

INVITED REVIEW

## Arthropod responses to the experimental isolation of Amazonian forest fragments

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**ABSTRACT.** Arthropods are the most diverse and abundant group of animals found in tropical lowland forests, and in light of ongoing global change phenomena, it is essential to better understand their responses to anthropogenic disturbances. Here we present a review of arthropod responses to forest deforestation and fragmentation based on studies conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), located in central Amazonia. These studies involved a wide range of arthropod groups. All but one of the studies evaluated changes in total species number or species density in relation to fragment size, (i.e. area effects), and one-third also evaluated edge effects. Our review indicates that almost every arthropod group studied showed some kind of response to reduction in forest area, including altered abundances, species richness or composition in comparisons of different-sized fragments, fragmented and non-fragmented areas, or comparisons of forest edges and forest interiors. These responses tended to be idiosyncratic, with some groups showing predicted declines in abundance or diversity in the fragments while others show no response or even increases. However, some of the observed effects on arthropods, or on the ecological processes in which they are involved, were transient. The most likely explanation for this was the rapid development of secondary growth around fragments, which greatly increased the connectivity between fragments and the remaining forest. Although the BDFFP has provided many insights regarding the effects of forest fragmentation on arthropod assemblages, many diverse groups, such as canopy arthropods, have received scant attention. For those that have been studied, much remains to be learned regarding the long-term dynamics of these assemblages and how landscape context influences local biodiversity. The BDFFP remains an exceptional site in which to investigate how the ecological interactions in which arthropods are engaged are altered in fragmented landscapes.

**KEY WORDS.** Area effects; edge effects; insects; secondary succession; tropical forest conservation.

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Arthropods are – by far – the most diverse and abundant group of animals found in tropical forests. Their biomass far outweighs that of all other animal species combined and they play every functional role imaginable, meaning they are critical to the structure and functioning of tropical forests. Understanding their ecology, their interactions with other species, and their responses to anthropogenic environmental impacts therefore continue to be active and important areas of ecological research.

Among the primary threats to the diversity of tropical forests, including arthropod diversity, are deforestation and habitat fragmentation (reviewed in LAURANCE *et al.* 2002, 2011). Deforestation usually proceeds unevenly, leaving behind a patchwork of forest fragments that are isolated at varying degrees from one another and the nearest expanses of forest. These fragments are embedded in an intervening habitat, referred to as the “matrix habitat”, whose use varies in intensity from re-

generating forest, to cattle pasture, to human settlements. Habitat fragmentation was first identified as a threat to the integrity of ecosystems almost thirty years ago (HARRIS 1984, WILCOVE *et al.* 1986), and understanding the consequences of fragmentation has since emerged as one of the principal areas of research in conservation biology (reviewed in LAURANCE & BIERREGAARD 1997, HARRISON & BRUNA 1999, DEBINSKI & HOLT 2000).

One of the most widely observed consequences of fragmentation in the tropics is a reduced number of species in remnants, particularly when compared to similarly-sized areas of continuous habitat (e.g., METZGER 2000, FERRAZ *et al.* 2003). These reductions are often attributed to the local extinction of species from fragments. However, it is frequently difficult to eliminate alternative hypotheses without pre-fragmentation data and because of the high spatial heterogeneity among sites. This is further complicated by the differences in disturbance history

of individual fragments, including such factors as post-isolation selective logging and hunting and the elevated risk of fires entering fragments. Consequently, there has been a call to complement surveys in naturally fragmented landscapes with manipulative experiments conducted at realistic spatial scales to elucidate the consequences of habitat fragmentation (DEBINSKI & HOLT 2000).

The Biological Dynamics of Forest Fragments Project (BDFFP), located 70 km north of Manaus, Brazil (2°30'S, 60°W), is the world's largest-scale and longest-running experimental study of fragmentation in tropical forests. Collaboratively administered by the Smithsonian Tropical Research Institute and Brazil's National Institute for Amazonian Research (INPA), the BDFFP was originally implemented to elucidate a major debate over the ideal size of nature reserves (i.e., Single Large vs. Several Small, SLOSS). In addition to addressing the way in which reserve area influences biodiversity, the BDFFP has also yielded major insights into how forest clearing and the regeneration and management of land surrounding fragments influence nutrient cycling, patterns of species diversity, interspecific interactions, and forest dynamics (BIERREGAARD *et al.* 2001, LAURANCE *et al.* 2002, 2011).

Here we review the over three decades of research conducted on arthropods at the BDFFP. Using the BDFFP technical series, we identified all papers on arthropods published between 1979 and 2011. We then grouped these articles by taxonomic group and recorded: 1) the duration of the study and when it was conducted, 2) the location of the sampling – e.g., continuous forest, forest fragments of different sizes, the matrix habi-

tat – and number of sites in each category sampled, 3) whether the research team had any pre-fragmentation data, and the 4) the potential responses to fragmentation evaluated by the research team, including reductions in species diversity, density, or abundance in fragments (i.e., area effects), reductions in diversity or abundance with increasing proximity for forest of fragment edges (i.e., edge effects), and the effects of the presence or composition of regrowth vegetation surrounding fragments (i.e., matrix effects). Finally, we use these results to propose new directions in the study of arthropod responses to fragmentation.

### THE BDFFP STUDY SITES

The BDFFP sites are located ca. 70 km north of Manaus, Brazil, in a 20 x 50 km landscape dominated by lowland *terra-firme* forest (Fig. 1). The topography is rugged, varying in elevation from 50-150 m. The forests have a 30-37 m tall canopy with emergent trees up to 55 m (RANKIN-DE MÉRONA *et al.* 1992), and are amongst the most floristically diverse forests in the world (GENTRY 1990, OLIVEIRA & MORI 1999). About 25% of the diversity is in herbaceous and understory species (GENTRY 1990), and the understory is dominated by stemless palms (SCARIOT 1999). Soils are nutrient-poor yellow oxisols, known as yellow latossols in the Brazilian soil classification system, which despite having a relatively high clay content have poor water retention capacity (FEARNSIDE & LEAL FILHO 2002). Mean annual temperature is 26°C (range 19-39°C), and mean annual rainfall ranges from 1900-2300 mm. There is a pronounced dry season from June-October (RIBEIRO & ADIS 1984).

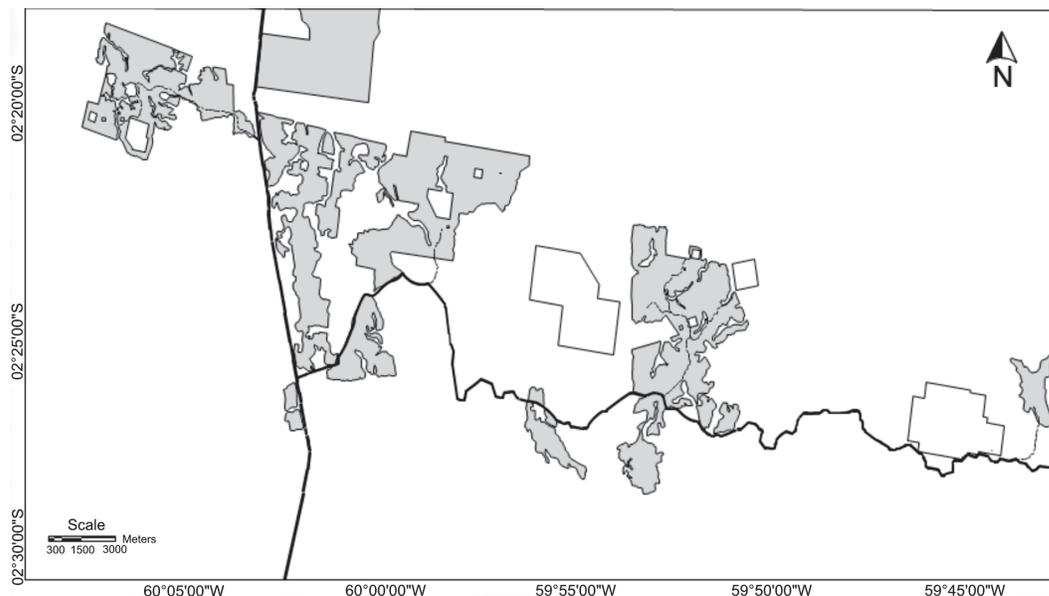


Figure 1. Map of the 20 x 50 km study area of the Biological Dynamics of Forest Fragments Project (BDFFP). Gray areas represent the forest area that was cleared to create cattle pastures. Squares and rectangles within the white area represent some of the BDFFP control sites.

In the 1970's the Brazilian government initiated a program aimed at expanding cattle ranching in the Amazon as a means of promoting the economic development of the region. Brazilian law at the time required owners of ranches leave 50% of the forest on the property standing, and researchers from INPA were able to convince the owners of three large ranches near Manaus to leave the required forest in fragments of different sizes (Fig. 2). In doing so the researchers were able to study the fragments on these ranches both prior to and after their isolation – a major advantage over prior studies of fragmentation in the tropics. Most BDFFP fragments were isolated from 1980-1984 by felling the trees surrounding the fragment and, in some cases, burning the downed trees once they dried (Tab. I, BIERREGAARD & GASCON 2001).

A major result to emerge early in the history of the BDFFP was that whether or not the felled trees were burned had a profound effect on secondary forest succession in the newly cleared pastures. Areas cleared for pasture that were not burned were rapidly covered with a secondary forest dominated by trees in the genus *Cecropia* (Cecropiaceae) (Tab. I). In contrast, the abandoned pastures established where felled trees had been burned (Fig. 2) were dominated by trees in the genus *Vismia* (Clusiaceae). In addition to these differences in the dominant tree genera, woody plant species richness in *Cecropia* stands is higher than in *Vismia* stands, and few species are shared between the two types of secondary forest (MESQUITA *et al.* 2001, RIBEIRO *et al.* 2010). Finally, *Cecropia* stands are much taller and have more closed canopies than *Vismia* stands (WILLIAMSON *et al.* 1998).

Due to economic failure and subsequent nearly abandonment of the ranches, only 11 of the 23 originally planned BDFFP fragments were created (Fig. 1). To maintain the isola-



Figure 2. View of one of the experimentally-created 1-ha fragments (Photo by R.O. Bierregaard Jr) surrounded by a cattle pasture.

tion of these fragments, a 100 m band around these fragments is periodically cleared (Tab. I). For a complete review of the BDFFP and its history, see BIERREGAARD *et al.* (2001).

#### ARTHROPOD GROUPS AND EFFECTS STUDIED

Twenty-seven studies involving a wide range of arthropod groups, including aquatic insects, ants, beetles, bees, butterflies, Drosophilids, spiders, termites and wasps, have been conducted at the BDFFP (Tab. II). Most of these studies evaluated community level responses, such as changes in species richness and composition, but some focused on population level responses to fragmentation (e.g., MESTRE & GASNIER 2008). All but one of the studies evaluated area effects (Tab. II). About

Table I. History of isolation of the BDFFP forest fragments.

Year	Events
1980	First two fragments (one of 1- and one of 10-ha) were isolated at Esteio Ranch.
1983	Four more fragments were isolated at Esteio and Porto Alegre Ranches (two of 1 ha, two of 10 ha). No burning in the cleared area. Two fragments of 100 ha were partially isolated.
1984	Three more fragments were isolated at Dimona Ranch (two of 1 ha, one of 10 ha). Completion of isolation of the first 100 ha fragment at Porto Alegre Ranch.
1985	Fragments of 1 and 10-ha isolated in 1983 already surrounded by 4-5m tall regrowth forest dominated by <i>Cecropia</i> spp. Woody vegetation invading the pasture areas around the fragments isolated in 1980 cut and burned by farmers.
1987	Woody vegetation invading the pasture areas around the fragments isolated in 1980 and 1984 cut and burned by farmers.
1988	<i>Cecropia</i> -dominated regrowth-forest surrounding the fragments isolated in 1983 approximately 10 m tall.
1989	<i>Vismia</i> -dominated regrowth-forest completely replaced the pasture areas established around the fragments isolated in 1980 and 1984. Re-isolation of most fragments (except two isolated in 1983) by cutting and burning a band of 100 m of secondary vegetation around the fragments.
1990	Completion of isolation of the second 100-ha fragment (Dimona Ranch).
1994	Re-isolation of most fragments by cutting and burning a band of 100 m of secondary vegetation around the fragments.
2000	Re-isolation of most fragments by cutting and burning a band of 100 m of secondary vegetation around the fragments.

one-third of the studies also evaluated edge effects. It was notable that few evaluated the potential effects of matrix type on the responses observed in fragments, i.e., whether the effects observed differed depending on whether a fragment was surrounded by pasture, *Vismia*- or *Cecropia*-dominated regrowth forest. The effects of distance from the nearest continuous forest on the arthropod biota in fragments was not evaluated in any study, probably because the range of distances between BDFFP fragments and continuous forest areas is low (ca. 100-900 m). In addition to responses to reduction in area, some studies also evaluated how changes in land cover, such as the replacement of mature forest by pastures or secondary forests, influenced species diversity.

The duration of each study and the sampling effort involved was quite variable. Most of the studies sampled for  $\leq 1$  y and/or sampled only a subset of the isolated fragments. The most notable exception was the study of butterflies by BROWN & HUTCHINGS (1997) which ran for 15 y and involved sampling in all 11 of the BDFFP's fragments (N = 5 1-ha, N = 4 10-ha, N = 2 100-ha). This study was also one of the few with pre-isolation data (Tab. II).

Below we briefly describe the main results of the studies conducted at the BDFFP. In addition, we present results from

six additional studies that did not focus on the arthropod responses *per se*, but rather on the ecological processes in which arthropods are the sole or primary actors.

## RESPONSES OF SPECIES ASSEMBLAGES TO FOREST FRAGMENTATION

### Butterflies

The study of true butterflies (Papilionoidea) led by K.S. Brown and collaborators represents the longest and most comprehensive study of an arthropod group ever conducted in the BDFFP landscape. Twenty-five sites were monitored over a 15-year period – from 1980 to 1995 – resulting in about 110,000 butterfly records over the course of 1,239 census hours (BROWN & HUTCHINGS 1997). A total of 455 species belonging to the butterfly families Nymphalidae, Pieridae, Papilionidae, and Lycaenidae were recorded. Almost half of these species were relatively rare, being found in five or fewer sites. In contrast, a single species, *Hypothyris euclea* (Godart, 1819) (Ithomiinae), constituted ca. 30% of all butterfly records. This species was extremely abundant in the BDFFP landscape during years immediately following the clearing of forests due to the proliferation in disturbed areas of its host-plant (*Solanum asperum* Rich.). Interestingly, however, within years of forest clearing it had

Table II. List of studies conducted at the BDFFP that analyzed some of the effects associated with deforestation and forest fragmentation on the abundance, species richness and/or species composition of arthropods. Shown are the groups studied, the period of studies, the sampling effort (no. sampling sites in different habitats), and the effects analyzed.

Arthropod group	Study period	No. sampling sites					Pre-isolation data?	Effects analyzed				Source
		1 ha frag.	10 ha frag.	100 ha frag.	Continuous forest	Matrix		Area	Edge	Matrix type	Land cover changes	
Aquatic insects	2001	0	1	2	9	8	No	Yes	No	No	Yes	NESSIMIAN <i>et al.</i> (2008)
Ants in myrmecophytes	2001/02	4	0	0	4	0	No	Yes	No	No	No	BRUNA <i>et al.</i> (2005)
Butterflies	1980-1995	5	4	2	14	0	Yes	Yes	No	Yes	No	BROWN & HUTCHINGS (1997)
Drosophilids	1980-1995	1	1	1	1	1	For one site	Yes	Yes	No	Yes	MARTINS (1989, 2001)
Dung beetles	1986	3	3	0	3	3	No	Yes	No	No	Yes	KLEIN (1989)
Dung beetles	1996/97	2	2	0	1	0	No	Yes	No	No	No	ANDRESEN (2003)
Dung beetles	2000	3	3	0	3	3	No	Yes	No	Yes	Yes	QUINTERO & ROSLIN (2005), QUINTERO & HALFFTER (2009)
Euglossine bees	1982/83	2	1	1	3	1	For three sites	Yes	No	No	No	POWELL & POWELL (1987)
Euglossine bees	1988/89	2	2	1	2	0	No	Yes	No	No	No	BECKER <i>et al.</i> (1991)
Ground-dwelling ants	1995	3	3	2	1	3	No	Yes	No	No	Yes	VASCONCELOS (1999), VASCONCELOS & DELABIE (2000)
Ground-dwelling ants	1993/96	0	0	2	2	0	No	Yes	Yes	No	No	CARVALHO & VASCONCELOS (1999)
Leaf-cutter ants	1985/96	5	4	0	9	0	No	Yes	No	No	No	VASCONCELOS (1988)
Leaf-cutter ants	~2009	0	0	0	45 transects	0	No	No	Yes	No	No	DOHM <i>et al.</i> (2011)
Leaf-litter beetles	1994	2	2	2	4	0	No	Yes	Yes	No	No	DIDHAM (1997)
Termites	1986	1	1	0	4	0	No	Yes	No	No	No	SOUZA & BROWN (1994)
Solitary wasps and bees	1988/90	2	2	1	7	2	No	Yes	No	No	Yes	MORATO & CAMPOS (2000)
Spiders	1999	4	3	2	4	3	No	Yes	Yes	No	No	MESTRE & GASNIER (2008)
Spiders	2001/02	5	4	0	9	0	No	Yes	Yes	No	No	REGO <i>et al.</i> (2005, 2007)

disappeared almost entirely, possibly do to a proliferation of its parasitoids (BROWN & HUTCHINGS 1997).

Surveys conducted prior and soon after the fragments of 1- and 10-ha were isolated indicated that the short-term response of the butterfly assemblage varied depending whether or not the felled vegetation was burned. Immediately after burning the number of species in the isolated fragments declined dramatically (from 25 to 12 species in the 1 ha fragment, and from 40 to 32 species in the 10 ha fragment). However, this pattern was not seen in fragments where ranchers failed to burn vegetation surrounding fragments (LOVEJOY *et al.* 1984, 1986). Additionally, BROWN & HUTCHINGS (1997) compared the total number of species recorded in fragments and areas of comparable size embedded in continuous forest. After adjusting for differences in sampling effort, they found that the type of matrix around the fragments was a strong predictor of species richness in the fragments. Isolated fragments surrounded by pastures contained a depressed number of species relative to fragments surrounded by tall second-growth forest. Nevertheless, the number of species found in fragments surrounded by tall regrowth forest was no greater than the one recorded in continuous forest areas with large internal clearings, which are key habitats for many butterfly species (BROWN & HUTCHINGS 1997).

When matrix type was not taken into account, differences in species richness between fragments and continuous forest were found to depend upon fragment size (LEIDNER *et al.* 2010). Fragments of 1-ha presented about 20% less species than comparable areas in continuous forest. In contrast, the 100-ha fragments contained comparatively more species (ca. 10-15% more species) than similar-sized areas in continuous forest. Small fragments (1-ha) appear unable to support butterfly species that are forest specialists. On the other hand, large fragmented forests ( $\geq 100$  ha) have both forest specialists and edge species, resulting in higher than expected species richness (LEIDNER *et al.* 2010).

The number of butterfly species in fragments varied markedly with time since isolation, but the observed changes were not consistent among fragments of different sizes (LEIDNER *et al.* 2010). Overall, however, fragments presented a significantly greater temporal and spatial variation in species richness than did the continuous forest sites. Forest fragmentation also caused strong shifts in the species composition of the butterfly assemblages, with the highest rates of turnover detected when the isolation status of fragments changed (i.e., when censuses performed prior and just after isolation were compared) (BROWN & HUTCHINGS 1997). Following isolation, fragments showed significantly lower turnover rates than sites in continuous forest. Even so, relative to continuous forest, fragments showed a significant decrease in the proportion of understory specialist species and an increase in the proportion of edge species, most notably in the fragments of 1-ha (LEIDNER *et al.* 2010).

### Drosophilids

Studies on drosophilids in the BDFFP focused on a guild associated with decomposing fruits that comprises ca. 40 fly

species in the area. These studies evaluated the influence of fragment area, distance from edge, and time since isolation (MARTINS 1987, 1989, 2001). Only a single fragment of each size (1, 10, or 100 ha) was studied, but the same fragments were inventoried repeated times between 1980 and 1995. In addition, the 100-ha fragment was sampled both before and after isolation. Species abundances in each fragment and period were estimated using standardized, fermented banana baits. The initial survey, conducted in the 1-ha and 10-ha fragments a few years after they were isolated, showed that both fragments and continuous forest were dominated by species of the subgroup *willistoni* (*Drosophila*, subgenus *Sophophora*). Nevertheless, the abundance of species from this subgroup was nearly twice as high in the fragments as in continuous forest (MARTINS 1989, 2001). Species of the subgroup *willistoni* were also more abundant along the border than in the center of the 10-ha fragment, despite the fact that they were rare in the young secondary growth forest surrounding this fragment. This was also true in the 100-ha fragment one month after its isolation. The latter showed an influx of individuals from a species typical of the surrounding regrowth forest (*Drosophila latifasciaeformis* Duda, 1940).

One exotic species (*Drosophila malerkotliana* Parshad & Paika, 1965) was found in all sites surveyed and showed an increase in abundance from 1980 to 1995, although this increase was more marked in the 1- and 10-ha fragments. Overall changes in species composition between 1980 and 1995 were stronger for the 1- than for the 10- and 100-ha fragments (MARTINS 1989, 2001).

### Euglossine bees

The effect of forest area on visitation rates to scent baits by male euglossine bees was evaluated in two independent studies; these found the community consisted of 15-16 species of the genera *Eufriesea*, *Euglossa*, *Eulaema*, and *Exaete* (POWELL & POWELL 1987, BECKER *et al.* 1991). In the initial study, three fragments – one of 1 ha, one of 10 ha and one of 100 ha – were censused prior and a few months after they were isolated in 1983 (POWELL & POWELL 1987). In spite of the close proximity between the fragments and the continuous forest (in some cases separated by only 100 m) and in spite of the fact that euglossine bees are long-flighted organisms (JANZEN 1971), visitation rates to baits in all fragment classes declined after forest isolation (Fig. 3). As predicted, responses of the individual species to fragmentation were variable. For instance, while visitation rates of *Eulaema meriana* (Olivier, 1789) and *Eulaema bombiformis* (Packard, 1869) was not affected by forest area, those of *Euglossa chalybeata* (Friese, 1925), *Euglossa stilbonata* Dressler, 1982 and *Euglossa crassipunctata* Moure, 1968 tended to increase as the forest area increased (POWELL & POWELL 1987).

A subsequent inventory in some of the same fragments five years later (June 1988-May 1989) showed a more complex relationship between forest area and the visitation rate of male bees (BECKER *et al.* 1991). In one site visitation rates were highest at the 10-ha fragment, while in the other at the 100-ha

fragment. Nevertheless, in both sites visitation rates in the 1-ha fragment was lower than in larger fragments or in continuous forest. Furthermore, changes in species composition were still clear, with five species captured exclusively in 1- and 10-ha fragments and another six species found exclusively in the 100 ha fragment or continuous forest (BECKER *et al.* 1991).

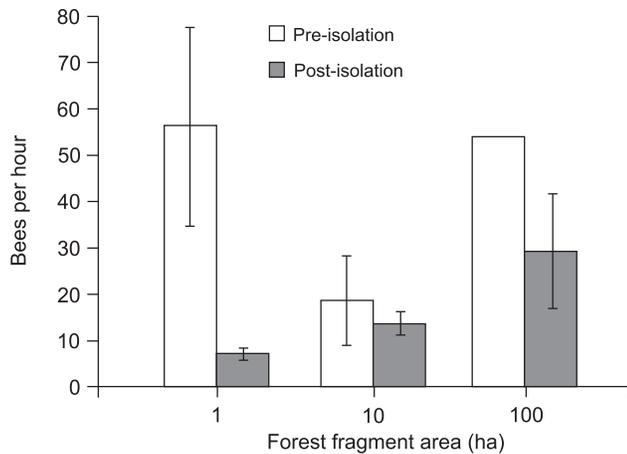
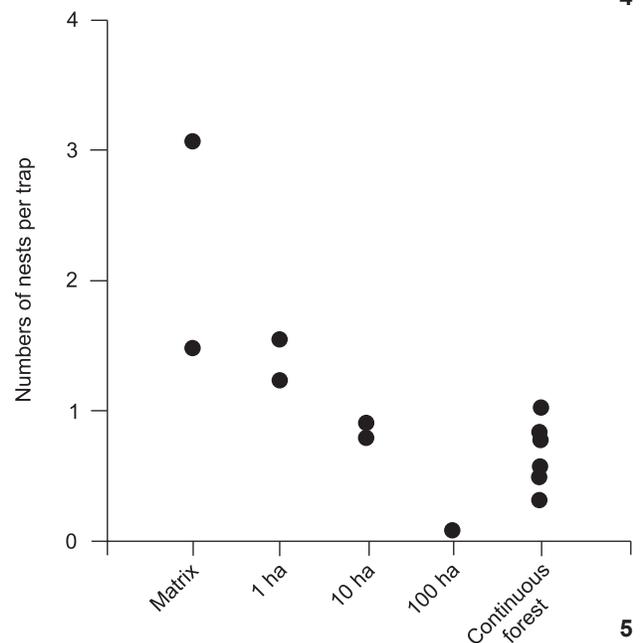
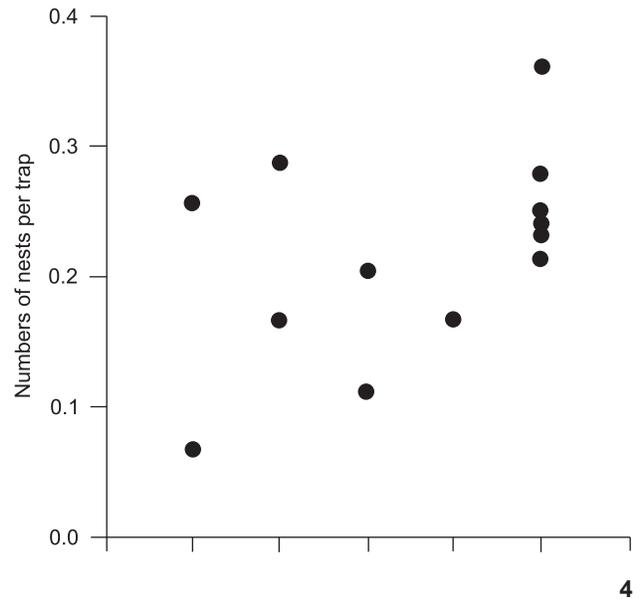


Figure 3. Visitation rates of male euglossine bees prior and after the isolation of different sized forest fragments. Bars represent mean values ( $\pm$  S.D.) Data from POWELL & POWELL (1987).

### Tree-hole nesting solitary wasps and bees

Solitary bees and wasps that use small wood cavities to make their nests were studied from 1988 to 1990. Using wooden trap nests placed at different heights on trees, MORATO & CAMPOS (2000) were able to quantify the number of nests built by different species in continuous forest, fragments, and in some of the regenerating matrix including an abandoned pasture and a regrowth forest dominated by *Cecropia* spp. Overall, they found 24 species of solitary wasps from the families Sphecidae, Eumenidae, and Pompilidae, and 14 species of solitary bees from the families Anthophoridae, Megachilidae, and Apidae (MORATO & CAMPOS 2000). For both bees and wasps, the number of species found in continuous forest tended to be greater than the one found in the different sized fragments or in the matrix habitats (wasps: 7-11 species in continuous forest versus 6-9 species in the fragments or in the matrix; bees: 12-16 species versus 10-14 species). Nevertheless, bees and wasps showed contrasting patterns of nest abundance (Figs 4 and 5). For bees there was a slight trend towards finding more nests in continuous forest than in the fragments or the matrix. In contrast, comparatively more wasp nests were built in the matrix and in the 1-ha fragments than in continuous forest, 10-ha fragments and 100-ha fragments. There were also changes in species composition (Figs 6 and 7). For instance, nests of the bees *Megachile orbiculata* Mitchell, 1930 and *Anthodiocetes moratoi* Urban, 1999



Figures 4-5. Number of nests founded by solitary bees (4) and wasps (5) during a one-year period in continuous forest sites, in different sized forest fragments, and in the matrix habitats surrounding these fragments. Data from MORATO & CAMPOS (2000).

were rare or absent in the matrix and the smaller fragments – habitats in which *Centris dichrotricha* (Moore, 1945) was the most frequently observed species (Figs 6 and 7). Nests of the wasp *Trypoxylon lactitarse* Saussure, 1867 were very common in the matrix and in the fragments but were quite rare in the continuous forest, while the reverse was true for *Podium sexdentatum*

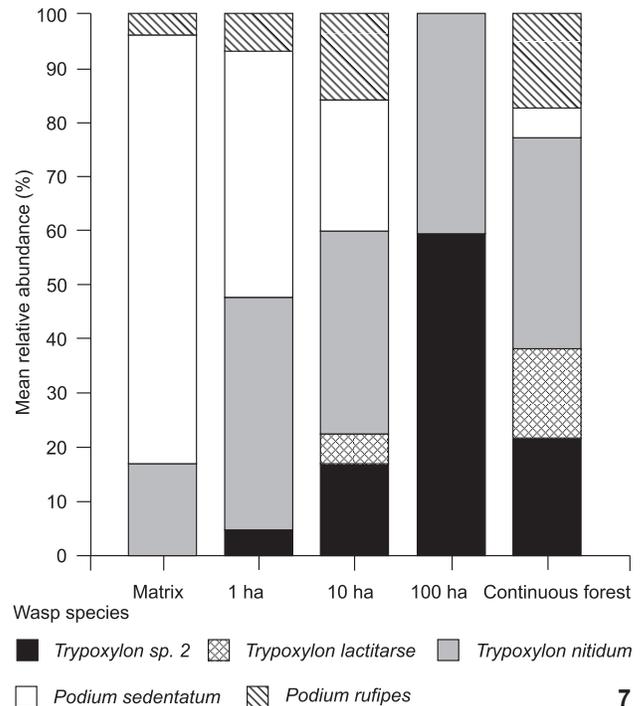
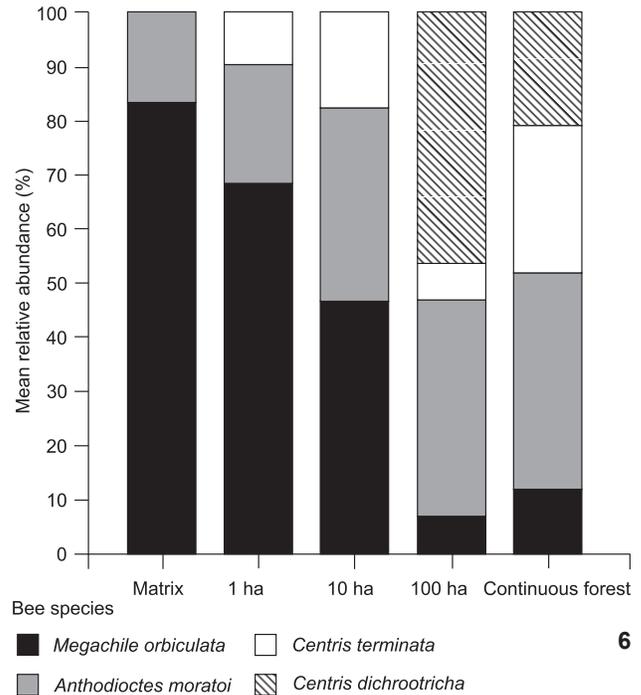
Taschenberg, 1869 (Figs 6 and 7). Interestingly, habitat fragmentation had a significant influence on the vertical distribution of wasp nests but not on those of bees (MORATO 2001). In continuous forest the number of wasps nests built at 1.5 m in height was greater than expected whereas in the forest fragments was lower than expected, with the reverse trend being observed for trap nests placed at 8 m in height (MORATO 2001).

**Termites**

SOUZA & BROWN (1994) compared the structure of termite assemblages between fragments (one 1-ha and one 10-ha fragments) and continuous forest (two sites); overall they found 64 species from 32 genera. Species richness was much greater in continuous forest than in fragments (54 and 28 species, respectively) and greater in the 10-ha fragment than in the 1-ha fragment (21 and 13 species, respectively). The feeding guild structure of termite assemblages was also altered in fragments. A greater proportion of the species exclusively found in continuous forest were soil feeders (59.8 versus 20% of soil feeder species in continuous forest and fragments, respectively) whereas in the fragments litter-feeders and species intermediate between soil-feeding and wood-feeding types were numerically more important (SOUZA & BROWN 1994). Most of the termite nests found in fragments and continuous forest were associated with rotting logs, while in continuous forest there were proportionally more nests in live trees and palms (SOUZA & BROWN 1994).

**Leaf-cutter ants**

Studies on leaf-cutter ants of the genus *Atta* Fabricius, 1804 analyzed the effects of forest area, edge proximity and forest regeneration on nest densities (VASCONCELOS 1988, VASCONCELOS & CHERRETT 1995, DOHM *et al.* 2011). The original forest landscape contained only two species, *Atta cephalotes* (Linnaeus, 1758) and *Atta sexdens* (Linnaeus, 1758), but following forest clearing for pasture establishment a third species, *Atta laevigata* (Smith, 1858), appeared (VASCONCELOS & CHERRETT 1995). A survey conducted 2-5 years after the 1- and 10-ha fragments were isolated showed no significant difference in *Atta* nest densities between fragments and continuous forest (VASCONCELOS 1988). However, nest densities were spatially variable and one particular 10-ha fragment presented a density of nests three times greater than any of the other four sites with equivalent area surveyed in continuous forest (Fig. 8). None of the nests found in this initial survey of the BDFFP fragments belonged to *A. laevigata* (VASCONCELOS 1988). Nevertheless, a much more recent study analyzing the influence of distance to forest edge on nest densities showed that *A. laevigata* represented 29% of the total number of nests (DOHM *et al.* 2011). In contrast to the other two species, whose nests were found at all distances surveyed, *A. laevigata* was only found in close proximity to the forest edge. This indicates that *A. laevigata*, which is poorly adapted to undisturbed forest habitats, has a high potential to proliferate at the forest edge. Overall, the density



Figures 6-7. Relative abundance of the most common species of solitary bees (6) and wasps (7) in continuous forest sites, in different sized forest fragments, and in the matrix habitats surrounding these fragments. Data from MORATO & CAMPOS (2000).

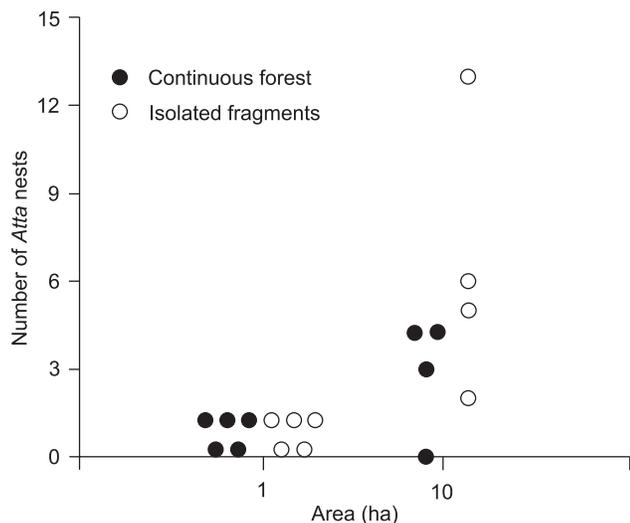


Figure 8. Abundance of leaf-cutter ant (*Atta* spp.) nests in isolated fragments and in continuous forest sites with equivalent area. Data from VASCONCELOS (1988).

of leaf-cutter ant colonies at the BDFFP landscape was much greater (ca. 20 times greater) near the edge than away from the edge towards the forest interior, a result comparable to that observed in regions with a longer history of habitat disturbance and fragmentation (DOHM *et al.* 2011).

### Ground- and litter-dwelling ants

The community of ants that nest or forage on the ground or in the litter layer in forests of the BDFFP study area is quite diverse, with over 100 species recorded in an area of just one hectare (VASCONCELOS & DELABIE 2000). Collections of ants in the center of the different sized forest fragments and in continuous forest revealed no consistent influence of fragment area on the density of ant species (i.e., number of species per ha). In two study sites, the density of species increased with fragment size, whereas in a third site there were more species in the 1-ha fragment than in the fragments of 10- or 100-ha. Nevertheless, in all three study sites relatively large dissimilarities in species composition were encountered among the small (1-ha) and the large fragments (100-ha) and the continuous forest (VASCONCELOS & DELABIE 2000, VASCONCELOS *et al.* 2001), indicating that small fragments support a somewhat distinct ant fauna.

Ant species composition was also affected by distance to forest edge, as revealed by collections of ant nests in decaying twigs along transects located at varying distances from the edges of two continuous forests and two fragments of 100 ha (CARVALHO & VASCONCELOS 1999). In fact, edge effects are likely to explain the observed differences in ant species composition between fragments of different sizes, since sampling plots in small fragments were located much closer to the forest edge than those in larger fragments or in continuous forest. Edge

proximity seems to favor those ant species more typical of disturbed, second-growth areas, since these species are comparatively more frequent along the edge than in the forest interior (VASCONCELOS *et al.* 2001). Similarly, the overall abundance of ants in the leaf-litter tends to be greater near the edge. DIDHAM (1997a) found that in two of his study sites ant abundance in the leaf litter was significantly higher at 0 and 26 m from the edge than in deep forest.

Although edge effects appear to have a predominant role in explaining changes in ant community structure following forest fragmentation, area and isolation effects cannot be completely discarded. In fact, at comparable distances from the forest edge there were more species of litter-nesting ants found in continuous forest than in isolated fragments of 100-ha. In addition, 27 out of 41 the species shared between continuous forest and fragments presented greater nest densities in continuous forest (CARVALHO & VASCONCELOS 1999). Finally, strong differences in species richness and composition between pasture areas and secondary forests of varying structure (VASCONCELOS 1999) suggest that the effect of habitat fragmentation on ground- and litter-dwelling ants is likely to be depend upon the type of habitat surrounding the fragments. Few forest ant species were found in the semi-abandoned cattle pastures, a pattern which is in sharp contrast to that observed in secondary forests, particularly in tall secondary forests dominated by *Cecropia* spp. (VASCONCELOS 1999). Therefore, ant populations in fragments surrounded by pastures are effectively isolated, while those surrounded by tall regrowth forest are not.

### Ants in myrmecophytes

Myrmecophytes, also known as 'ant-plants', are plants with leaf-pouches, hollow branches, or other specialized structures in which a specialized suite of ant species nest. BRUNA *et al.* (2005) studied the community of ants inhabiting these plants in both 1-ha fragments and similar sized areas in continuous forest to determine if plants in fragments were colonized by a different suite of ants than those in continuous forest, and if the proportion of plants housing ant colonies differed between the two habitat types (BRUNA *et al.* 2005). A total of 33 ant species were recorded, of which 11 were obligate ant-plant nesters and 22 were opportunistic inhabitants of one or more of the 12 species of ant-plants found in the study plots. In general, each ant-plant species hosted no more than two species of obligate ant partners, of which one was much more frequent than the other (BRUNA *et al.* 2005). In contrast to what might be predicted for such a specialized mutualistic interaction, overall ant species richness did not differ between fragments and continuous forest sites, and the proportion of plants colonized by obligate species was similar in forest fragments and continuous forest. For three of the four ant-plant species analyzed the overall ant occupancy rates did not differ between plants in fragments or in continuous forest, while for one species (*Cordia nodosa* Lam.) ant occupancy was actually higher in the fragments. This relatively high degree of specialization in the

association between ants and ant-plants, coupled with the fact that most BDFFP fragments are less than 1 km from the nearby forest areas that are sources of founding queens, may help to explain why communities of ant-plants and their ant mutualists appear resistant to the detrimental changes associated with habitat fragmentation, as demonstrated by more recent analyses of the structure of these ant-plant mutualist networks (PASSMORE *et al.* 2012).

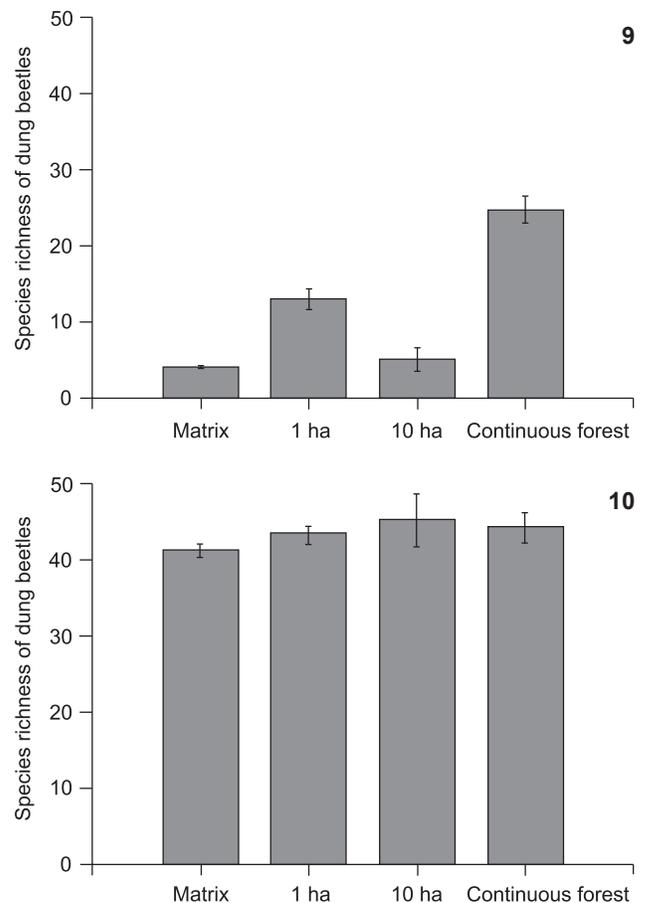
### Dung beetles

Dung beetle (Coleoptera: Scarabaeinae) assemblages were inventoried at various times since inception of the BDFFP with the intent of assessing the effects of habitat fragmentation on the abundance, size, species richness, and on some of the functional attributes of these insects (KLEIN 1989, ANDRESEN 2003, QUINTERO & ROSLIN 2005, QUINTERO & HALFFTER 2009). The initial study, which compared beetle assemblages in continuous forest, forest fragments (1- and 10 ha), and the matrix, was performed 2-6 years after the initial isolation of the fragments (KLEIN 1989). The second study, which involved a subset of the habitats and sites used by the first one, was performed in 1996-97 (ANDRESEN 2003); this was followed by one which was conducted in the identical sites and habitats (QUINTERO & ROSLIN 2005, QUINTERO & HALFFTER 2009).

Over 60 dung beetle species have been recorded in the BDFFP landscape. Significant differences in species richness between fragments and continuous forest were recorded in 1986 and in 1996-97, but not in 2000. In 1986 both the 1- and 10-ha fragments had fewer species than the continuous forest (Figs 9 and 10), whereas in 1996-97 only the 1-ha fragments had significantly fewer species than the continuous forest. The 2000 survey, however, failed to detect any differences in species richness (Figs 9 and 10) or in the abundance of individual species between any of the fragment size classes and continuous forest (QUINTERO & ROSLIN 2005). According to QUINTERO & ROSLIN (2005) the development of secondary vegetation around the fragments is the most likely explanation for these temporal changes in beetle assemblages, as by 2000 most of the BDFFP fragments were surrounded by tall secondary growth forest (up to 20 y old) which itself contained as many species of dung beetles as the undisturbed continuous forest (Figs 9 and 10). In contrast, the open areas surrounding the fragments in 1986 were dominated by four non-forest dung-beetle species in *Glaphyrocantion* Martinez, 1948 (KLEIN 1989).

Forest fragmentation also affected the abundance and size of dung beetles, but once more some of these effects were only temporary. In 1986 beetle abundance was significantly greater in continuous forest than in the 1- and 10-ha fragments, whereas in the subsequent surveys beetle abundance did not differ between fragmented and continuous forests (QUINTERO & ROSLIN 2005) or was even higher in the 10-ha fragments than in the other sites (ANDRESEN 2003). Beetles captured in continuous forest in the initial surveys were significantly larger than those captured in the 1-ha and 10-ha forest fragments (KLEIN 1989), a

difference that persisted, albeit weakly, in the 1996-97 surveys (ANDRESEN 2003; note that differences in beetle size were not evaluated in the 2000 survey). Since the most important source of food for dung beetles is the dung of mammalian herbivores (ANDRESEN 2003), the observed changes in beetle size and abundance likely reflect temporal changes in mammalian densities in the fragments.



Figures 9-10. Species richness of dung beetles at two times since deforestation and forest fragmentation. In 1986 (9) fragments were surrounded by pastures or by a 3 year-old secondary forest, whereas in 2000 (2) all fragments were surrounded by a tall secondary forest 10-17 years old. Data from KLEIN (1989) and QUINTERO & ROSLIN (2005).

### Leaf-litter beetles

Studies on leaf-litter beetles at the BDFFP have analyzed the influence of fragment area and edge distance on beetle abundance, species richness and composition (DIDHAM 1997b, DIDHAM *et al.* 1998a), as well as on the extinction probabilities of species in different trophic guilds (DIDHAM *et al.* 1998b). Beetles were extracted from leaf-litter samples taken in the cen-

ter of 1- and 10-ha fragments and at varying distances from the forest edge of 100-ha fragments and continuous forest sites. Additional collections were performed in control sites located > 10 km from the nearest forest edge.

The diversity of leaf-litter beetles observed in these studies was astonishing: 993 species in an overall sample of 8,454 beetles. The dominant families were Staphylinidae, Scydmaenidae, Ptiliidae, and Curculionidae, with 50-150 species each. Overall beetle abundance increased with edge proximity but did not change with fragment area, even though there was a clear trend towards finding lower beetle densities in the larger fragments (DIDHAM 1997b). Interestingly, beetle abundance did not change linearly with distance from the forest edge. Instead, there was often a bi-modal pattern of abundance, with one peak on the fragment edge and the other at mid-distances (26-105 m) into the forest. Beetle abundance and richness were highly inter-correlated, and as a consequence absolute species richness increased significantly with increasing proximity to the forest edge; it was also higher in small fragments than in larger ones (DIDHAM *et al.* 1998a). In contrast, rarefied species richness (i.e., species richness controlling for differences in beetle abundance) was not significantly affected by habitat fragmentation.

There were clear differences in the composition of leaf-litter beetle assemblages between continuous forest and isolated forest fragments, with the latter lacking many of the species characteristic of continuous forest. Of the 29 most abundant species, which together accounted for 48% of total beetle abundance in the continuous forest sites, 49.8% of species were absent from samples taken in 1-ha fragments, 29.8% were absent from 10-ha fragments, and 13.8% were absent from 100-ha fragments (DIDHAM *et al.* 1998a). It is important to note, however, that some of the observed variation in the composition of beetle assemblages appears associated with sampling site location within the study area and not with the effects of fragment area *per se* (DIDHAM *et al.* 1998a). This is because most of the fragments sampled for leaf-litter beetles were located in the west of the BDFFP study area, whereas the control sites were located on the east. This geographic separation of control sites and experimental fragments (Fig. 1) is an intrinsic – albeit unplanned – limitation of the BDFFP design. More recent studies have tried to minimize this problem by establishing control sites in continuous forest areas closer to the fragments (e.g., REGO *et al.* 2007).

Beetle assemblages also differed between edge and interior sites, with more marked differences in fragments than in the edges and interiors of continuous forest. Interestingly, different edges did not share a common beetle fauna composed of widespread or 'weedy' species. In fact, beetle species composition was surprisingly more variable among edge sites than among undisturbed forest sites (DIDHAM *et al.* 1998a). However, DIDHAM *et al.* (1998b) did find that overall the proportion predatory species was higher near edges, whereas the proportion of xylophagous species increased with increasing distance from edges. While edge effects also influenced the extinction prob-

abilities of some species (defined as the absence of the species from samples within a given site), for most of the species analyzed fragment area was the most important determinant of extinction probability. Extinction probabilities were also variable among trophic guilds, being higher for predatory than for xylophagous species and higher for these guilds than either saprophagous or fungivorous species (DIDHAM *et al.* 1998b).

## Spiders

Wandering spiders from two different families (Ctenidae and Sparassidae) were collected in seven forest fragments ( $\leq 10$  ha) and in nine areas of continuous forest (REGO *et al.* 2005). These spiders are widely distributed over the Amazon region; they have strictly nocturnal habitats, do not use webs to capture their prey, and are found mainly in the leaf-litter. However, in spite of their similar habits, they showed opposite responses to habitat fragmentation. While the overall density of Sparassidae (all species combined) was higher in the fragments, that of Ctenidae was significantly higher in continuous forest than in the fragments (REGO *et al.* 2005). A total of 14 ctenid species were recorded in the BDFFP study area, of which *Ctenus manauara* Höfer, Brescovit & Gasnier, 1994, *Ctenus cruksi* Mello-Leitão, 1930, *Ctenus amphora* Mello-Leitão, 1930, and *Ctenus villasboasi* Mello-Leitão, 1949 were the most abundant (REGO *et al.* 2007). An analysis of the responses of these four species to edge and area effects showed that the latter two species had significantly higher population abundances in continuous forest than in fragments, whereas *C. manauara* and *C. cruksi* showed similar abundances in fragmented and non-fragmented habitats (REGO *et al.* 2007). However, none of the four *Ctenus* species showed significant differences in abundance with respect to the forest edge (REGO *et al.* 2007). MESTRE & GASNIER (2008), in a study conducted two years earlier in some of the same sites studied by REGO *et al.* (2005, 2007), detected an impressive seasonal variation in the abundance of all four *Ctenus* species. Furthermore, they did not detect any significant differences in abundance when comparing species individual abundances between "small" (1 and 10 ha) and "large" (100 ha and continuous forest) forest areas (MESTRE & GASNIER 2008).

## Aquatic insects

One of the more recent groups to have been investigated is the aquatic insects (NESSIMIAN *et al.* 2008). Using 20 streams throughout the BDFFP study area, the possible influence of land cover and habitat fragmentation on the richness and composition of aquatic insect assemblages was compared in four habitats: pastures, secondary forests of varying ages and structure, forest fragments (of 10 and 100 ha), and continuous forest. A total of 150 reaches were surveyed, resulting in the capture of 5,746 individuals from 151 taxa in 10 orders. Continuous forest, forest fragments, and secondary presented similar mean numbers of insect species per reach, and the number of species found in these three habitats was about 1.5 times greater than the one found in pasture reaches (NESSIMIAN *et al.* 2008). Com-

parable results were found for analysis using rarefied species richness, as well as those using only species of Ephemeroptera, Plecoptera and Trichoptera (considered indicators of water quality). Streams in pastures had different communities from those in primary and secondary forest, whereas those in pastures and forest fragment were only marginally different. Streams in continuous, fragmented, and secondary forests had very similar faunas – only a few species were considered characteristic of primary forest streams, and none for secondary forest streams. Overall, the results of this study suggest that only drastic changes in the vegetation cover, as those observed when forest is replaced by pasture, can induce significant changes in the aquatic insect community.

## CHANGES IN ARTHROPOD-RELATED ECOLOGICAL PROCESSES

### Herbivory

Densities of mammalian herbivores are often quite low in forests of the central Amazon (EMMONS 1984, MALCOLM 1995) and consequently most of the herbivore damage seen on forest plants is caused by a highly diverse suite of insects. Two studies have evaluated the effects of Amazonian forest fragmentation on herbivory in plants of the forest understory. A seedling transplant experiment compared herbivore damage of three plant species between continuous forest and different sized fragments (BENITEZ-MALVIDO *et al.* 1999). Damage was variable among the four study sites (one continuous forest site, one 100 ha fragment, one 10 ha fragment and one 1 ha fragment), but for some species the observed differences were not consistently related to fragment size. For instance, in *Chrysophyllum pomiferum* (Eyma) T.D. Penn. there was significantly more damage in seedlings transplanted to a 10-ha fragment than to those transplanted to continuous forest or to fragments of 1- or 100-ha, whereas for *Micropholis venulosa* (Mart. & Eichler ex Miq.) Pierre damage was higher in plants from the 1 and 100 ha fragments than for those in continuous forest or the 10 ha fragment (BENITEZ-MALVIDO *et al.* 1999). In contrast, herbivore damage in *Pouteria caimito* (Ruiz & Pav.) Radlk. over a 14 month period showed a positive relationship with fragment area (BENITEZ-MALVIDO 2001).

Similarly, the relationship between forest area and herbivore damage was found to be species specific in leaves of naturally occurring tree saplings (FAVERI *et al.* 2008). Nevertheless, the community-wide level of herbivory increased positively and significantly with forest area, with plants from continuous forest suffering on average twice as much as damage as plants in the 1-ha fragments (FAVERI *et al.* 2008). This occurred despite no significant changes in the species composition of the tree sapling community according to fragment size, or in the nutritional or defensive leaf traits of the species studied. In addition, predation of herbivores, estimated using artificial caterpillars, also showed no significant relationship with forest area. Therefore, neither of these top-down and bottom-up forces could explain the observed effects of forest frag-

mentation on leaf herbivory. One alternative hypothesis put forward is that forest fragmentation may affect the dispersal of insect herbivores, thereby reducing their abundances in small forest isolates (FAVERI *et al.* 2008).

### Pollination

Perhaps the most comprehensive studies on pollination at the BDFFP are those of *Dinizia excelsa* Ducke (Fabaceae), which is an emergent, canopy tree that reaches up to 60 m in height. Deforestation and forest fragmentation alter the breeding structure of *D. excelsa* – forest fragments contain few reproductive trees, and all but the largest trees, which farmers maintain for timber or shade, are felled in the cleared areas. Furthermore, deforestation also alters the assemblage of *D. excelsa*'s insect pollinators (DICK 2001a, b). In continuous forest, stingless bees (Meliponini) were the primary pollinators of *D. excelsa*; small beetles were common visitors, but because their movement was limited they appear to be at most vectors of self-pollination (DICK 2001b). A total of 14 species of stingless bees and 10 species of small beetles were recorded. These same species were found in the forest fragments and at similar abundances as in continuous forest. However, trees in forest fragments were also visited by large numbers of African honeybees (*Apis mellifera scutellata* Lepeletier, 1836). These were the primary pollinators of trees isolated in pasture areas, since in these areas beetles were not present and stingless bees were quite rare. Interestingly, African honeybees resulted in the greatest *D. excelsa* seed pod production in pasture trees and those from a 10-ha fragment (Fig. 11) (DICK 2001a, b). In addition, microsatellite analyses suggest that replacement in degraded habitats of native bees by african hon-

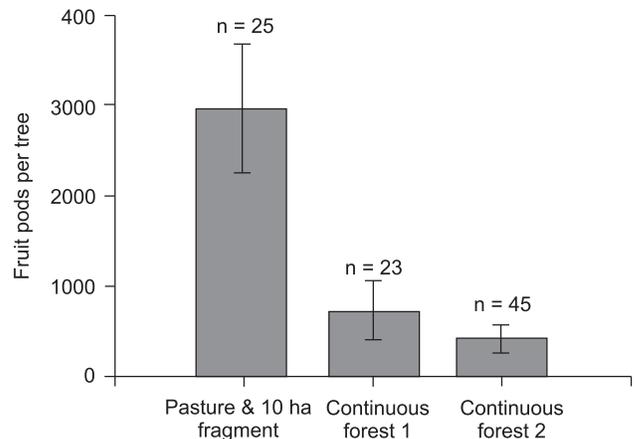


Figure 11. Number of pods produced by *Dinizia excelsa* trees growing in different habitats. *N* represents the number of trees sampled in each habitat. Adapted from DICK (2001b). African honeybees are the main pollinators of *D. excelsa* in pastures and isolated forest fragments, whereas native bees are the main pollinators of this tree species in undisturbed, continuous forest.

eybees may have helped to ameliorate the deleterious effects associated with the increased isolation of these remnant trees – african honeybees are capable of long-distance pollen transport (e.g. up to 3.2 km; DICK 2001a, DICK *et al.* 2003). It is important to mention, however, that results found for *D. excelsa* cannot be generalized for other forest tree species. Although african honeybees are good pollinators of *D. excelsa* and other plants with simple flowers and a rich supply of nectar and pollen, they can be harmful to those species with specialized flowers (DICK 2001b).

### Removal of dung and carrion and seed burial by scarab beetles

As indicated above, forest fragmentation strongly affected the community of dung beetles, though these effects tended to dissipate as the forest regenerated in the areas surrounding the fragments. These changes in the beetle community had a cascading effect on some of the ecological processes these beetles are responsible for, namely the removal of dung and carrion and the burial of seeds present in dung piles. Two independent studies indicated that dung removal rates decrease significantly with fragment area (KLEIN 1989, ANDRESEN 2003) most likely due to a concomitant decrease in beetle abundances, size, or both. Similarly, the removal of carrion (quail carcasses) was smaller in fragments than in continuous forest one day after exposure of the carcasses. However, this initial difference disappeared two days later, perhaps as result from shifts in the decomposition guild, with omnivores ants replacing scarab beetles in the carcasses after the second day (KLEIN 1989).

ANDRESEN (2003) also compared the percentage of seeds buried by dung beetles between fragmented and continuous forest and found that, for two of the three plant species evaluated, it was significantly higher in continuous forest. Furthermore, there was a trend, albeit not a statistically significant one,

for beetles to bury seeds deeper in the continuous forest than in forest fragments. Seeds buried by dung beetles have a lower chance of being found by rodent seed predators, and seedling establishment was higher for buried seeds than for seeds that remained on the forest floor (ANDRESEN 2003).

### CONCLUSIONS AND FUTURE DIRECTIONS

Our review indicates that almost every arthropod group studied showed some kind of response to forest fragmentation, including altered abundances, species richness or composition when comparing fragments of different sizes, fragmented and non-fragmented areas, and/or forest edges versus interior forest. However, these changes in abundance and species richness tended to be idiosyncratic, with some groups showing predicted declines in abundance or diversity in fragments, while others showed no response or a positive one (Tab. III). Idiosyncratic responses were also seen within each group and even between closely related species. These variable responses are most likely explained by changes in the availability of resources in or around the fragments. For instance, litter production increases sharply near forest edges (VASCONCELOS & LUIZÃO 2004) and this may help to explain the increased abundance of leaf-litter invertebrates near edges (DIDHAM 1997a). On the other hand, increased tree mortality in fragments (LAURANCE *et al.* 1998) may help to explain the observed decline in the abundance and species richness of wood-nesting solitary bees (MORATO & CAMPOS 2000). Although the number of studies is still limited, there is also clear evidence that changes in the structure of arthropod assemblages have consequences on many ecological processes. One of the most notable examples is the invasion of small fragments by african honeybees (DICK 2001b), which greatly affected the floral visitors and consequently the pollination and fruit production of *D. excelsa*.

Table III. Effects of forest fragmentation (area, isolation, and/or edge effects) on the abundance, species richness and composition of different arthropod groups. (+) Increase, (-) decrease, (0) no change.

Arthropod group	Abundance	Species richness	Species composition	Effects depend on matrix type/time since isolation?
Aquatic insects	0	0	Not altered	No information
Ants in myrmecophytes	-	0	Not altered	No information
Butterflies	+/0/-	+/0/-	Altered	Yes
Drosophilids	+	0	Altered	No information
Dung beetles	-/0	-/0	Altered, at least temporarily	Yes
Male Euglossinae bees	-/+	0	Altered	Yes
Ground-dwelling ants	+/0/-	-/0	Altered	No information
Leaf-cutter ants	+	+	Altered	No information
Leaf-litter beetles	+/0	+/0	Altered	No information
Solitary bees nesting in wooden cavities	-	-	Altered	No information
Solitary wasps nesting in wooden cavities	+	-	Altered	No information
Ctenus Spiders	-/0	0	Altered, at least temporarily	Yes
Termites	No information	-	Altered	No information

However, another major conclusion we draw is that many of the observed responses to reduction in forest area of arthropods and the ecological processes in which they are involved were often transient. The most likely explanation for this is the development of a second growth forest around the fragments, which greatly increases the connectivity between the fragments and the remaining forest areas. In this sense, it is interesting to notice that most of the studies conducted in the late 1990's and early 2000's (Tab. II), when second growth forests established around the fragments were already well developed, tended to not detect differences between fragments and continuous forest (Tab. III). Even though some of the secondary vegetation surrounding the fragments has been cut and burned several times, it is clear that the degree of isolation of the BDFFP fragments declined sharply through time. Therefore, although the research conducted at the BDFFP has provided many insights into the effects of fragmentation on arthropod assemblages, little is known regarding the long term dynamics of these assemblages considering a (more realistic) scenario where fragments remain in effective isolation through time.

Our review also demonstrates that more than thirty years after the founding of the BDFFP there are still ample opportunities for novel and exciting research documenting the effects of forest fragmentation on Amazonian invertebrates. First, there remains a dearth of information on most groups of Amazonian arthropods. We were unable to find any published papers about the fauna of the canopy, where arthropods are at their highest diversity and abundance (ERWIN 1982). While the taxonomic obstacles in working with many of these groups remain substantial, DNA barcoding has emerged as a promising tool for overcoming these challenges, as demonstrated in other tropical invertebrate systems (SMITH *et al.* 2005). Genetic tools may also help address some of the hypotheses put forward by BDFFP researchers regarding the role of dispersal and matrix permeability in promoting the persistence of arthropods in fragments (BRUNA *et al.* 2011), which has consequences for the genetic structure of isolated populations.

Second, arthropods are exceptional systems with which to test hypotheses for how landscape structure, complexity, and composition influence biodiversity (reviewed in DIDHAM *et al.* 2012, TSCHARNTKE *et al.* 2012). Using arthropods to address these issues at the BDFFP, however, is complicated by the fact that this site's original design was rooted in Island Biogeography Theory. As such, it has fragments of multiple sizes but not the multiple landscape types necessary to address issues of landscape structure (the regeneration of different matrix types was the fortunate outcome of an early rainy season, BIERREGAARD & GASCON 2001). Nevertheless, it remains one of the few sites in the tropics in which there are fragments of similar size and of known history that are surrounded by different matrix types, making it a valuable reference point against which to compare results from temperate systems (KRAUSS *et al.* 2003, HAYNES & CRIST 2009). In addition, while one cannot explicitly disentangle the effects of

edge and area using the BDFFP fragments – the effects of edge and isolation are confounded – the large expanses of continuous forest in this landscape make it an invaluable location in which to document edge-related changes in arthropod abundance and diversity in the tropics. Complementing the results of such studies from the BDFFP with those from other landscape-scale experiments of habitat loss and isolation (MARGULES 1992), especially those such as the SAFE Project (EWERS *et al.* 2011) that manipulate both patch and landscape-level characteristics could greatly advance our understanding of how landscape context influences biodiversity in fragmented regions.

Finally, while ecologists have long hypothesized ecological interactions involving arthropods could be severely modified in fragmented landscapes (JANZEN 1987), research on this topic at the BDFFP remains limited. Advancing our understanding of interactions involving arthropods has implications not only for the maintenance of biodiversity in fragmented forests, but may also help elucidate broader issues regarding the evolution and ecology of tropical biodiversity (NOVOTNY *et al.* 2006, 2007).

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