 1202, and 3209) and four in 1-ha fragments (Reserves 1104, 3114, 2107, and 2108). Plots in 1-ha fragments were established by dividing the fragment equally into two adjacent 50×100 parcels and randomly choosing one of them in which to establish the plot, while plots in 10-ha fragments were located in the fragment's center. Plots in continuous forest were haphazardly placed at locations 500–4,000 m from any secondary forest/mature forest borders.

Natural patterns of seedling establishment and survivorship

In January 1998 I marked all *H. acuminata* plants (seedlings and adults) in the ten plots used in this study. I then returned to the plots in January 1999 and 2000 to record the establishment of any new seedlings. For both 1999 and 2000, I compared the number of seedlings emerging in 1-ha, 10-ha, and continuous forest plots with Kruskal-Wallis tests. I also compared the proportion of seedlings emerging in 1999 that survived to the 2000 census using the Kruskal-Wallis test. Finally, I evaluated how seedling abundance varied with local population density and flowering plant abundance. I used Spearman rank correlations to compare the abundance of seedlings in each plot with (1) the abundance of flowering *H. acuminata* individuals in that plot in the previous flowering season and (2) the total *H. acuminata* abundance in that plot the previous year (seedlings and adults).

Experimental patterns of seedling establishment and survivorship

During the 1998 fruiting season (March–April), I collected fruit from over 200 *H. acuminata* plants found in continuous forest Reserve 1501. The seeds were separated from the pulp by abrasion with a strainer under running water, then bathed in a dilute bleach solution for 5–10 min to inhibit fungal pathogens. I stored seeds in peat moss until I established the experiments (Berry and Kress 1991). A total of 1,668 seeds were collected; these seeds are referred to as the "1998 experimental cohort" throughout the remainder of this paper.

In late April 1998 these seeds were used to conduct the following experiment: I planted seeds every 10 m along five 100 m transects that were spaced 10 m apart from each other. These transects were at sites immediately adjacent to the 10 demographic plots used to record natural patterns of seedling emergence. At each location on the transect I planted a total of three seeds, one in each of the following experimental treatments: (1) mimicking natural dispersal by placing seeds directly on the ground, (2) the seed placed in a plastic cup that was planted half-way into the ground and filled with local soil, allowing both seed predation and the accumulation of leaf litter on the seed, and (3) the seed placed in a cup as above but covered with a fine mesh to prevent all seed predation and leaf litter accumulation. Seeds from the same maternal plant were evenly distributed among all sites and treatments to avoid confounding potential maternal effects with fragmentation-related effects. I checked seeds monthly for 2 years and recorded all predation, germination, seedling establishment, and seedling survivorship. Any leaf litter that accumulated on cups covered with mesh was removed during these surveys; however litter was allowed to accumulate in open cups and on seeds placed on the ground.

In May 1999 I repeated this experiment, this time using 1,320 seeds (the "1999 experimental cohort"). Most (84.8%) were from over 100 plants located in Reserve 1501; however the remainder

came from a 20-year-old secondary forest near Reserve 3209. Seeds collected from the same plant were again evenly distributed among sites and treatments.

I compared the proportion of seeds establishing as seedlings (arcsine-transformed) at the end of 1 year using ANOVA. Experimental treatment (open cup, covered cup, ground), habitat type (1-ha, 10-ha, CF), and cohort (1998 or 1999 experimental cohort) were fixed main effects. I also used the 1998 experimental cohort to compare the proportion of seeds establishing as seedlings after 2 years with repeated measures ANOVA. Experimental treatment and habitat type were again fixed main effects, and there were two measurement dates (12 and 24 months). Results of this experimental cohort's germination success after the first year are presented in Bruna (1999).

To determine if the seedlings from the 1998 experimental cohort that emerged in continuous forest were more likely to survive than those emerging in fragments, I compared the proportion of seedlings from each habitat type that survived from 1998 until 1999. Sample sizes from some of the treatments and locations were low; I therefore pooled seedlings from all treatments and compared the proportion of seedlings surviving in 1-ha fragments, 10-ha fragments, and continuous forest using Kruskal-Wallis tests.

To determine if seedling growth differed by habitat type, I analyzed the final leaf-areas of 2-year-old (1998 experimental cohort) and 1-year-old (1999 experimental cohort) seedlings. From 26 April to 14 May 2000, I measured the length of each seedling's leaves to the nearest millimeter and calculated leaf area using the regression equation

$$\sqrt{\text{Leafarea (cm}^2)} = 0.53 + 0.831 \times \text{leaflength}$$

($F_{1, 65}$=1,441.25, R^2=0.957, P<0.0001, based on 67 leaf tracings measured with a LICOR 3000A leaf area meter). The individual leaf areas were summed for each seedling, and total leaf area was square root-transformed to improve normality. Due to limited numbers of seedlings in fragments, seedlings were pooled from different sites within the same habitat class (i.e., 1-ha, 10-ha, or CF) and treatments (i.e., ground, open cup, and covered cup). Final leaf area was then used as a dependent variable in an ANCOVA, with habitat size class as a fixed main effect and the number of months since germination as a covariate. Note that this assumes that experimental treatments affect seed germination but not subsequent seedling growth, which preliminary analysis indicated was valid.

Results

Natural patterns of seedling establishment and survivorship

In 1999 the median number of emerging seedlings in the three continuous forest demographic plots was 52 (mean =61.00±27.62 SD, range 39–92). This was slightly higher than in 10-ha fragments, where the median was 43 (mean =39.33±33.36 SD, range =4–71) and substantially greater than in 1-ha fragments, where the median was 16 (mean =17.25±14.96 SD, range =2–36). However these differences were not significant (H=4.34, P=0.11, Fig. 1). In 2000, the median number of seedlings in plots was significantly different (median densities: CF=130, 10-ha =44, 1-ha =16.5; H=6.16, P=0.047). An average of 124.33±17.21 SD new seedlings were recorded in continuous forest plots in the 2000 census (range =105–138), whereas in 10-ha fragments an average of only 51.33±45.45 SD seedlings were recorded (range =10–100). In 1-ha fragments the mean number of new seedlings emerging was only 21.00±15.98 SD (range =7–44, Fig. 1).
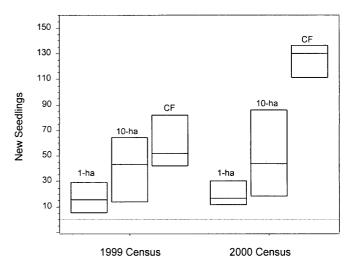

Fig. 1 Box plots depicting the number of new seedlings counted in 0.5 ha demographic plots in the 1999 and 2000 censuses. The line through the box is the median value, while the upper and lower limits of each box represent the 75th and 25th percentile
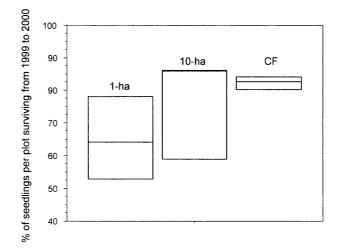

Fig. 2 Box plots depicting the proportion of new seedlings marked in 0.5 ha demographic plots in the 1999 census that were still alive in 2000. The line through the box is the median value, while the upper and lower limits of each box represent the 75th and 25th percentile. For 10-ha fragments the median value is adjacent to the upper limit of the box

The difference in survivorship of the seedlings emerging in forest fragment and continuous forest demographic plots was not significant (H=1.97, P=0.38; median in CF plots=0.83, mean =0.82±0.03 SD; median in 10-ha =0.86, mean =0.74±0.21 SD; median in 1-ha =0.64, mean =0.65±0.15 SD). However while survivorship in plots located in continuous forest was consistently high, it was 7.6–9.1-fold more variable in fragments (CV of average seedling survivorship per plot in CF=3.1%, CV for 10-ha =28.1%, CV for 1-ha =23.5%, Fig. 2).

In both 1999 and 2000, the number of seedlings emerging in a plot was positively correlated with the number of plants flowering there the previous year

Table 1 Results of the ANOVA testing for an effect of habitat type, experimental treatment, and cohort on the proportion of seeds germinating and establishing as seedlings. Significant results are in bold

Factor	df	MS	F	P
Habitat type[a]	2	0.147	13.59	**<0.0001**
Treatment[b]	2	0.062	5.79	**0.006**
Cohort[c]	1	0.028	2.62	0.113
Habitat type×Treatment	4	0.004	0.39	0.812
Habitat type×Cohort	2	0.011	1.01	0.375
Treatment×Cohort	2	0.004	0.40	0.673
Habitat type×Treatment×Cohort	4	0.011	1.03	0.404
Residual	42	0.011		

[a] 1-ha fragment, 10-ha fragment, or continuous forest
[b] Ground, open cup, or covered cup
[c] 1998 or 1999 experimental cohort

Fig. 3 The mean proportion of seeds (±1 SE) from the experimental cohorts germinating after 1 year

[seedlings vs flowering plant abundance (1999): $r=0.661$, $P=0.05$; seedlings vs flowering plant abundance (2000): $r=0.860$, $P=0.01$; $n=10$ plots in both years]. Seedling abundance was also strongly positively correlated with total plant density (1999 seedlings vs 1998 density: $r=0.705$, $P=0.03$; 2000 seedlings vs 1999 density: $r=0.875$, $P=0.01$).

Experimental patterns of seedling establishment, survivorship, and growth

The mean proportion of seeds that germinated and established as seedlings after 1 year was 2.6–4 times higher in continuous forest than in 1-ha or 10-ha fragments (overall germination across all treatments and cohorts in CF=0.08±0.05 SD, 10-ha =0.02±0.02 SD, 1-ha =0.03±0.04 SD, $P<0.0001$, Table 1, Fig. 3). The difference between experimental treatments was also significant ($P=0.006$), with germination of seeds in cups covered by mesh significantly higher than that of seeds in open cups or those placed directly on the ground (Fig. 3). There was, however, no significant habitat type×treatment interaction ($P=0.81$). Although germination was substantially lower for the 1999 experimental cohort (e.g., 1998 experimental cohort in CF=0.10±0.06 SD vs 0.05±0.03 SD for the 1999 cohort in CF), there was no significant effect of cohort, either as a main effect ($P=0.11$) or in any interaction terms (Table 1).

The patterns of germination 2 years after sowing were consistent with those after 1 year. Mean proportion germinating was 3.3–4.3-fold greater in CF than in 1-ha and 10-ha fragments (overall germination across treatments: CF=0.13±0.05 SD, 0.03±0.03 SD in 10-ha, 0.04±0.05 SD in 1-ha; $P<0.0001$, Table 2, Fig. 4). The effects of treatment were again significant ($P=0.04$), but there was no treatment×habitat type interaction ($P=0.72$, Table 2). There was a significant main effect of time ($P<0.0001$), meaning the proportion of seeds germinating increased significantly between 12 and 24 months af-
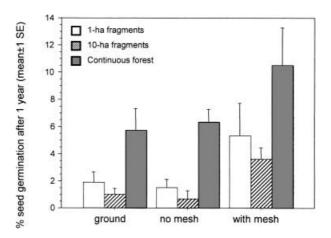
Table 2 Results of the repeated measures ANOVA testing for an effect of habitat type, experimental treatment, and time since planting on the proportion of seeds from the 1998 Experimental Cohort germinating and establishing as seedlings. Significant results are in bold

Factor	df	MS	F	P
Habitat Type[a]	1	0.49	29.75	**<0.0001**
Treatment[b]	2	0.05	3.26	0.06
Habitat type×Treatment	2	0.001	0.09	0.91
Subject (Group)	24	0.02		
Time[c]	1	0.03	18.85	**0.0002**
Time×Habitat type	1	0.001	0.45	0.51
Time×Treatment	2	0.0004	0.30	0.74
Time×Habitat type×Treatment	2	0.002	1.75	0.20
Time×Subject (Group)	24	0.001		

[a] 1-ha fragment, 10-ha fragment, or continuous forest
[b] Ground, open cup, or covered cup
[c] 12 or 24 months

ter the experiment was initiated. However "time" was not significant in any interaction terms (Table 2).

The proportion of seedlings from the 1998 experimental cohort surviving until 1999 was very high in all locations, although median survivorship was slightly higher in forest fragments (CF: median=0.83, mean =0.85±0.16 SD; 10-ha: median=1.00, mean =0.93±0.19 SD; 1-ha: median=1.00, mean =0.83±0.35 SD). This difference was not significant ($H=1.79$, $P=0.46$).

Seedlings from the 1999 experimental cohort emerging in the different habitat types were similar in size when measured in 2000 (CF: 18.68 cm^2±18.70 SD; 10-ha: 15.73 cm^2±7.29 SD; 1-ha: 19.71 cm^2±14.03 SD). By 2000, seedlings from 1998 cohort emerging in continuous forest had 21% more leaf area than those in 1-ha fragments and they had 59% more than those in 10-ha fragments (CF: 60.54 cm^2±49.98 SD; 10-ha: 38.16 cm^2±34.36 SD; 1-ha: 50.10 cm^2±47.99 SD). This difference between habitat types was not significant, however ($F=1.712$, MS=12.80, $df=2$, $P=0.18$). Instead, the differences in leaf area are better explained by seed-
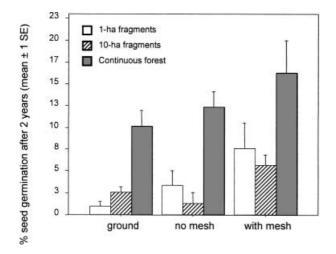
Fig. 4 The mean proportion of seeds (±1 SE) from the 1998 experimental cohort germinating after 2 years

ling age, as indicated by the significant effect of the covariate "months since germination" on final seedling leaf area (F=22.02, MS=164.56, df=1, P<0.0001). The habitat type×months since emergence interaction was not significant (F=0.49, MS=3.65, df=2, P=0.61).

Discussion

Recruitment via seeds is important for maintaining genetic diversity in plant populations (Crawley 1997; Hamilton 1999) and is essential for long-term population persistence (Rees 1997). In 1999, naturally occurring *H. acuminata* seedlings in the BDFFP's continuous forest were, on average, 1.5 times more abundant than in 10-ha fragments and 4 times more abundant than in 1-ha fragments. In 2000 these disparities were even more dramatic – seedlings were 2.4 and 6 times more abundant in continuous forest than fragments (10-ha and 1-ha, respectively). In previous studies documenting reduced abundances of shade-tolerant or understory seedlings in fragments, reductions in density were hypothesized to result from both limited seedling recruitment and the increased mortality of established seedlings (Benitez-Malvido 1998; Jules 1998; Santos et al. 1999). The result of the experiments described here, coupled with observations from demographic plots, suggest this is also true for *H. acuminata*. Below I address the impact of fragmentation on both within-fragment and landscape-level processes potentially limiting seedling recruitment, as well as how the patterns of seedling growth and survivorship vary with fragment size.

Within-fragment mechanisms influencing recruitment

Several studies have found that seed predation increases significantly in habitat fragments or near forest edges (Burkey 1993; Santos and Telleria 1994; Diaz et al. 1999;

Jules and Rathcke 1999). However increased seed predation is not responsible for the reduced *H. acuminata* seedling density observed in these forest fragments. In 1998, rates of experimental seedling establishment were similar for seeds planted directly on the ground and those in open cups protected from seed removal, and germination was actually higher for unprotected seeds from the 1999 cohort. At the conclusion of the experiment 40.1% and 32% of the seeds failing to germinate in open cups were recovered (1998 and 1999 cohort, respectively), and none showed any signs of seed predation. Finally, during the 2 years of surveying only 5 out of 2,998 seeds had any marks on them that were indicative of predation.

Fragment size can also influence seedling abundance (Benitez-Malvido 1998), and the density of naturally occurring *H. acuminata* seedlings was substantially higher in 10-ha fragments than in small ones. Surprisingly, germination rates were equally low in both fragment size classes. This was an unexpected result, given that the detrimental consequences of fragmentation frequently diminish with increasing distance from fragment edges (Laurance et al. 1997). As a result, the patterns observed in the interiors of large fragments are often similar to those from continuous forest (Benitez-Malvido 1998; Laurance et al. 1998b). In this case, however, it appears the factors reducing seedling germination and subsequent establishment are operating even in the seemingly protected interiors of larger fragments.

Seeds of tropical plants frequently have a limited range of light, temperature, and humidity within which they can germinate, and specific temperature and light levels are often cues that induce germination (reviewed in Vázquez-Yanes and Orozco-Segovia 1993; Rees 1997). These environmental variables are strongly altered in many forest fragments (Chen et al. 1992; Gehlhausen et al. 2000), including those in the BDFFP landscape. For example, Didham and Lawton (1999) found temperatures on the edges of two fragments adjacent to the ones used in this study were 1–40°C higher than in nearby continuous forest, while earlier studies conducted in those reserves found the differences ranged from 3 to 80°C (Kapos 1989; Kapos et al. 1997). These higher temperatures, in concert with increased levels of wind turbulence, result in augmented evaporative water loss in fragments (Didham and Lawton 1999). In addition while soil moisture levels in fragments can be highly variable, surface soil moisture can be completely depleted within 20 m of edges (Kapos 1989) and reduced considerably up to 60 m from edges (Camargo and Kapos 1995). Finally, increased tree mortality and crown damage in fragments (Laurance et al. 1998a) have allowed for greater penetration of sunlight, and as a result the level of photosynthetically active radiation can be higher up to 40 m from fragment edges (Kapos 1989). It seems likely that environmental changes in fragments have a strong impact on *H. acuminata* seed germination (Bruna 1999).

Changes in abiotic conditions such as these frequently cause trees in fragments to shed leaves in response to physiological stress (Lovejoy et al. 1986). In addition

rapidly growing pioneer tree species, such as those favored in forest fragments (Ferreira and Laurance 1997), frequently have higher rates of leaf production and abscission (e.g., Sundarapandian and Swamy 1999). The rate of leaf litter production in the BDFFP fragments is higher than in continuous forest (Sizer et al. 2000), and the decomposition of this leaf litter can be 2–13 times slower (Didham 1998 but see Rubenstein 2001). As a result, leaf litter depth can be as much as 50% greater in fragments and near forest edges (Didham 1998). While litter can prevent seed desiccation during the dry season (Vázquez-Yanes and Orozco-Segovia 1993) or augment local nutrient levels (Facelli 1991), it can also alter the cues that induce germination (Molofsky and Augspurger 1992). Seeds trapped in litter are also more susceptible to fungal pathogens (Vázquez-Yanes and Orozco-Segovia 1993), while seedling roots can be physically prevented from reaching the soil surface (Ahlgren and Ahlgren 1981; Hamrick and Lee 1987). Protecting *H. acuminata* seeds from litter accumulation increased seedling establishment for both experimental cohorts (Figs. 3, 4), and while there was no significant habitat type × treatment interaction the increase in germination and establishment of protected seeds was proportionally greater in fragments (e.g., 2.65–13.25-fold increase in fragments vs 1.6-fold increase in CF, 1999 experimental cohort). This suggests higher leaf litter accumulation in fragments is partially responsible for inhibiting seed germination.

Experiments conducted in the BDFFP's continuous forest have shown the germination responses of seeds sown under litter can be quite species-specific, even when the species are ecologically similar (Ganade 1996, 2002; Benitez-Malvido and Kossmann-Ferraz 1999). To date, no other studies have investigated the consequences of increased litter accumulation in the BDFFP reserves for germination and seedling establishment. However in a comprehensive study conducted in the abandoned pastures surrounding these reserves, Ganade (1996) found the presence of litter substantially enhanced seedling establishment for four primary forest species. This was true even for the species whose establishment in continuous forest was detrimentally affected by litter, indicating litter created a favorable microhabitat in these otherwise highly disturbed areas (Ganade 1996, 2002). It is therefore probable that some species will respond favorably to the presence of increased litter in fragments while others will respond negatively. If idiosyncratic responses to leaf litter are indeed an important factor influencing the distribution of seedlings in tropical forests (Benitez-Malvido and Kossmann-Ferraz 1999), then experiments aimed at quantifying these responses are needed to predict potential shifts in plant community composition following fragmentation (Andersen et al. 1997).

Finally, in both years seedling abundance in a plot was strongly correlated with the previous season's flowering plant density, and the number of flowering *H. acuminata* can be very low in fragments (Bruna and Kress 2002). During the 1998 flowering season, the 0.5 ha demographic plots in the seven forest fragments had an average of only 12.86±29.17 SD flowering plants in them, while the continuous forest plots used in this study had 52.67±32.39 SD individuals in them that flowered (Bruna and Kress 2002). If sites are largely dependent on local flowering plants for seeds, the low numbers of flowering plants in fragments could be partly responsible for reductions in seedling abundance. Ongoing analyses with genetic markers are attempting to determine the extent to which seedling recruitment is a function of local seed production versus input from other sites (W.J. Kress, P. Aldrich, E.M. Bruna, unpublished data).

Landscape-level mechanisms influencing recruitment

Three important extrinsic mechanisms that could influence these results bear discussing. First, *Heliconia* seeds are bird-dispersed (Berry and Kress 1991), and the behavior and abundance of frugivorous birds have been shown to respond strongly to anthropogenic landscape modifications (Restrepo et al. 1999; Ortiz-Pulido et al. 2000). In a 9-year mist-netting study conducted at the BDFFP, the capture rates of 12 common frugivorous bird species declined significantly in forest fragments following fragment isolation (Bierregaard and Stouffer 1997). At least some of these species disappeared completely from 1-ha fragments or were captured there only sporadically. If *H. acuminata* populations in fragments depend on seed dispersal from nearby areas of continuous forest, then reductions in seedling establishment resulting from abiotic changes could be exacerbated by reduced abundances of frugivorous birds. While a seed bank could temporarily compensate for the loss of dispersers (Rees 1997), the seed banks of tropical rain forest plants have among the shortest longevity of any plant community (Vázquez-Yanes and Orozco-Segovia 1993). Some *H. acuminata* seeds are capable of remaining viable for up to 2 years, as has been found for other understory herbs (Horvitz and Schemske 1994). However most (>80%) of the seeds germinating in the second year were from the experimental treatments that offered some form of protection to seeds. It seems unlikely that a long-term *H. acuminata* seed bank could offset continued reductions in seedling emergence.

Second, germination rates of experimental seeds could be lower in fragments if the seeds were adapted to conditions at continuous forest sites where they were collected (e.g., Galen et al. 1991). In this particular case, however, local adaptation seems unlikely unless it occurs on very broad spatial scales. Most seeds were collected from a large area (>3.5 km^2) that had substantial variation in topography, canopy cover, and plant density. In addition one of the continuous forest sites (Reserve 1301) was approximately 17 km from the source of seeds used in the experiment, and this site never had the lowest seed germination rates for any treatment in either year. However even if local adaptation were a mechanism reducing seedling emergence in the experimental transects, natural pop-

ulations in fragments would still be vulnerable to the demographic consequences of reduced germination by nonlocal seeds. Due to low numbers of flowering individuals (Bruna and Kress 2002), the primary source of seeds for many of fragments is nearby areas of forest rather than fruiting plants found within each site.

Finally, seedling abundance at a site was positively correlated with total *H. acuminata* abundance, and the continuous forest sites used in this study all had higher population densities than the forest fragments (Bruna and Kress 2002). The experimental results strongly suggest that seedling abundance is reduced in fragments as a function of fragmentation-related changes in such factors as environmental conditions and disperser abundance. However it is possible that seedling numbers could also vary with landscape-level factors independent of fragment isolation that influence plant density, such as gradients in soil chemistry or rainfall. There are continuous forest locations where *H. acuminata* abundance is comparable to that found in forest fragments (Bruna and Kress 2002); it would be interesting to conduct seed germination trials in these low-density continuous forest sites to evaluate the strength of factors potentially limiting population density as well as the importance of local recruitment limitation.

Impact of fragmentation on seedling growth and survivorship

Seedling growth, damage, and mortality can all be strongly influenced by environmental conditions, often in unexpected ways (e.g., Clark and Clark 1989, 1991; Ellison et al. 1993; Molofsky et al. 2000). The high variation in seedling survivorship observed in fragments (Fig. 2) may reflect the spatially variable nature of both microclimatic changes (Kapos et al. 1997) and litter production rates (H. Vasconcelos, unpublished data) in these locations. In addition to temperature stress (Benitez-Malvido 1998), increased rates of herbivory (Benitez-Malvido 2002), fungal infection (Benitez-Malvido et al. 1999), and damage from falling debris (Scariot 2001) have all been hypothesized to reduce seedling growth rates and survivorship in fragments. While evidence directly linking these mechanisms to decreased survivorship is limited, Benitez-Malvido (2002) did find that herbivory of shade-tolerant tree seedlings transplanted to BDFFP fragments increased with decreasing fragment size. She also found the growth rates of *Chrysophylum pomiferum* seedlings transplanted to a 10-ha fragment increased with increasing distance from the fragment edge (Benitez-Malvido 2002). In contrast, I found no difference in final *H. acuminata* leaf area when comparing seedlings from fragments with those in continuous forest, suggesting neither herbivory nor growth differed between habitat types. While this could have been because plants that grew poorly in one of the habitat types died prior to being measured, the proportion of seeds surviving from germination to measurement did not differ significantly between habitat types

(1998 cohort: $\chi^2=0.13$, $P=0.94$; 1999 cohort: $\chi^2=0.80$, $P=0.67$). It appears that while the altered environmental conditions found in fragments may reduce *H. acuminata* seed germination and seedling survivorship, their effect on the growth of *H. acuminata* seedlings is negligible.

Implications for the conservation of tropical plants

The effects of fragmentation on tropical plants are not uniformly detrimental – some taxa show enhanced reproduction, recruitment, or growth in fragments (Ferreira and Laurance 1997; Sizer and Tanner 1999; Dick 2002). However the results of this study suggest that for understory herbs, reduced recruitment resulting from altered plant-animal interaction could be exacerbated by abiotic changes. Furthermore, even seeds dispersed into the seemingly protected interiors of large fragments appear susceptible to these effects. This suggests the impact of fragmentation on the factors influencing plant recruitment may be felt over much larger spatial scales than previously thought (Laurance 2000). In addition to reducing the fitness of individuals whose seeds are dispersed into fragments, these reductions could have a major impact on plant population dynamics. Unlike some temperate ecosystems, where seeds can remain in a seed bank for extended periods of time (e.g., Kalisz 1991), seeds of tropical plants must move quickly into a "seedling bank" to escape intense pressure from seed predators and pathogens (Vázquez-Yanes and Orozco-Segovia 1993). The dynamics of many species are dependent on pulses of recruitment from these seedling banks during periods of favorable environmental conditions (e.g., Alvarez-Buylla 1994), and plants can remain in this bank for years or even decades until environmental conditions become suitable for growth (Clark and Clark 1992; Horvitz and Schemske 1995). If severe enough, long-term reductions in seedling abundance could potentially lead to reductions in population size and local extinction (Jules 1998). Strategies aimed at promoting the movements of dispersers between fragments and reducing the intensity of abiotic edge effects – including the creation of corridors and active management of matrix habitat (Gascon et al. 2000) – are therefore an essential element of strategies designed to protect viable populations of tropical understory plants.

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