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The effect of habitat fragmentation on communities of mutualists: Amazonian ants and their host plants

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Abstract

The consequences of fragmentation for communities of mutualist partners are for the most part unknown; moreover, most studies addressing this issue have been conducted on plant–pollinator communities. We evaluated how the experimental fragmentation of lowland Amazonian rain forest influenced a community of ant–plant mutualists. We inventoried a total of 1057 myrmecophytes in four fragments and four continuous forest sites; the twelve plant species recorded were occupied by 33 ant morphospecies, of which 11 were obligate plant inhabitants. Neither plant species richness, ant species richness, nor total ant–plant density were significantly lower in forest fragments. However, eight of the plant species, including three of the four most common, had higher mean densities in continuous forest than fragments. Of these four species, only one (*Cordia nodosa*) had significantly different colonization rates between habitat types, with higher colonization rates of plants in fragments. This may be because the *Azteca* species it is associated with increases in abundance in forest isolates. Although our results suggest that communities of ant–plant mutualists are likely to persist in fragmented tropical landscapes 25 years after fragment isolation, most species are rare and populations sizes in fragments are extremely low. Environmental and demographic stochasticity could therefore limit long-term population viability. We suggest future studies focus on evaluating how fragmentation has altered herbivore pressure and the dispersal of ants and plants to fragments, since the interaction of these factors is likely to have the greatest impact on long-term patterns of population persistence.
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1. Introduction

Interspecific mutualisms, such as pollination and seed dispersal, play an important role in structuring ecological communities and are critical to the population dynamics of many plant and animal species (reviewed in Bronstein, 1994). Consequently, it is hypothesized that the disruption of mutualisms in fragmented habitats could cause a cascade of short and long-term effects, including the local extinction of partner taxa (Janzen, 1987; Kearns et al., 1998). Empirical work testing this hypothesis remains limited, however, and the consequences of fragmentation for communities of mutualist partners are for the most part unknown (but see Aizen and Feinsinger, 1994a,b; Memmott and Waser, 2002).

Most studies investigating the effects of fragmentation on mutualisms have been conducted on plant–pollinator interactions (reviewed in Kearns et al., 1998) and seed-dispersal mutualisms (e.g., Jules and Rathcke, 1999). Some of these studies found that fragments had reduced pollinator diversity or that the densi-

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ties of pollinators were lower in fragments (Aizen and Feinsinger, 1994a; Powell and Powell, 1987). Still others showed that pollinator communities were unaffected by fragmentation (Becker et al., 1991; Steffan-Dewenter and Tscharntke, 1999) or that declines in native pollinator communities were ameliorated by the invasion of exotic species from nearby disturbed areas (Aizen and Feinsinger, 1994b; Dick, 2001). Unfortunately, few of these studies simultaneously assessed the effects of fragmentation on both plant and pollinator populations, so it is unclear how changes in the abundance of one set of partners influences the other (but see Aizen and Feinsinger, 1994a,b). Additional studies, especially those focusing on non-pollination mutualisms, are needed to elucidate the consequences of fragmentation for communities of mutualist partners.

Mutualisms between ants and plants are one of the defining features of tropical rainforests (Benson, 1985), and they are model systems for studying the ecology and evolution of mutualistic interactions (Bronstein, 1998). Some tropical plants, called myrmecophytes or ant–plants, have specialized structures known as domatia (e.g., leaf pouches, swollen petioles, or hollow stems) in which ants nest. Resident ants frequently defend their host plants from herbivores or competitors, and for many ant–plants the loss of ant colonies results in severe defoliation or mortality (Bruna et al., 2004; Vasconcelos, 1991). There is also mounting evidence that ant–plant interactions can exert strong effects on host–plant reproduction (Stanton et al., 1999; Vasconcelos, 1991). Fragmentation-related extinctions of myrmecophytes or associated ants could therefore affect many plant and animal species, as well as alter multiple aspects of ecosystem functioning. Despite their importance to tropical ecosystems, however, ant–plant mutualisms have remained conspicuously overlooked by conservation biologists.

As a first step towards evaluating how fragmentation influences the dynamics of ant–plant interactions, we compared mutualist partner communities in rain forest fragments and nearby areas of continuous forest. We conducted our study at Brazil's Biological Dynamics of Forest Fragments Project (BDFFP), a large-scale experiment initiated in the early 1980s to evaluate the effect of fragmentation on tropical biotas (Bierregaard et al., 2002). Comprehensive work conducted in the BDFFP's continuous forest by Fonseca and Ganade (1996) and Fowler (1993) has described a rich community of myrmecophytic plants and ant associates. We used these previously published descriptions, as well as additional surveys in both continuous forest and forest fragments, to address the following three questions: First, is the density and species richness of myrmecophytic plants different in fragments and continuous forest? We predict that while overall species diversity would decrease in fragments, the density of myrmecophytes from

pioneer genera such as *Cecropia* will increase. Second, does the proportion of plants housing ant colonies differ between the two habitat types? We predict that because of the limited dispersal capability of ant queens, plant colonization rates will be lower in fragments. Third, are plants in fragments colonized by different suites of ants than those in continuous forest? We predict the proportion of plants colonized by non-mutualist species will increase in fragments.

2. Methods

2.1. Study sites and surveys

The BDFFP is located ca. 70 km north of Manaus, Brazil (2°30′S, 60°W) in lowland forest with rugged topography (Fig. 1). Soils at the site are nutrient-poor ferralsols with poor water-retention capacity. While tree diversity is extremely high (>1600 species), the understory is relatively species poor and dominated by stemless palms. Mean annual temperature is 26 °C (range: 19–39 °C), and annual rainfall ranges from 1900 to 2300 mm (BDFFP records). There is a pronounced dry season from June to October.

In addition to large expanses of continuous forest, the BDFFP reserve network includes several forest fragments isolated in the 1980s by the creation of cattle pastures. Fragments 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. Fragment isolation is maintained by periodically clearing the secondary growth surrounding fragments. For a complete description of the study site and the BDFFP design see Bierregaard et al. (2002). This study was conducted in four of the BDFFP's 1-ha fragments and four haphazardly selected continuous forest sites (Fig. 1) from October 2001 to February 2002.

In each of our eight study sites, we established a 100 m × 100 m plot in which we mapped all ant–plants. This plot size encompassed the entire 1-ha fragment for all fragments except #1104, which actually measures ~2.3 ha (M. Santamaria, pers. comm.). We collected a voucher specimen of each ant–plant we encountered, and verified the presence or absence of an ant colony by inspecting leaves for patrolling workers or soldiers, inspecting all domatia (when possible), and attempting to elicit ant responses by shaking leaves or blowing into domatia. For plants with more than 10 domatia, we randomly selected at least one domatium from the upper, middle and lower portions of the plant to open and inspect for colonies. Whenever possible we collected workers or queens for future identification. We also noted the presence of eggs, larvae, or pupae to determine if ants were nesting in domatia or merely foraging on leaf surfaces. Upon identification or assignment to morpho-
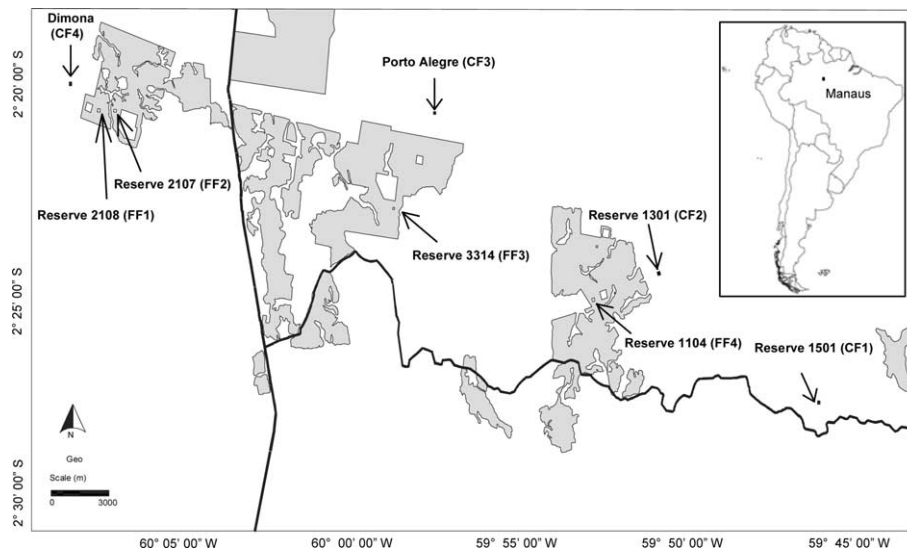
Fig. 1. Map of the Biological Dynamics of Forest Fragments Project reserves in which survey plots were located. White areas are continuous forest, stippled areas represent pasture and clearings surrounding fragments, dark lines represent roads. Abbreviations: CF, continuous forest plots; FF, forest fragment plots.

species, ants were classified as primary obligates, secondary obligates, or opportunists. Primary and secondary obligates are defined based on their relative frequency of occurrence in continuous forest, with primary obligates occupying >80% of the individuals of a species and secondary obligates found in 20% or fewer (all plots combined). We define 'opportunists' as generalist ant taxa that occasionally forage on myrmecophytes but rarely nest in them. Our definitions are consistent with those based on previous comprehensive surveys of the local ant and ant–plant community (Fonseca and Ganade, 1996; Vasconcelos et al., 2003). Plant vouchers are maintained at the BDFFP herbarium, while insect vouchers were deposited in the entomological collection of the Instituto Nacional de Pesquisas da Amazônia (INPA).

Workers of the ant genus *Azteca* are difficult to identify to the species level without collecting queens. Since doing so would increase the probability of colony failure, we conducted all analyses by grouping the *Azteca* morphospecies we identified into a single taxon (*Azteca* spp.). Preliminary analyses using separate morphospecies yielded results that were qualitatively similar to those presented below. Species-level identification is also difficult for the plant genera *Tachigali* (Fabaceeae) and *Pouruma* (Cecropiaceae) when individuals are seedlings or saplings. Therefore, all statistical analyses were conducted by grouping individuals from these genera into single taxa (i.e., *Tachigali* spp. and *Porouma* spp.).

2.2. Statistical analysis

We compared taxonomic richness of plants and ants in fragments and continuous forest using Mann–Whitney *U* tests. To test for an effect of fragmentation on ant–plant density, we (a) compared the total density of myrmecophytic plants in fragment and continuous forest plots using a Mann–Whitney *U* test and (b) used a sign test to determine if significantly more species had higher mean densities in continuous forest than in forest fragments. To determine if the proportion of plants housing ant colonies differed between fragments and continuous forest, we used only those plant species found in all eight study sites: *Hirtella physophora*, *H. myrmecophila*, *Tachigali* spp., and *Cordia nodosa*. We compared the percentage of plants colonized in the two habitat types (by any type of ant associate) using Mann–Whitney *U* tests. Finally, to determine if unique suites of ants were colonizing plants in the different habitat types, we compared the percentage of plants colonized by primary or secondary associates only. This analysis was done with Mann–Whitney *U* tests; each plant species was compared separately. We used the non-parametric tests for all comparisons because our sample sizes were low and we were unable to transform the data to meet the assumptions of parametric statistics; one-tailed tests were used because we had pre-established directional hypotheses.

3. Results

We inventoried a total of 1057 myrmecophytes from 12 plant taxa in our plots. The 78.9% of plants that were occupied contained a total of 33 ant morphospecies, 18 of which were recorded in forest fragments and 28 of which were found in continuous forest. These ants included both 11 obligate associates (e.g., *Crematogaster laevis*, *Pseudomyrmex nigrescens*) and 22 opportunistic

species (e.g., *Crematogaster brasiliensis*, *Wasmannia auropunctata*). The most common myrmecophytes were *H. myrmecophila* (55.2% of all stems sampled), *C. nodosa* (19.9%), *Tachigali* spp. (9.0%), and *H. physophora* (7.1%). Consequently, the most common ant species we recorded were their primary associates (*H. myrmecophila* and *H. physophora* = *Allomerus octoarticulatus*; *C. nodosa* = *Azteca* spp.; *Tachigali* spp. = *Pseudomyrmex concolor*). A complete list of the ant and plant species surveyed in this study is available at www.wec.ufl.edu/faculty/BrunaE/BrunaPapers.htm.

Contrary to our prediction, neither plant nor ant species richness was significantly lower in forest fragments. The median number of plant species recorded per plot was 7 in continuous forest and 6.5 in forest fragments (range = 4–10; $U' = 10.5$, $p = 0.23$). The median number of ant species or morphospecies recorded per plot was 8 in forest fragments vs. 14.5 in continuous forest (range 7–15; $U' = 13$, $p = 0.10$). Although plots in continuous forest had almost twice the median number of myrmecophytes that plots in fragments had (162 vs. 89.5, respectively, range = 55–268 plants/plot), ant–plant density was not significantly different among habitat types ($U' = 13$, $p = 0.10$). Nine of twelve species had higher mean densities in continuous forest (Fig. 2), although this was not significantly different based on the highly conservative sign test ($p = 0.14$).

Colonization frequencies of *H. myrmecophila* and *H. physosphora* were consistently high (Fig. 3), and the percentage of plants occupied by obligate ant species in the two habitat types was not significantly different (*H. myrmecophila*: $U' = 14$, $p = 0.08$; *H. physophora*:

$U' = 10$, $p = 0.51$). The colonization rates of *Tachigali* spp. in fragments and continuous forest were also not significantly different ($U' = 13$, $p = 0.10$), though this is probably the result of pronounced intersite variability in colonization rates rather than uniformly high colonization (Fig. 3). Only in *C. nodosa* were the colonization rates different between continuous forest and fragments ($U' = 15$, $p = 0.05$). However, the pattern was the opposite of that we predicted – fragments had a higher percentage of plants occupied than continuous forest sites did (Fig. 3). *C. nodosa* also had a higher frequency of colonization by opportunists than did the other species (Fig. 3), though the percentage of plants colonized by opportunist and obligate ant associates did not differ between habitat types for any of the four most common species (*C. nodosa*: $U' = 12$, $p = 0.14$; *H. physophora*: $U' = 10$, $p = 0.16$; *H. myrmecophila*: $U' = 12$, $p = 0.12$; *Tachigali* spp.: $U' = 12$, $p = 0.12$).

4. Discussion

Domatia-bearing plants and their resident ants are a diverse and conspicuous component of Amazonian biodiversity. We hypothesized the highly obligate relationship between them would make this community particularly susceptible to the detrimental effects of fragmentation, resulting in declines in density and species richness. Although we found that the density of ant–plants in fragments 20–25 years after isolation was almost half that in continuous forest, the effects on partner species richness appear limited. However, the rarity of most myrmecophytes, and hence their resident ants, suggests long-term population viability in fragments may be low.

Numerous studies have found assemblages of habitat fragments are species-poor relative to large, undisturbed areas (e.g., Bruhl et al., 2003; Ferraz et al., 2003). In contrast, we found the species richness of both partners was similar for plots in continuous forest and forest fragments. We also found comparable numbers of species at the landscape level, i.e., when summing species richness across all fragments and continuous forest sites. Nevertheless, several caveats suggest it would be premature to conclude fragmentation will have only a limited effect on species composition in this and other ant–plant communities. First, we sampled ant–plant partners in only four paired sites, and a lack of statistical power may have limited our ability to detect differences in specie richness or population density between fragments and continuous forest. Second, we almost certainly underestimated species richness in continuous forest. A number of habitat types were not included in our survey plots (e.g., large gaps), and some myrmecophytes are restricted to these areas (e.g., *Cecropia ulei*). These observations are supported by previous research in our
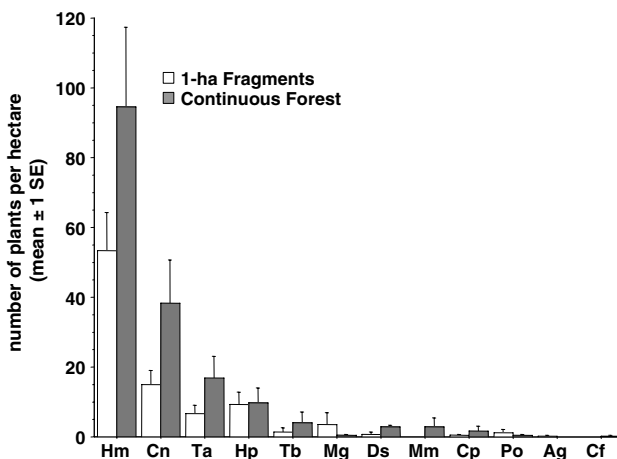

Fig. 2. Bar graph showing the average number of plants of each species found in continuous forest (filled bars) and forest fragments (open bars). Species are shown in decreasing order of abundance, summed across all plots. Abbreviations: Hm, *Hirtella myrmecophila*; Cn, *Cordia nodosa*; Ta, *Tachigali* spp.; Hp, *H. physophora*; Tb, *Tococa bullifera*; Mg, *Maieta guianensis*; Ds, *Duroia saccifera*; Mm, *Myrcia madida*; Cp, *Cecropia purpuracens*; Po, *Pouruma* spp.; Ag, *Amaioua guianensis*; Cf, *Cecropia ficifolia*.
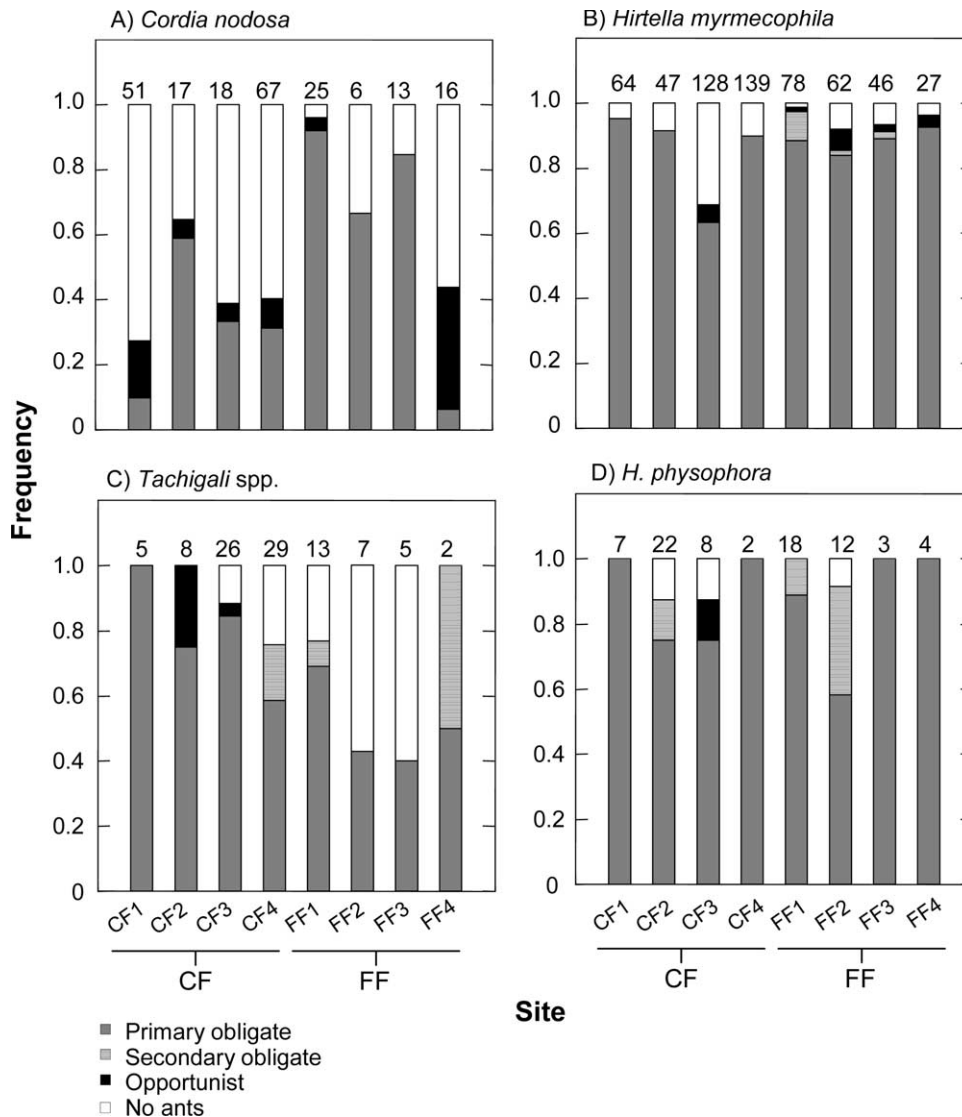
Fig. 3. Colonization frequency of the four most common ant–plants recorded in our surveys. Plants were either vacant (open bars) or colonized by ants that were primary obligates (grey bars), secondary obligates (hatched bars), or opportunistic (black bars). Primary obligates are the most commonly recorded residents, secondary obligates are rarer species, and opportunists are generalist ant taxa that occasionally forage on or nest in myrmecophytes but are not obligate domatia dwellers (Fonseca and Ganade, 1996; Fowler, 1993). Numbers above bars represent the number of plants recorded in that location. Abbreviations for plot locations correspond to those in Fig. 1.

field sites (Fonseca and Ganade, 1996; Fowler, 1993). Third, for many species of myrmecophytes the probability they will be found in isolated patches will be very low because they are extremely rare in continuous forest (e.g., *Duroia saccifera*, *Amaioua guianensis*, *Myrcia madida*). This "sampling effect" (cf. Norton et al., 1995) will be exacerbated for species restricted to specific habitat types. For instance, the plant species *Maieta guianensis* and *M. poeppiggi* (Melastomataceae) are found primarily along stream sides and other low-lying areas; this habitat is found in only one of our forest fragments. Fourth, several genera of ants inhabiting myrmecophytes are comprised of morphologically-similar species (e.g., *Allomerus, Azteca*) whose taxonomy and systemat-

ics have yet to be thoroughly reviewed (Benson, 1985). Taxonomic revisions may well reveal additional species not included in our analyses. Finally, seed dispersal from the nearby areas of continuous forest may be rescuing the populations in forest fragments (Brown and Kodric-Brown, 1977).

Although not statistically significant, our results also suggest a trend towards the reduced density of ant–plants in fragments, both overall and when species are considered individually. Most species, including five of the six most common ones, had average densities that were lower in fragments than continuous forest. Furthermore, for most species the population sizes in fragments are probably too low to remain viable for the

long-term. Only *H. myrmecophila* had more than 10 individuals in all forest fragments, and five species had fewer than two individuals in at least one of the fragments (*Duroia saccifera*, *Maieta guianensis*, *Tachigali* spp., *Amaioua guianensis*, *Cecropia purpuracens*). Surprisingly, even the pioneer ant–plants genera *Cecropia* and *Pourouma* were rare in the fragments – the most common pioneer found in these highly disturbed areas is *Cecropia sciadophylla*, which does not have ant associates. It is also worth noting that there may also be reductions in density as a result of mechanisms that are independent of modifications in ant partner communities. For instance, altered abiotic conditions in fragments can elevate mortality rates (Laurance et al., 1998) as well as reduce seedling recruitment (Bruna, 2002). Furthermore, the post-fragmentation densities, we observed are probably conservative, since the BDFFP's fragments are protected from fire, cattle, logging, and other factors that elevate individual mortality.

An additional mechanism that could drive reductions in species composition is the reduction in colonization rate of plants by ant queens. Vacant plants in which queens can establish colonies are widely considered a limiting resource for which there is intense competition (Longino, 1989; Yu et al., 2001), and previous surveys of ant–plant systems have found the proportion of plants colonized by ants is generally high. For instance, Fiala et al. (1999) found that over 98% of *Macaranga* had at least one *Crematogaster* queen in them; Longino (1989) and Yu et al. (2001) found slightly lower colonization rates for *Cecropia* species and *C. nodosa* (86% and 90%, respectively). In contrast, we found a community-wide colonization rate of less than 80%. Furthermore, our surveys revealed substantial variation in colonization rates both between species and sampling localities. At least some species have rates similar to those found in previous studies – for example, we found over 90% of the *Hirtella physophora* were colonized in each of the eight sites we sampled. In contrast, the overall colonization rate of *C. nodosa* was only 51.8%, with the percentage of plants colonized in each site ranging from 27.5% to 96%. Similar results were seen for *Tachigali* species – while in three of our sites all the plants we surveyed were colonized, colonization rates in two others were as low as 40%. Some plant species appear more dependent on ant colonists than others, particularly at early ontogenetic stages (Del Val and Dirzo, 2003; Fiala et al., 1994). If colonization rates for these species are reduced in forest isolates, these populations may be more susceptible to local extinction.

Even when colonization rates are similar in fragments and continuous forest, the dynamics of these mutualisms in fragments may be altered as a result of differences partner identity. In our field sites, for example, *Tococa bullifera* individuals that are colonized by secondary obligates suffer higher rates of herbivory than those colonized by primary obligates (Bruna et al., 2004). We found *H. myrmecophylla* individuals were colonized by secondary obligates (*Azteca* species) in three of four forest fragments, while in three of four continuous forest sites they were colonized exclusively by their primary obligate (*Allomerus* species). Interestingly, the *Tachigali* spp. individuals in fragments also had a higher incidence of colonization by *Azteca* than by their primary obligate (*Pseudomyrmex* species).

Several non-mutually exclusive mechanisms could be driving these subtle changes in partner identity. For instance, it may be that unoccupied plants are being colonized by queens dispersing from other myrmecophytes in the same fragment. Alternatively, queens could be dispersing into fragments from the secondary growth in which fragments are embedded. While these successional habitats are often highly degraded, many species of ant–plant partners are found there (T. Izzo, pers. comm.). Finally, queens may capable of dispersing across matrix habitat to plants in fragments from nearby areas of continuous forest. Although experimental work evaluating the dispersal capability of ant queens is limited, work in the Peruvian Amazon suggests *Azteca* queens are excellent fliers that are capable of long-distance dispersal (Yu et al., 2001). Taken together, this evidence suggests the increased abundance of *Azteca* species in fragments may be the result of either superior dispersal ability or increased colony survivorship in transitional habitats. Future empirical work will evaluate the consequences of these changes.

4.1. Implications for conservation of ant–plant communities

The fragmentation of tropical habitats is considered one of the greatest threats to the world's biodiversity, in part because of potential changes in the dynamics of interspecific mutualisms (Laurance et al., 1997). Our results suggest that communities of ant and plant partners are likely to persist in fragmented landscapes, at least in the 20–25 years following isolation. As a function of their rarity in continuous forest, however, population sizes in individual fragments are often extremely low. Environmental and demographic stochasticity could therefore limit long-term population viability, particularly if dispersal of seeds or queens to fragments is limited or there are Allee effects influencing the persistence of the mutualism (e.g., Anstett et al., 1997). Long-term persistence may be further compromised by reductions in ant partner composition, since these partners can differ significantly in the quality services provided to plants (Bruna et al., 2004; Ness, 2003). Unlike plant–pollinator mutualisms, in which the generalist species that increase in abundance in fragments can still be effective partners (Aizen and Feinsinger, 1994a; Dick, 2001), opportunist ant taxa provide limited defense

against herbivores (e.g., Suarez et al., 1998). We suggest future studies focus on evaluating how fragmentation has altered herbivore pressure and the dispersal of ants and plants to fragments, since the interaction of these factors is likely to have the greatest impact on long-term patterns of population persistence.

Acknowledgements

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