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Metapopulation Extinction Thresholds in Rain Forest Remnants

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abstract: Although habitat fragmentation is a major threat to global biodiversity, the demographic mechanisms underlying species loss from tropical forest remnants remain largely unexplored. In particular, no studies at the landscape scale have quantified fragmentation's impacts on colonization, extinction, and local population growth simultaneously. In central Amazonia, we conducted a multiyear demographic census of 292 populations of two leaf-inhabiting (i.e., epiphyllous) bryophyte species transplanted from continuous forest into a network of 10 study sites ranging from 1, 10, and 100 to >10,000 ha in size. All populations experienced significantly positive local growth ($\lambda > 1$) and a nearly constant per-generational extinction probability (15%). However, experimental leaf patches in reserves of ≥100 ha experienced nearly double (48%) the colonization probability observed in small reserves (27%), suggesting that the proximate cause of epiphyll species loss in small fragments (≤10 ha) is reduced colonization. Nonetheless, populations of small fragments exhibit rates of colonization above patch extinction, positive local growth, and low temporal variation, which are features that should theoretically reduce the probability of extinction. This result suggests that for habitat-tracking metapopulations subject to frequent and stochastic turnover events, including epiphylls, colonization/extinction ratios must be maintained well above unity to ensure metapopulation persistence.

Keywords: Amazon, bryophyte, demography, extinction, fragmentation, metapopulation.

Tropical forest fragmentation increases the local extinction rates of many remnant plant populations (Turner et al. 1994; Fischer and Stöcklin 1997; Cardoso da Silva and Tabarelli 2000). However, the causal mechanisms underlying plant species loss from habitat isolates remain poorly understood (Bruna 2003). Increased extinction risk in isolates can result from interactions between local and regional population dynamics (Holt et al. 1995; Lande 1999; Davies et al. 2001). At the regional scale, increased insularity associated with fragmentation potentially reduces interisolate migration rates relative to patch extinction, resulting in a nonequilibrium metapopulation dynamic (Harrison 1991; Hanski et al. 1996). Locally, the altered environments of border habitats, especially in tropical regions (i.e., edge effects), have been shown to promote extinction and thereby induce highly variable or negative population growth in a wide range of species (reviewed by Laurance [2002]). However, experimental studies on plant populations have yet to simultaneously explore how habitat fragmentation affects local population growth, colonization, and extinction.

Although reductions in local recruitment resulting from disrupted plant-pollinator interactions (Aizen and Feinsinger 1994), seed/spore dispersal limitation (Santos and Telleria 1994; Cardoso da Silva and Tabarelli 2000; Lindén et al. 2003), or low seedling survivorship (Bruna 1999) are generally invoked as primary mechanisms of local extinctions from habitat fragments, few studies have quantified the importance of such demographic parameters on long-term population growth (Andersen 1989; Bruna 2003).

For example, observed rates of seedling mortality in the Amazonian herb *Heliconia acuminata* (Bruna 1999) incorporated into a matrix demographic model predict significantly lower λ (i.e., population growth) than expected based on the present population sizes in the fragments investigated. Indeed, such results would suggest that the migration of seeds from neighboring habitat patches contributes to the long-term demographic stability of fragmented *H. acuminata* populations (Bruna 2003). However, since Bruna's (2003) empirical estimates of λ were made over a short time period relative to the generation period

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of *H. acuminata*, temporal variation in growth, seed production, and seed bank contributions may also contribute to the reported differences between model predictions and empirical evidence. Nonetheless, more long-term demographic studies focusing on tropical plant species with fast generation times are needed to comprehensively assess the impacts of habitat fragmentation across all life cycle phases.

Species assemblages composed of members with similar ecological requirements are, more often than not, characterized by a positive interspecific correlation between local population abundance and regional distribution (Hanski 1982; Lawton 1994). In particular, species with large local populations are regionally common (i.e., high probability of occurring at any given habitable site), whereas those characterized by small population sizes are regionally rare. Although several hypotheses, ranging from niche-breadth differences to sampling artifact, provide equally plausible explanations for this relationship (Gotelli and Simberloff 1987; Hanski et al. 1993; Collins and Glenn 1997; Gaston et al. 1997; van Rensberg et al. 2000), only one hypothesis predicts how modifications to the regional distributional extent of a species assemblage is expected to alter both demographic and community-level processes.

The metapopulation-based "rescue effect" hypothesis posits that immigration, which increases in proportion to a species' regional abundance, reduces the probability of local extinction (Brown and Kodric-Brown 1977; Hanski and Gyllenberg 1993). By extension, this hypothesis predicts that habitat destruction will result in declines in both a species' local abundance and site occupancy as a result of lower per-patch colonization rates (Harrison 1991; Gonzalez et al. 1998). However, previous studies of the rescue effect dynamic in the context of habitat fragmentation have been mostly limited to controlled laboratory (Burkey 1997) or mesocosm (Gonzalez et al. 1998; Kneitel and Miller 2003; Rantalainen et al. 2004) experiments (but see Davies et al. 2001 for an example at the landscape scale).

Epiphyllous (leaf-inhabiting) bryophytes are ideal organisms for measuring demographic parameters within experimentally tractable time periods because they typically establish reproductively viable populations on leaf surfaces in less than 6 months (Zartman 2004). In tropical regions, epiphyllous bryophyte communities are composed of a diverse assemblage of monoicous taxa hypothesized to be dependent on intragametophytic selfing and asexual reproduction to ensure dissemination of copious quantities of spores and gemmae during their brief life span (Schuster 1988). Most epiphyllous bryophyte taxa are members of a large, cosmopolitan family of leafy hepatics known as the Lejeuneaceae (Spruce 1884), and in Amazonia as many as 20 species may occur on a single understory leaf (Zartman 2004). Because patch (i.e., within-leaf) extinctions are commonly, but not exclusively, independent of the fate of the patch (e.g., leaf death and senescence), epiphyllous bryophytes are most accurately characterized as taxa operating under a habitat-tracking metapopulation dynamic (Thomas 1994; summarized by Snäll et al. [2003]).

The local abundance-regional distribution patterns of the 67 epiphyll species occurring at the Biological Dynamics of Forest Fragmentation Project (BDFFP) near Manaus, Brazil (Zartman and Nascimento, forthcoming), corroborate predictions from metapopulation models incorporating strong rescue effects (Gotelli 1991; Hanski and Gyllenberg 1993), suggesting that dispersal limitation accounts for their reduced species richness and lower local abundance in small (1- and 10-ha) rain forest reserves. Indeed, previous research at BDFFP showed that 100-ha reserves and continuous forest are nearly twice as rich in species per hectare and harbor population densities 10 times those of smaller (1- and 10-ha) reserves (Zartman 2003).

We quantified rates of intrinsic growth and colonization-extinction probabilities in experimentally transplanted populations of two common Amazonian epiphyllous bryophytes (*Radula flaccida* Gott. and *Cololejeunea surinamensis* Tixier) at BDFFP to discover how changes in these demographic parameters in relation to reserve size may have contributed to their apparent metapopulation extinction threshold of fragments <10 ha in area (Zartman 2003). Specifically, we examine two hypotheses that focus on both regional- and local-scale demographic processes. First, epiphylls of small reserves may be subject to nonequilibrium metapopulation dynamics resulting in reduced patch (i.e., leaf) colonization probabilities when compared with populations inhabiting the larger (≥100-ha) reserves. Indeed, indirect evidence suggesting dispersal limitation for epiphylls into BDFFP fragments of ≥10 ha (Zartman and Nascimento, forthcoming) would predict, assuming constant extinction rates among reserve sizes, lower colonization/extinction ratios in small reserves. Second, reduced epiphyll species richness in small reserves may have resulted from either negative growth (i.e., mean λ values < 1) or increased temporal variation in growth (i.e., coefficient of variation in λ is greater for 1- and 10-ha reserves than for 100-ha and continuous reserves), demographic phenomena that demonstrably increase the probability of local extinction (Holsinger 2000). Likewise, it is equally probable that the hypervariable microenvironmental conditions of rain forest fragments due in part to increased tree mortality caused by windthrow (Laurance et al. 1998; Laurance 2002) may alter patch (i.e., leaf) quality, thus affecting the local epiphyll population dynamics.

Material and Methods

Field Site

The BDPFF, located 70 km north of Manaus, Brazil, was established in 1979 and is the world's largest and longest-running study on forest fragmentation (Lovejoy et al. 1986; Debinski and Holt 2001). It covers 10,000 km^2 of continuous rain forest and forest reserves ranging in size from 1 to 100 ha surrounded by cattle pasture (fig. 1). The continuous forest at BDFFP consists of nonflooded tropical lowland rain forest ranging from 50 to 150 m in elevation (Bierregaard et al. 1992) and is characterized by a complex canopy architecture of trees 30–40 m tall with emergents reaching up to 55 m (Rankin-de-Merona et al. 1992).

Experimental Design and Study Organisms

In December 2000, we transplanted a total of 98 epiphyll host plants of a common Amazonian understory palm species (*Astrocaryum sciophilum* Miq. Pulle) occupied by 292 populations of two focal epiphyll species (*Radula flaccida* Gott. and *Cololejeunea surinamensis* Tixier) into forest fragments, of which three were 1 ha, two 10 ha, and one 100 ha in size, as well as into two continuous (control) forest sites (table 1). Little is known about how the local densities of epiphyllous bryophyte species vary throughout central Amazonia; however, a taxonomic study of this group (Zartman and Mota, forthcoming) provides qualitative evidence that the two focal species are the most common epiphyllous bryophytes of BDFFP and the greater Manaus region. Furthermore, these two species were selected for study because they are readily identifiable in the field without destructive sampling, and they both experience significant reductions in their local densities in response to forest fragmentation, a pattern shared with a vast majority of the other epiphyll species at BDFFP (Zartman 2003; see Ecological Archives E084-019-A1).

We relocated experimental host plants from interior (i.e., ≥0.5 km from the forest edge) continuous rain forest near the Dimona and Colosso camps at BDFFP and randomized their transplant sites before establishing them along transects aligned perpendicular to the forest border in both 1-, 10-, and 100-ha fragments and continuous-forest reserves (table 1). Adult leaves of the palm *A. sciophilum* are pinnately dissected, reaching 3 m in height; therefore, only juvenile members of this species with small (ca. 0.5 m in length) leaves harboring either of the two focal epiphyll species on at least one-third of their leaves were selected for transplanting.

The importance of interspecific competition in shaping epiphyll population dynamics remains entirely unexplored. In an effort to avoid the confounding effects of competition in this experiment, only *A. sciophilum* host plants harboring colonies of the two species physically separated by at least 10 cm were selected for study. Meeting these criteria was facilitated by the fact that both species grow in dense disk-shaped clusters in which colonies grow

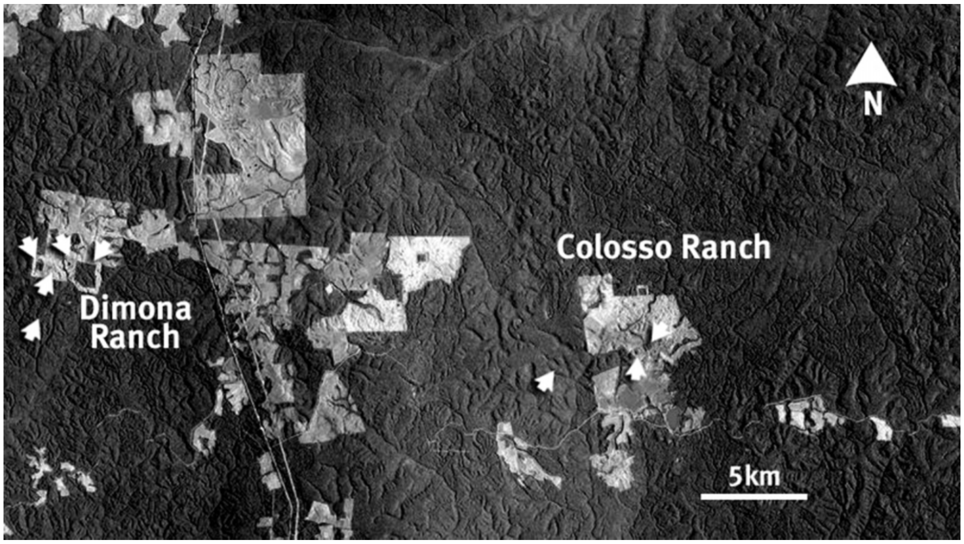

Figure 1: Map of the Biological Dynamics of Forest Fragments Project. Light-colored areas represent permanently cleared forest habitat and cattle pasture. Dark areas embedded in the lighter regions are forest fragments of 1, 10, and 100 ha. Black areas surrounded by white background are reserves located inside contiguous primary forest. White arrows indicate sites where the transplant experiment was conducted. All fragments at the Dimona and Colosso camps were used in this experiment.

Table 1: Experimental design for epiphyll host transplant study

Reserve size	Number of sites	Number of host plants	Number of occupied leaves
1 ha	3	32	78
10 ha	2	24	74
100 ha	3	14	48
Continuous	2	28	92
Total	10	98	292

Note. The three sites for the 100-ha reserve represent three separate transplant sites separated by 500 m within the single 100-ha reserve at the Dimona camp (see "Material and Methods").

in a radial fashion. Experimental host plants were carefully dug up and carried in plastic buckets to the transect sites for replanting in the same afternoon. All leaves, whether or not initially occupied by the focal epiphyll species, were individually marked and labeled with aluminum tags for identification. From December 2000 to June 2003, we conducted biannual demographic censuses measuring population sizes and tallying the number of colonization and extinction events.

Distance intervals between each transplant varied with fragment size. For example, 1-ha reserves received 10 transplants spaced at 10-m intervals from the north-facing to south-facing borders. The 10-ha reserves received 20 transplants positioned 10 m apart for the 50 m in proximity to the forest borders, with spacing in the fragment interior increasing to approximately 20 m between transplants. Prior research indicated that fragment size, rather than proximity to edge, best explains changes in epiphyll density among reserve sizes (Zartman and Nascimento, forthcoming); host palms were nonetheless planted along transects perpendicular to forest edges in an effort to sample the entire gradient of microenvironmental conditions associated with BDFFP forest fragments (Kapos et al. 1997).

We established two of the three study sites in the 100-ha reserve at Camp Dimona along transects perpendicular to the western and northern borders. Each site included a total of 10 host palm plants spaced at 10-m intervals. The third site in the 100-ha reserve was located along a transect on a gently sloping grade in the fragment interior, near where the "600 m" trail crosses a small unnamed stream passing through the center of the reserve. Because of the logistical challenges of transplanting the host palm species, we utilized only one 100-ha reserve for this experiment. Although this sampling design precludes the use of statistical analyses from separating treatment effects from site-to-site variation (Hurlbert 1984), previous research (Zartman 2003) indicates that there is no significant difference in local epiphyll density and species richness between the two 100-ha reserves of the BDFFP (i.e., Dimona and Porto Allegre camps; fig. 1). Furthermore, the transplant site located along the western border of the 100-ha Dimona reserve is closer to the nearby 1-ha reserve than it is to either of the other two transplant sites within the 100-ha reserve (fig. 1), thereby reducing the chance that spatial proximity among the study sites in the 100-ha reserve could by itself cause overestimation of the fragment size effect. Two continuous-forest sites were also established at both the Dimona and Colosso camps with plants relocated from nearby (≥0.5 km) areas to control for the physiological shock associated with transplanting the host palms.

Colonization, Growth, and Extinction

We defined a colonization event as the appearance of one of the two epiphyll species on any marked palm leaf unoccupied by that same species in the previous census. We estimated local population growth by measuring the surface area (cm^2) covered by the epiphylls with a piece of transparency paper marked with a grid of squares 1 cm × 1 cm in size superimposed over the study leaves, and we tallied the number of squares occupied by the two species separately (sensu Lücking 1995, 1999). Within-leaf growth rates (λ) are defined as the proportional change in population size between censuses ($n = 7$ census intervals over 30 months) calculated separately for each leaf and for each of the two species. Only study leaves and focal epiphyll populations that survived the entire census period accrued a total of six λ calculations.

Local extinction is herein defined in one of two different ways: population extinction and substrate loss. Evidence from both the Amazon (Zartman and Mota, forthcoming) and other Neotropical regions (Monge-Najera 1989; Lücking 1999) indicates that epiphyllous bryophyte species do not exhibit any apparent host plant specificity, suggesting that the long-term fate of epiphyll populations in forest fragments is not entirely influenced by the fate of one particular host plant species. However, in order to disentangle the effects of fragmentation on *A. sciophilum* mortality rates from fragmentation's direct effects on the population dynamics of *R. flaccida* and *C. surinamensis*, we analyze these two forms of local extinction separately. Population extinction is defined as the disappearance of an epiphyll colony from a leaf surface surviving from one interval to the next, whereas substrate loss is defined as the death of the entire study leaf on which an epiphyll colony was recorded in the previous census interval.

Statistical Analyses

We calculated the colonization probability of *R. flaccida* and *C. surinamensis* as the fraction of initially vacant *A. sciophilum* palm leaves subsequently colonized by either of the two focal epiphyll species during the course of the censuses. We employed a χ^2 test to determine whether significant differences in the colonization probability exist between reserves of differing sizes. In order to control for differences in the absolute number of unoccupied leaves among the study sites, the expected χ^2 values, grouped into small (1- and 10-ha) and large (100-ha and continuous) reserve categories, were calculated based on the proportion of uninhabited, marked leaves that received an epiphyll colony.

We tested for interspecific differences in λ for each reserve size class using two-tailed *t*-tests assuming equal variances. Because only a relatively small subset of the focal epiphyll populations (i.e., leaf scale) was measured at all seven census intervals, we employed a repeated-measures ANOVA by averaging λ values for all leaves on each *Astrocaryum* plant for the last five censuses. Utilizing only a subset of these data in this analysis was necessary in order to maximize the inclusion of epiphyll populations because of the wholesale loss of transplants at two sites (Dimona 100-ha site and Colosso 1-ha site), as well as the addition of the Colosso continuous-forest site after the second census. We also tested the effect of reserve size on local population growth (λ) at the leaf scale for the entire data set with single-classification ANOVAs. We performed the ANOVAs as well as Tukey's multiple-means comparisons tests using the GLM procedure in SAS, version 6 (SAS Institute 1996; Steel et al. 1997). Keppel's (1991) modified Bonferroni (1936) method was used to adjust the α value and was calculated using six means comparisons and an ANOVA model with df $= 3$. This modified version of the more conservative Bonferroni (1936) method was used in order to reduce the probability of committing a Type II error (Perneger 1998). We quantified temporal variation in growth rates among fragment sizes by calculating the coefficient of variation from the means and standard deviations of λ.

We estimated the per-generational probability of population extinction of the two epiphyll species using Slatkin's (1977) equation from population genetic theory, which assumes a constant extinction probability among populations:

$$X = (1 - e_0)^T, \tag{1}$$

where the extinction probability per generation (e_0) is estimated from the proportion X of populations identified at some time and still extant T generations later (e.g., McCauley 1989). Although accurate estimates of epiphyllous bryophyte generation times are unavailable, the restricted period of annual rains at the BDFFP (Bierregaard et al. 1992), combined with the fact that the transmission of male bryophyte gametes requires water, suggests that sexual reproduction is seasonal. For the purposes of calculating extinction probabilities based on Slatkin's (1977) model, epiphyll generation times were estimated at 1 year. For example, the combined proportion X of *R. flaccida* and *C. surinamensis* populations of small (1- and 10-ha) fragments identified at the beginning of the experiment and still extant two generations (T) later is 0.725. These two values are then used to calculate the per-generational extinction probability (e_0) employing equation (1).

We used the Mann-Whitney *U*-test to determine whether average population size for those that went extinct was statistically different from the mean initial population size. We also employed basic binary logistic regression using SYSTAT 10.2 (SYSTAT, Evanston, IL) to model the effects of reserve size on the relationship between survival probability and initial population size. We tested the effect of fragmentation on the rate of substrate loss (i.e., palm leaf mortality) using ANCOVA with time (i.e., days since initiation of the transplant experiment) as the main variable and reserve size as the covariate.

Results

Colonization

Both *Radula flaccida* and *Cololejeunea surinamensis* experienced lower colonization probabilities in small fragments (1 and 10 ha) when compared with the 100-ha reserve and continuous-forest sites. *Cololejeunea surinamensis* colonized 33% of the uninhabited study leaves in the small 1- and 10-ha reserves, compared to 45% in reserves of ≥100 ha. *Radula flaccida* exhibited a slightly greater difference in colonization probabilities between the small (27%) and large (53%) reserves. From a total of 458 unoccupied *Astrocaryum sciophilum* host plant leaves ($n = 256$ for 1- and 10-ha sites; $n = 202$ for ≥100-ha sites), the combined colonization probability by *R. flaccida* and *C. surinamensis* in the 100-ha reserve and continuous forest (48%) was significantly greater than that for small reserves (27%; $\chi^2 = 21.7$, df $= 1$, $P < .001$; fig. 2).

Population Growth

Mean λ values of *R. flaccida* and *C. surinamensis* between reserve size classes did not differ significantly (table 2); therefore, we executed the ANOVAs by combining data for both epiphyll species. Populations at all sites experienced significantly positive local growth (i.e., $\lambda > 1$; fig.

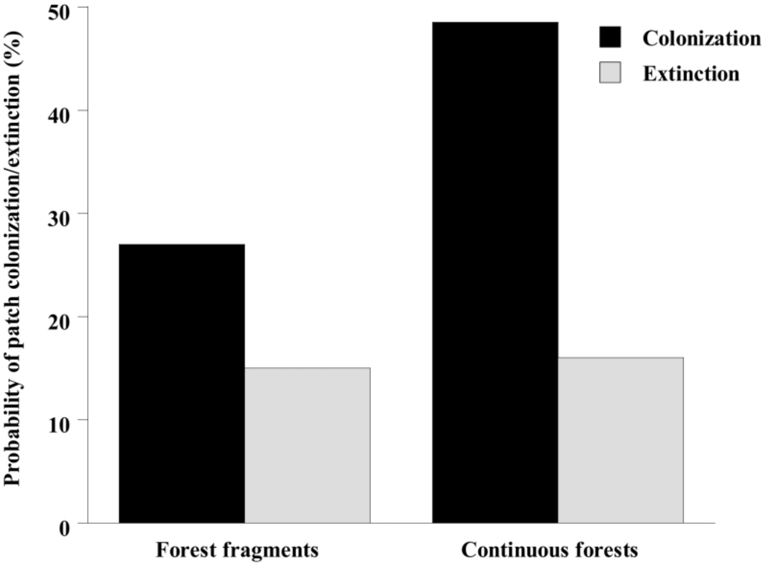

Figure 2: Colonization and per-generational extinction probabilities measured for populations of two epiphyll species, *Radula flaccida* and *Cololejeunea surinamensis*, transplanted into small (1- and 10-ha) and large (≥100-ha) reserves at the Biological Dynamics of Forest Fragments Project. Because the two species exhibited nearly identical values for leaf colonization and extinction in the two reserve size classes, they are combined in this figure for clarity. Refer to the text for species-specific demographic parameters as well as an explanation of how they are defined and calculated.

3). However, as indicated by both the repeated-measures ANOVA at the plant scale and single-classification ANOVA at the leaf scale, populations in smaller (1- and 10-ha) reserves grew at significantly slower rates than those from 100-ha fragments and continuous-forest sites (table 3). Tukey's pairwise means comparisons of 1-ha versus 100-ha reserves, 1-ha versus continuous reserves, 10-ha versus 100-ha reserves, and 10-ha versus continuous reserves all resulted in significance levels of $P \leq .01$ (adjusted $\alpha = 0.02$) at the leaf scale. No significant differences were detected in epiphyll growth rates between 100-ha and continuous reserves or between 1- and 10-ha reserves. Populations in fragmented habitats increased in size, on average, by 35% over census intervals (for 1- and 10-ha reserves, mean $\lambda \pm \mathrm{SE} = 1.35 \pm 0.07$), whereas those of continuous-forest sites more than doubled in size (for 100-ha and continuous reserves, mean $\lambda \pm \mathrm{SE} = 2.1 \pm 0.27$). Temporal variability in growth rates was highest in populations at the 100-ha site and lowest for those transplanted into the smallest (1-ha) reserves (fig. 4). Our *t*-test results comparing λ means among the two border sites and the one interior site in the 100-ha reserve confirm that the high temporal variability in growth in this reserve was not simply an artifact of the different habitats sampled ($t = 0.56$, df = 205, $P = .57$).

Extinction

Estimates of per-generational patch (i.e., within-leaf) extinction probabilities were nearly identical between species in both the small (1- and 10-ha) and large (100-ha and continuous) reserve classes. Whereas *C. surinamensis* exhibited 16% per-generational extinction probability from *A. sciophilum* leaves in both small and large reserves, *R. flaccida* exhibited a marginally lower extinction probability in small fragments (13%) when compared with large reserves (16%). Nonetheless, when grouped together, the resulting difference in combined per-generational extinction probabilities between the two reserve size classes was <1% (fig. 2).

However, logistic regression models indicate that patch

Table 2: Two-sample *t*-test comparing mean population growth values for *Radula flaccida* (λ^R) and *Cololejeunea surinamensis* (λ^C) at each reserve size

Reserve size	λ^R	λ^C	*t*	df	*P*
1 ha	1.5 (2.9)	1.2 (1.6)	.84	182	>.4
10 ha	1.0 (1.0)	1.2 (2.2)	1.01	195	>.3
100 ha	2.0 (4.9)	2.3 (4.0)	.36	205	>.7
Continuous	1.6 (1.4)	2.0 (2.4)	1.41	159	>.1

Note. Values of λ are shown with SD in parentheses. Significant differences were not detected at any reserve size.

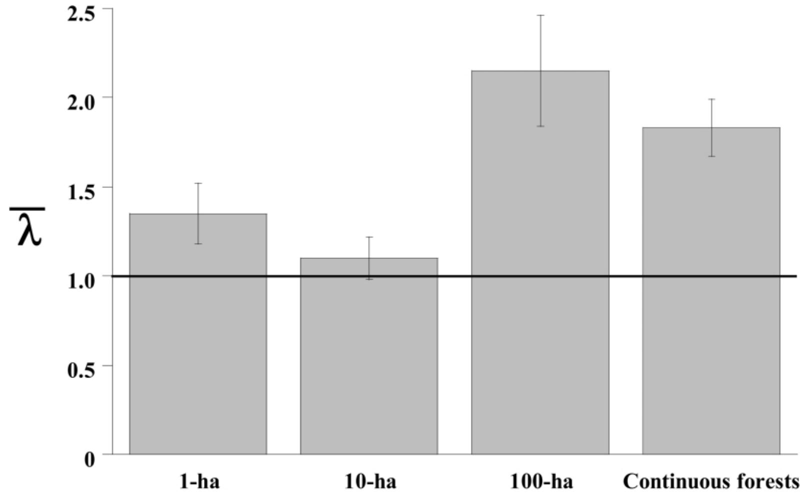

Figure 3: Mean relative population growth (λ; ±SE) in relation to reserve size. Black line indicates the threshold between population growth and decline. Although populations from all treatments experienced positive growth, those transplanted into 100-ha fragments and continuous forest grew faster than those in 1- and 10-ha fragments at the two spatial scales of individual leaves and host plant palms (see "Results"). The values presented above were calculated at the leaf scale and represent the mean λ calculated from the eight census intervals ($n = 7$) for each leaf averaged for each reserve size.

extinction risk decreases significantly in relation to increased initial population size only for continuous-forest sites (fig. 5). Large reserve populations of initial population sizes ≥30 cm^2 experienced a 90% survival probability, nearly 1.3 times higher than that recorded for similar-sized populations of small reserves. Furthermore, for all reserve sizes, the mean initial epiphyll population size was significantly larger than the mean population size that went extinct (table 4). The extinction probability for larger (>6 cm^2) epiphyll populations was significantly greater in fragments than in control sites (Mann-Whitney *U*-test; $U = 667$, $P < .001$, $n = 97$). However, *t*-test results ($t = 3.7$, df = 337, $P < .001$) indicate that mean (±SE) initial population sizes transplanted to fragments (13.2 ± 1.2 cm^2; range 1–50 cm^2) were significantly greater than those for continuous forests (7.2 ± 0.89 cm^2; range 1–51 cm^2), suggesting that skewed population sizes from the outset of the experiment may have contributed to the apparently larger populations experiencing extinction in small fragments.

Substrate Loss

Variation in mortality rates of transplanted palm leaves was not explained by reserve size (ANCOVA; $F = 0.14$, df = 3, 289, $P > .9$) but rather by time since the onset of the transplant study ($F = 40.3$, df = 6, 289, $P < .001$), suggesting that transplants experienced significantly higher chances of mortality toward the end of the census, probably because of natural aging and senescence. The 10-ha reserves experienced the highest leaf mortality (51%) and 1-ha reserves the lowest (25%), while both the 100-ha reserve and continuous-forest sites had relatively similar leaf mortality (32% and 35%, respectively). No significant interaction was detected between time and study site ($F = 0.64$, $P = .60$), indicating that the ANCOVA's as-

Table 3: Repeated-measures and single-classification ANOVA summary statistics

	df (model)	df (error)	Type III SS	MSE	*F*	*P*
Repeated-measures ANOVA:						
Reserve size	3	38	25.3	8.4	3.0	.04
Time	3	114	31.7	10.6	3.0	.03
Reserve size × time	9	…	49.3	5.5	1.5	.14
Single-classification ANOVA:						
Reserve size	3	745	132.2	44.2	5.1	.002

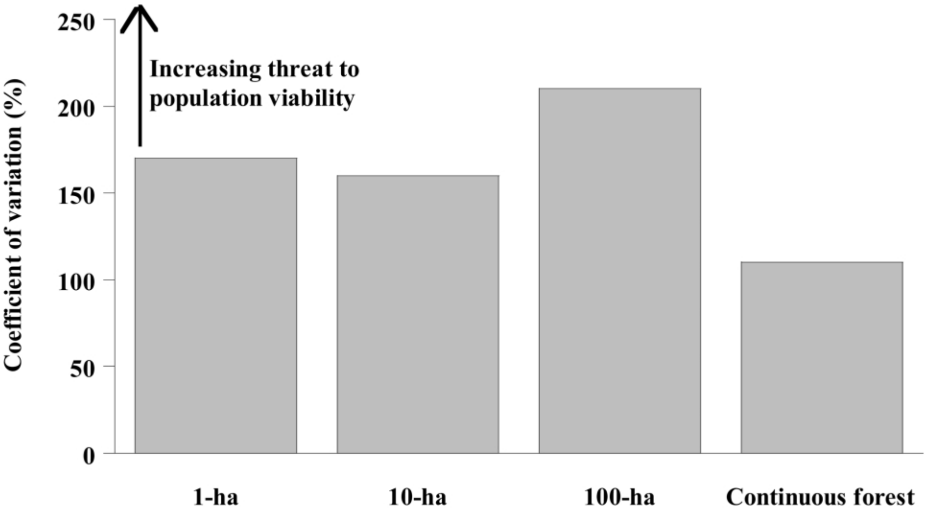

Figure 4: Temporal variation in mean population growth and fragment size. Coefficient of variation was calculated from the means and standard deviations presented in figure 3.

sumption of homogeneity of slopes was not violated (the nonsignificant term was removed from the final ANCOVA model).

Discussion

These findings offer a unique insight into how demographic processes shape metacommunity structure in the context of a landscape-scale network of tropical forest fragments. The sharply reduced colonization rates for the two focal epiphyll species in small (≤10-ha) BDFFP reserves corroborate previously documented abundance-distribution relationships of 67 epiphyll species, suggesting a disruption in rescue effect dynamics (Zartman and Nascimento, forthcoming) as a primary cause for fragmentation-induced declines in species richness (Zartman 2003). In this case, nonequilibrium metapopulation dynamics resulting from reduced colonization, as opposed to increased extinction probabilities (fig. 2), are the causal mechanism resulting in the erosion of epiphyll species richness in small BDFFP reserves.

Nonetheless, it should not be overlooked that local population dynamics, such as growth rates, did increase significantly in relation to fragment size, which is an indication that fragmentation demonstrably affected local processes as well (fig. 3). Clearly, edge effects have a profound influence on the population and community dynamics of lowland tropical rain forest taxa (reviewed by Laurance et al. [2002]), and the positive relationship between local growth and reserve size may be partly attributable to the complex abiotic changes associated with proximity to BDFFP forest edges (Kapos et al. 1997). However, populations from all reserve sizes were characterized by significantly positive growth, suggesting that fragmentation-induced changes to local epiphyll population dynamics are not sufficient by themselves to account for the dramatic impacts of fragmentation on epiphyll community structure (Zartman 2003). A basic tenet of metapopulation theory is that regional processes (i.e., colonization-extinction equilibrium), as opposed to local population dynamics, are most important in influencing metapopulation persistence (Levins 1969). Our results, demonstrating an abrupt, fragmentation-related decline in

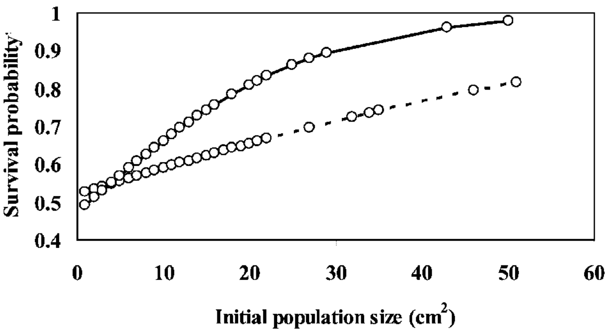

Figure 5: Logistic regression model of the probability of patch survival in relation to initial population size. These data are based on a 2-year demographic census from 136 experimental epiphyll populations in continuous-forest sites (*solid line*) and 108 populations from small (1- and 10-ha) forest fragments (*dashed line*). Survival probabilities increased significantly in relation to initial size only for populations inhabiting continuous forest ($t = 2.39$, $P = .017$). No significant relationship was detected between initial size and survivability in populations from small fragments.

Table 4: Mean initial population size and mean initial size for populations that went extinct for two focal epiphyll species in fragmented (1- and 10-ha) and continuous-forest sites

Site type	Population size (cm^2) Overall	Population size (cm^2) Extinct	*n*	*U*	*P*
Continuous	7.2 ± .89	2.7 ± .45	179	1,965	<.01
Fragmented	13.2 ± 1.24	5.7 ± .61	257	3,966	<.001

Note. Population sizes are shown as mean ± SE. Statistics are based on a Mann-Whitney *U*-test.

colonization-extinction ratios, offer a rare empirical confirmation of this fundamental prediction of metapopulation theory in the context of a landscape-scale fragmentation experiment (Thrall et al. 2000).

Colonization

Mounting indirect evidence from studies on epiphytic (i.e., tree-inhabiting) cryptogams of temperate regions suggests that dispersal limitation, as opposed to microsite variability, best explains local distribution patterns in both anthropogenically disturbed (Dettki et al. 2002; Lindén et al. 2003; Snäll et al. 2003) and old-growth (Sillet et al. 2000) forest habitats. Likewise, our results, which uniquely include direct measurements of epiphyll colonization rates, corroborate the results of such studies conducted in temperate areas. In particular, small (1- and 10-ha) reserves ≤700 m from the nearest continuous-forest border (fig. 1) were characterized by a significant disruption in epiphyll colonization (fig. 2).

Whether reduced epiphyll recruitment into forest fragments is attributable to overall reductions in spore rain density or to negative impacts of edge effects on spore germination has not been tested. That is, reduced colonization may be attributable to lowered overall propagule abundance, lower establishment success of these propagules, or both. However, fragment size per se, rather than proximity to the forest edge, better predicts variation in local epiphyll abundance (Zartman and Nascimento, forthcoming), an indication that lower spore rain density probably underlies reduced colonization in forest fragments. Nonetheless, this result is merely an indirect assessment of whether a disruption in colonization dynamics in small fragments results from altered regional (e.g., limited interfragment dispersal) or local (e.g., edge-related impacts on local epiphyll densities) processes. Indeed, the apparently low genetic structure of *Radula flaccida* Gott. populations among BDFFP forest reserves (C. E. Zartman, S. F. McDaniel, and A. J. Shaw, unpublished data) suggests that interfragment dispersal patterns have at least not weakened to the point of demonstrably altering gene flow patterns over the 30 years since their initial isolation. Experimental field studies estimating demographic parameters across a range of manipulated population densities in continuous forest are needed to disentangle the effects of local environment and spatial isolation on epiphyll colonization rates.

The dispersal behavior of epiphyllous bryophytes may be most accurately characterized as "aerial plankton" (Richter 1970) because the trajectories of their spores are entirely dependent on the vicissitudes of local convective currents. Since epiphylls, like other spore-producing plants, have little control over their ultimate destination, they are dispersed into sites independent of habitat quality, a behavior that has led to predictions that such species should exhibit no relationship between patch size and density (Andrén 1994; Bowman et al. 2002). However, as demonstrated by patterns of epiphyll abundance and distribution (Zartman 2003), such a prediction does not hold for epiphylls. This is probably due to the fact that the density of bryophyte spore deposition declines precipitously with increased distance from the source (Wyatt 1982; reviewed by Shaw [2000]), potentially leaving fragments without a sufficient spore rain to support colonization rates necessary for metapopulation persistence.

Local Population Dynamics and the "Rescue Effect"

Theory predicts that either negative population growth or high environmental stochasticity may increase extinction risk in fragmented populations (Burkey 1997; Holsinger 2000). On the contrary, epiphylls experienced positive growth (table 2; fig. 3) and low temporal variation (fig. 4) in vital rates in small (1- and 10-ha) fragments despite their demonstrably reduced species richness in these reserves (Zartman 2003). Clearly, positive local growth alone is not a reliable indicator of the long-term stability for habitat-tracking metapopulations in fragmented habitats, and, as these data suggest, changes in vital rates need to be evaluated in the context of regional-scale processes, such as dispersal and colonization.

The peripheral role of local population dynamics in influencing epiphyll metapopulation persistence is probably due to the ephemeral nature of their habitat patches. The leaf life span of many understory dicotyledonous plants in Neotropical forests is typically less than 18 months (Bentley 1979; Coley et al. 1993), suggesting that the precocious development of gametangia to ensure rapid dissemination of spores before leaf senescence, rather than the production of vegetative biomass per se, would be more advantageous for epiphyll metapopulation persistence. In this case, the temporal instability of patch (i.e., leaf) dynamics may adequately explain why local (i.e., within-leaf) demographic parameters, such as overall growth, are not accurate indicators of metapopulation viability. Indeed, variation in host plant leaf mortality rates for *Astrocaryum sciophilum* was better explained by time than by reserve size (see "Results"), suggesting that the natural process of palm leaf death had already set in even within the 2-year time frame of this experiment.

However, the relationship between local population size and reproductive potential in epiphyllous bryophytes has yet to be studied. It is equally plausible that the combined effects of slower growth (fig. 3) and increased extinction risk (fig. 5) for larger epiphyll populations of 1- and 10-ha reserves would render these populations less likely than those of larger (≥100-ha) reserves to reach an adequate size for sufficient reproductive output. Moreover, the disproportionate loss of large populations from small reserves (fig. 5) may reduce overall local rates of recruitment and increase the role of both demographic (Goodman 1987; Pimm et al. 1988; Holsinger 2000) and genetic (Menges 1991; Newman and Pilson 1997; Richards et al. 2003) stochasticity in influencing the fates of the remaining, smaller populations. However, such hypotheses can only be tested upon further detailed studies of the reproductive biology and population genetic structure of these taxa.

Nonetheless, the fact that both focal epiphyll species experienced positive local growth as well as colonization-extinction ratios above unity at all study sites raises a fundamental question: why are epiphyll populations unable to persist in the small BDFFP fragments? One of two explanations probably accounts for this apparent incongruity. We separated analyses of extinction events into two categories: population extinction and substrate loss. Calculations of per-generational population extinction (fig. 2; eq. [1]), which do not include extinction events caused by substrate loss, may then underestimate overall rates of local extinction, defined as the combination of patch extinction and substrate loss. Since variation in host leaf mortality (i.e., substrate loss) is not explained by reserve size, it is plausible that reduced colonization in small fragments falls sufficiently below overall local extinction rates, resulting in a colonization-extinction ratio below unity. However, epiphyllous bryophytes are not host plant specific (Zartman and Mota, forthcoming), and they potentially inhabit a variety of host plant species (Lücking 1995), thus rendering it difficult to test such a hypothesis without information on leaf mortality for scores of potential host plant species. Nonetheless, the demonstrable importance of patch longevity in the extinction-colonization dynamics for other epiphytic bryophyte metapopulations (Snäll et al. 2005) would suggest that epiphylls, because of the unstable nature of their patch (i.e., leaf) dynamics, must maintain colonization rates well above that of local extinction to ensure long-term persistence.

The "rescue effect" hypothesis posits that immigration, which is positively correlated with habitat occupancy density, decreases the rate of patch extinctions (Gotelli 1991; Hanski and Gyllenberg 1993). Although both epiphyll habitat occupancy density (Zartman 2003) and colonization potential (fig. 2) differ significantly between small and large reserves at BDFFP, overall rates of patch extinction remain nearly equal (fig. 2). The apparent lack of influence of colonization and patch occupancy densities on local extinction rates, as predicted by rescue effect theory, elicits one of two potential explanations. First, despite the demonstrably fast generation times of epiphyllous bryophytes, the duration of this demographic census is perhaps too short to accurately quantify temporal variability in rates of patch extinction. Second, it is plausible that reduced colonization rates in small remnants, despite maintaining a colonization-extinction ratio greater than unity (fig. 2), are sufficient to affect metapopulation persistence. Nonetheless, patterns in patch extinction are significantly different, indicating bolstered survivability of larger populations in reserves larger than 100 ha (table 2; fig. 5). The proximate explanation for this phenomenon remains unclear because it is apparently not a result of unstable local population dynamics (figs. 3, 4).

Conservation Implications

Although a growing base of data exists on the impacts of habitat fragmentation on early plant life-history stages (Benitez-Malvido and Martinez-Ramos 2003; Bruna 2003; Hokit and Grant 2003), this study represents the first hierarchically based synthesis, in the context of a single system, that evaluates the population-level consequences of forest fragmentation in light of its effects at the community scale. Because of their rapid generation times and the absence of potentially confounding plant-pollinator/disperser interactions, epiphyllous bryophytes provide a well-suited system for disentangling the impacts of increased habitat insularity on both regional and local demographic processes. In particular, these demographic data corroborate evidence from community-level patterns that minimum viable metapopulation sizes for epiphyllous bryophytes are not attained in rain forest remnants smaller than 100 ha.

However, the exceptional features that make epiphylls ideal for conducting experimental demographic studies are possibly the same characteristics that may preclude generalizing such findings to other plant taxa. Although few terrestrial plant groups inhabit patches as unstable as the surface of an understory tropical leaf, vascular plant epiphytes and hemiepiphytes are a significant component of the Amazonian flora (Ribeiro et al. 1999), and, because of the unstable nature of their substrates (e.g., tree bark and secondary branches of emergent trees), they are also subject to ecological constraints similar to those experienced by epiphylls. Nonetheless, results from this study indicating a disruption in epiphyll colonization dynamics in rain forest remnants of ≤10 ha potentially provide insight into the long-term demographic impacts of recent widespread fragmentation events in the Amazon (Skole and Tucker 1993) on other tropical plant taxa, such as palms (Scariot 1999), and on trees (Phillips et al. 2004) that are characterized by much longer generation times.

Epiphyllous bryophytes are a conspicuous component of most rain forests, and they contribute significantly to tropical biodiversity (Lücking 1995; Zartman 2004), host plant fitness (Mueller and Wolf-Mueller 1991), and ecosystem processes (Frieberg 1998). Considering that leaf surface communities are the biological source of approximately one-fifth of all the available nitrogen in Neotropical rain forests (Frieberg 1998), dramatic reductions in their local abundances due to habitat fragmentation may have untold repercussions on tropical ecosystem processes throughout the world.

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