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Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration

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I compared dung beetle communities and assessed some of their functional effects (dung removal, seed burial, seedling establishment) in continuous forest with those in 1-ha and 10-ha forest fragments in Central Amazonia. I followed the fate of seeds until seedling establishment for three native tree species, using clean seeds and seeds surrounded by dung. The 1-ha fragments had half the number of dung beetle species captured in continuous forest and in 10-ha fragments. The continuous forest sites and the 1-ha fragments had similar number of individuals, but in the 10-ha fragments dung beetles were twice as abundant. Mean beetle size increased with increasing forest area. Dung removal and seed burial rates were higher in continuous forest than in forest fragments. Seed predation rates were higher in the forest fragments. In all sites, the proportion of seedlings established from seeds surrounded by dung vs clean seeds was the same, and it was the same in continuous forest vs fragments. When comparing seeds that remained on the forest floor with seeds buried by dung beetles, a higher percentage of seedlings established from the latter. Conservation programs that aim to maintain the regeneration ability of forest fragments must incorporate all the important components involved in seedling establishment; in Central Amazonia these include dung beetles as secondary dispersers. It is important that studies start measuring directly not only the first-order effects of forest fragmentation on species, but also the higher-order functional effects.

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Rainforests all over the world are disappearing at an alarming rate, with net tropical deforestation exceeding 150 000 km^2 per year (Whitmore 1997). Deforestation inevitably results in fragmentation, with both constituting great threats to biodiversity (Harris 1984, Wilson 1988, Laurance and Bierregaard 1997).

Most studies on the effects of forest fragmentation have focused on direct first-order effects, i.e. fragmentation induced changes in the abundance and diversity of plant and animal populations and communities (see Laurance and Bierregaard 1997 for a review). Such studies have shown that while some species are negatively affected by fragmentation, others benefit. While it is true that reserve planning and management require detailed studies on the direct effects of fragmentation on target species and communities (Bierregaard et al. 1992), it is also necessary to adopt a more integrative approach. One alternative is to study higher-order functional responses, thus focusing on the role that the affected populations or communities play in ecosystem processes, such as pollination and seed dispersal (Didham 1997a). Although it is often stated that habitat fragmentation likely disrupts these plant-animal interactions, very few studies have actually addressed this issue (Laurance and Bierregaard 1997, Renner 1998, Debinski and Holt 2000).

The study of seed dispersal is especially relevant in rainforests, because fruit-eating animals dominate the

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vertebrate biomass in such ecosystems (Terborgh 1986) and because > 75% of tree species produce fruits that appear adapted for animal consumption (Howe 1990). A crucial aspect in understanding fruit-frugivore interactions, is the fate of seeds after deposition by the primary disperser (Chambers and MacMahon 1994). For example, seeds that are dispersed through defecation by mammals are often deposited in fecal clumps (Andresen 2000). This dung attracts dung beetles, which bury dung for feeding and/or oviposition (Halffter and Edmonds 1982). Dung beetles also bury some of the seeds present in the dung accidentally, thus acting as secondary seed dispersers (Estrada and Coates-Estrada 1991, Shepherd and Chapman 1998, Andresen 1999, Feer 1999, Vulinec 2000). Rodents are also attracted by the odor of fecal material, but unlike dung beetles they actively remove and consume seeds present in the dung and thus act primarily as seed predators (Janzen 1982, 1986, Andresen 1999). Visual or olfactory detection of seeds by rodents is affected by seed burial, and seed predation rates are substantially lower for buried seeds than for seeds exposed on the surface (Johnson and Jorgensen 1981, Crawley 1992, Andresen 1999). Consequently, seeds buried by dung beetles have a high probability of avoiding detection by rodents (Andresen 2000, 2001). Seeds that are surrounded by dung may therefore follow very different fate paths than seeds of the same species that are dispersed without fecal material (e.g., spit-out or dropped by mammals, regurgitated by birds, etc.). If we want to have a full understanding of the dispersal ecology and regeneration requirements of a plant species, we must study the factors affecting the fate of seeds after seed deposition, such as secondary dispersal by dung beetles.

It is known that the composition and/or structure of dung beetle communities in tropical forest habitats are greatly affected by the type of vegetation (Halffter et al. 1992, Escobar 2000, Davis et al. 2000, 2001, Halffter and Arellano 2002), and consequently they are very sensitive to forest disturbances such as logging (Davis 2000), forest conversion to plantations, crops and pasture (Nummelin and Hanski 1989, Halffter et al. 1992, Davis et al. 2001), and forest fragmentation (Klein 1989, Davis 1994, Estrada et al. 1999). Although it is known that in general both species richness and the abundance of individuals are diminished in forest fragments, and that fragments often have an altered species composition when compared to continuous forest (Klein 1989, Didham et al. 1998, Estrada et al. 1999), second order or functional effects of altered dung beetle communities are mostly unknown for tropical forest fragments (Didham 1996, 1997a). Only the study by Klein (1989) showed that a decrease in dung beetle densities in small forest fragments was correlated with a sharp drop in dung decomposition rates. It is important that fragmentation studies start measuring the functional effects of fragmentation directly, rather than inferring functional responses based on data of first-order effects on species richness and abundance (Didham 1996).

In this study I use an experimental approach to measure both first-order as well as functional effects of forest fragmentation. I first quantify the changes in composition and structure of dung beetle communities in forest fragments, and then I assess the changes in the role that dung beetles play as secondary seed dispersers in affecting plant regeneration. Specific questions addressed were: 1) How does fragmentation affect the dung beetle community? 2) Are dung removal and seed burial rates different between forest fragments and continuous forest? 3) How is the long-term fate of seeds, as determined by their interaction with dung beetles and seed predators, affected by forest fragmentation?

Study site and methods

Study site

This study was conducted in five forest reserves that are part of the Biological Dynamics of Forest Fragments Project (BDFFP), located 80 km north of Manaus (2°30′S, 60°W), Brazil. The continuous forest site is an 800 ha reserve (reserve #1501) which is embedded in > 10 000 ha of continuous forest. The other four reserves are isolated forest fragments located in cattle ranches known as Colosso (CO) and Porto Alegre (PA). Two of the fragments are 1 ha in area (reserves #1104 and #3114, hereafter called 1-CO and 1-PA, respectively) and the other two are 10 ha in area (reserves #1202 and #3209, hereafter called 10-CO and 10-PA, respectively).

Reserves 1-CO and 10-CO were isolated in 1980 and reserves 1-PA and 10-PA in 1983 (Lovejoy et al. 1986). The fragments are almost perfect rectangles and during the two years of my study (May 1996–May 1998), all four fragments were surrounded by pasture and/or low (2–4 m tall) secondary growth vegetation composed mostly of *Vismia* spp. (Clusiaceae) and *Cecropia* spp. (Cecropiaceae).

Dung beetle communities

To assess the effects of forest fragmentation on the dung beetle communities, I captured dung beetles three times in the 1-ha fragments (between August and November 1997), five times in the 10-ha fragments (between November 1996 and September 1997) and five times in two transects in the continuous forest area (cont-E and cont-W, 1 km apart, between November 1996 and September 1997). At least one month elapsed between trapping periods at each site. For each trapping period, beetles were captured at all sites within two months, to avoid the confounding effect of seasonality (Andresen 2000).

Six pitfall traps were used in each of the trapping periods in each site. Traps consisted of plastic containers 15 cm high and 10 cm in diameter. Each trap was filled to about two thirds of its capacity with soapy water and buried at ground level. Fifty grams of fresh howler monkey *Alouatta seniculus* (L.) dung were put inside a plastic mosquito-netting bag and suspended ca 5 cm above the center of the trap. Traps were placed along transects under intact canopy (at least 20 m away from treefall gaps), with at least 30 m between traps. The locations of the traps were the same during each trapping event. Traps were set out between 16:00 and 16:30 h and dung beetles were collected the next day between 08:00 and 08:30 h.

Voucher specimens were sent for identification to Fernando Z. Vaz-de-Mello (Univ. Federal de Viçosa).

Dung removal and seed burial by dung beetles

Experiment 1: Dung removal and seed burial by beetles in continuous forest vs forest fragments

To assess dung removal and seed burial by dung beetles I used single seeds inside 10 g howler-monkey dung piles. I used 10 g of dung because this is a representative dung-pile size for several Neotropical frugivores (Estrada et al. 1993, Andresen 1999, 2000). To be able to find seeds buried by dung beetles, a 50 cm long white nylon thread was glued to each seed. The other end of the thread was loose, and when a seed was buried by a beetle this end of the thread protruded out of the ground. I used seeds of three tree species: *Pourouma guianensis* Aubl., Moraceae (seed length: 11 ± 0.8 mm, n = 10; here and elsewhere I report means ± one standard error), *Micropholis guyanensis* (A.DC.), Sapotaceae (length: 18 ± 0.3 mm, n = 10), and *Pouteria durlandii* (Standl.) Baehni, Sapotaceae (length: 27 ± 0.7 mm, n = 10). Hereafter species will be referred to by their generic name only. *Micropholis* was only used in the continuous forest and the two 10-ha fragments.

Dung piles with seeds were placed on the forest floor along transects between 15:00 and 18:00 h, one pile every 10 m. Transects varied in length (100–300 m) according to the site (continuous forest or fragment), and according to the amount of dung and number of seeds available on a given day. The numbers of seed-containing dung piles used for each species in each site are given in Fig. 3.

I checked seed-containing dung piles after one day, recording dung removal (all dung removed vs some dung remaining) and seed burial (seed buried vs seed on the surface). Seeds placed without dung were never found buried, thus I assumed that seeds with dung that were found buried, had been buried by dung beetles, and not by rodents. Furthermore, most buried seeds were never moved large horizontal distances, which further argues against burial by rodents. Finally, in an experiment conducted with plastic beads instead of seeds (Andresen 2000, 2002), in which all bead burial can consequently be safely assumed to have been done by beetles, beads were buried in exactly the same pattern as were experimental seeds in this study.

Buried seeds were dug out and burial depth was measured to the nearest 1 cm. Seeds that were not found, were not included in analyses (ca 5% of all seeds placed on the ground). Similarly, seeds in dung piles from which not all the dung had been removed were excluded from analyses, because such seeds could have been buried by beetles during the following days (unpubl.).

Experiment 2: Exclusion of large beetles in continuous forest

Because dung beetles in forest fragments have been reported to be of smaller sizes than beetles in continuous forest (Klein 1989, this study), and because beetle size is important in determining whether a seed is buried (Feer 1999, Andresen 2000), I hypothesized that if seeds were buried less often in fragments than in continuous forest, beetle size would be a causal factor involved in producing this pattern. To test this idea I manipulated the dung beetle community in continuous forest by excluding large beetles so as to mimic the dung beetle community in forest fragments.

Dung piles (10 g) containing experimental seeds of three species (see below) were set out on the forest floor along transects, one pile every 10 m. I used two treatments: exclusion of large beetles and no exclusion. Treatments were alternated along transects, and each treatment was replicated 6 times in each transect. Six transects were used for each species, yielding a total sample size of 36 for each species.

To exclude large beetles I placed a tray 30 cm long, 20 cm wide and 10 cm tall, upside down, above the seed-containing dung pile. The trays consisted of hard plastic mesh with mesh openings of 12 mm (to exclude the largest beetles, which are the most important for dispersal of seeds > 5 mm, Andresen 2000). For the treatment without exclusion I put a 4 cm high plastic "fence", with the same length and width dimensions as the exclusion tray, around the dung pile. This prevented dung beetles from taking seeds outside this area, but still allowed them full access to dung piles.

I used seeds of the following tree species: *Helicostylis scabra* (J. F. Macbr.) C. C. Berg, Moraceae (length: 5 ± 0.2 mm, n = 10), *Pourouma*, and *Pouteria*. I placed seeds of a single species in each dung pile, using 8 seeds in the case of *Helicostylis*, 4 seeds for *Pourouma* and 2 seeds for *Pouteria* (about the same "seed volume" was present in each dung pile). I checked each location after two days and counted the seeds remaining on the surface.

Long-term seed fates

I followed the fate of seeds in forest fragments and continuous forest to determine whether the effects of forest fragmentation on dung beetle community composition and activity were correlated with differences in seed fate. I used two treatments: clean seeds and seeds inside 10 g dung piles. The no-dung treatment simulated seeds that have been spit out or dropped by mammals or regurgitated by birds. I used the same seed species as in Experiment 1. I used *Micropholis* in continuous forests and 10-ha fragments, but not in 1-ha fragments due to lack of seeds.

I followed the same experimental setup as in Experiment 1, except that buried seeds were not removed from the ground. Seeds were checked after one day and then once a month until seed predation/removal, or seedling establishment. For each seed I recorded fate (seed alive, seed preyed upon/removed, seedling), location (buried or on the surface), and whether all dung had been removed after one day. When seeds had been moved from the original location, an effort was made to find the seed and/or thread; an area of ca 5 m around the location was searched. Of the seeds moved by rodents and found, in this experiment as well as others (Andresen 2000, 2001), all were either found preyed or hidden in a place unfavourable for seedling establishment (inside a hollow log, or deep rodent hole). Thus, seeds that were not found were assumed to have been removed by rodents and to be dead. It is important to keep in mind, however, that some of the removed seeds could have been scatterhoarded by rodents in sites suitable for germination and seedling establishment (Forget et al. 1998).

Statistical analyses

Data were analyzed through generalized linear models (GLMs), using the GLIM statistical package (Francis et al. 1993). In GLMs the deviance is a measure of the discrepancy between the observed data and the fitted values, thus, the significance of each term in a model can be tested through the deviance that the removal of the term adds to the model (Crawley 1993). For the response variables consisting of counts (number of dung beetle individuals and number of dung beetle species), the error structure was defined as having a Poisson distribution, the log link function was used, and the χ^2 statistic was used to test for significant changes in deviance (Crawley 1993). When the response variable was a proportion (proportion of dung piles with some dung remaining after 24 h, proportion of seeds buried by dung beetles, proportion of seeds establishing as seedlings, and proportion of seeds preyed), the binomial error structure and logit link function were used. When the residual term of the models with either Poisson or binomial error was inflated due to overdispersion, the data were rescaled as indicated in Crawley (1993), making the tests more conservative. After rescaling a model with binomial error structure the F statistic rather than the χ^2 statistic was used for testing the significance of changes in deviance (Crawley 1993). For the continuous response variable (mean beetle size) the error structure was defined as normal, the identity link was used, and the F statistic was used to test for significant changes in deviance. Beetle size was ln-transformed to obtain constant variance (Crawley 1993, Sokal and Rohlf 1995).

When post-hoc tests were necessary to compare pairs of treatment levels, the differences between parameter estimates, calculated based on the minimal adequate model, were divided by their corresponding standard errorr, to yield t-statistics (Crawley 1993). Data on burial depths were analyzed with a Kruskal-Wallis test.

For the analyses on number of individuals, number of species, mean beetle size, proportion of dung piles with dung remaining after 24 h, and proportion of seeds buried, a nested design was used, with area (continuous forest, 1 ha, 10 ha) being the main factor, and individual sites (two for each area treatment) nested within the main factor. For the analyses on proportion of seeds establishing as seedlings and the proportion of seeds preyed, a nested design was used, with area as the main factor, the dung treatment (seeds with dung vs seeds without dung) nested within area, and the burial treatment (seeds buried vs not buried by dung beetles) nested within the dung treatment.

Because I collected data in two 1-ha fragments, two 10-ha fragments and one continuous forest area (with two independent transects, in the case of dung beetle captures), I did not use sites as individual samples. Rather I used individual samples within sites (e.g., five dung beetle trapping periods in 10-CO) as replicates for statistical analyses. This would result in pseudoreplication if I generalized my results to "all" continuous forests vs 1-ha fragments vs 10-ha fragments. To avoid this artifact, my results will only apply to the sites I studied and the conclusions I reach will only be valid for them, and any generalization should be done keeping this limitation in mind.

Results

Dung beetle communities

A total of 14 608 beetles were captured (3549 in the continuous forest, 8515 in the 10-ha fragments, and 2544 in the 1-ha fragments), representing 58 species. Of all species, four were captured in the 10-ha fragments but not in the continuous forest, and five were found in the continuous forest but not in the 10-ha fragments. However, most of these species were represented by just

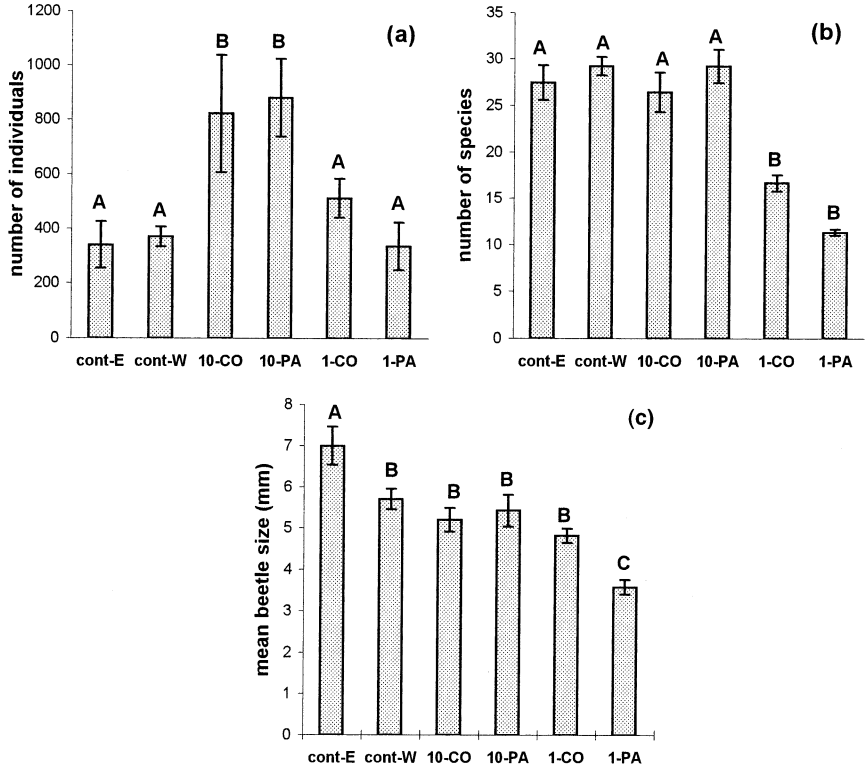

Fig. 1. Mean number of individuals (a), mean number of species (b), and mean beetle size (c), of beetles captured in continuous forest (cont-E and cont-W), 10-ha forest fragments (10-CO and 10-PA) and 1-ha forest fragments (1-CO and 1-PA). Sample sizes are five trapping periods for continuous forest and 10-ha sites, and three trapping periods for 1-ha sites (in each period data of the six traps were pooled). Error bars represent ± 1 standard error. Matching letters above bars identify statistically homogeneous samples ($p > 0.05$).

a few individuals. In the 1-ha fragments I captured only 28 of the 58 species (Appendix 1).

In terms of mean number of beetles per trapping period, there was a significant effect of area ($\chi^2 = 20.9$, $DF = 2$, $p < 0.001$), but no effect of sites ($\chi^2 = 1.1$, $DF = 3$, $p > 0.05$). The same number was captured in 1-ha fragments and in continuous forest sites. However, in the 10-ha forest fragments, dung beetles were about twice as abundant as in the continuous forest, or as in the 1-ha fragments (Fig. 1a).

In terms of mean number of species captured, there was again a significant effect of area ($\chi^2 = 41.8$, $DF = 2$, $p < 0.001$), but no effect of sites ($\chi^2 = 4.1$, $DF = 3$, $p > 0.05$). The same number of species was captured in continuous forest and 10-ha fragments, but was reduced by half in the 1-ha fragments (Fig. 1b).

Mean beetle size varied significantly with both area ($F_{2,23} = 14.0$, $p < 0.001$) and sites ($F_{3,20} = 5.3$, $p < 0.05$). In general, the mean size of beetles declined with decreasing area (Fig. 1c).

Dung removal and seed burial by dung beetles

Experiment 1: Dung removal and seed burial by dung beetles in continuous forest vs forest fragments

Dung removal rates decreased with decreasing area (Fig. 2). After 24 h, 10% and 14% of dung piles in continuous forest and 10-ha fragments, respectively, had some dung remaining, while 45% of dung piles in 1-ha fragments had some dung ($\chi^2 = 322.9$, $DF = 2$, $p < 0.001$; post-hoc pair-wise comparisons: continuous vs 10 ha: $t = 3.2$, $DF = 8$ $p < 0.05$; continuous vs 1 ha: $t = 12.7$, $DF = 6$ $p < 0.001$; 10 ha vs 1 ha, $t = 4.2$, $DF = 6$, $p < 0.01$). Significant variation was observed among sites within area treatments ($\chi^2 = 91.5$, $DF = 2$, $p < 0.001$).

The percentage of seeds buried by beetles was higher in continuous forest than in fragments (Fig. 3). This effect was statistically significant for *Pouteria* ($\chi^2 =$

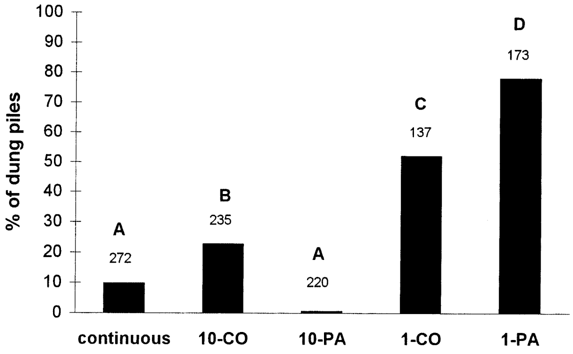

Fig. 2. Percentage of dung piles with some dung remaining after 24 h. Matching letters above bars identify statistically homogeneous samples ($p > 0.05$). Numbers of dung piles used are given above each bar. Site abbreviations are defined in Fig. 1.

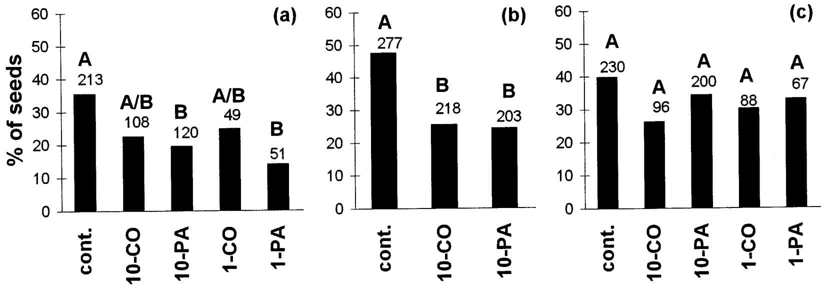

Fig. 3. Percentage of seeds of *Pouteria* (a), *Micropholis* (b) and *Pourouma* (c) buried by dung beetles in continuous forest and forest fragments. Matching letters above bars identify statistically homogeneous samples ($p > 0.05$). Numbers of seeds are given above each bar. Site abbreviations are defined in Fig. 1.

13.1, $DF = 2$, $p < 0.01$) and *Micropholis* ($\chi^2 = 37.9$, $DF = 1$, $p < 0.001$), but only suggestive of significance for *Pourouma* ($\chi^2 = 4.7$, $DF = 2$, $p = 0.15$). Regarding burial depths, a trend existed in which seeds were buried deeper in the continuous forest than in forest fragments. However, the differences were statistically significant only for *Micropholis* in the comparison between the continuous forest (median depth: 5 cm) and the Colosso 10-ha fragment (median depth: 2 cm; Kruskal-Wallis = 9.13, $p = 0.01$, adjusted post-hoc pairwise comparisons: continuous vs 10-CO, $p < 0.05$, continuous vs 10-PA, $p > 0.05$, 10-CO vs 10-PA, $p > 0.05$).

Experiment 2: Exclusion of large beetles in continuous forest

For the three plant species 13–19% fewer seeds were buried when large beetles were excluded. This effect was statistically significant for *Pouteria* ($\chi^2 = 9.0$, $DF = 1$, $p < 0.01$), suggestive of significance for *Helicostylis* ($F_{1,70} = 4.4$, $0.05 < p < 0.1$) and not significant for *Pourouma* ($F_{1,70} = 2.7$, $p > 0.05$).

Long-term seed fates

In terms of seedling establishment there was neither an effect of area treatment (continuous forest vs fragments) nor of dung treatment (seeds with vs without dung) for any of the three seed species (Area: *Micropholis*, $\chi^2 = 0.215$, $DF = 1$, $p > 0.05$; *Pouteria*, $\chi^2 = 3.51$, $DF = 2$, $p > 0.05$; *Pourouma*, $F_{2,3} = 2.0$, $p > 0.05$; Dung: *Micropholis*, $\chi^2 = 0.191$, $DF = 2$, $p > 0.05$; *Pouteria*, $\chi^2 = 3.14$, $DF = 3$, $p > 0.05$; *Pourouma*, $F_{3,3} = 0.694$, $p > 0.05$). However, the effect of burial treatment (seed buried vs not buried by dung beetles) was significant for *Micropholis* ($\chi^2 = 10.67$, $DF = 2$, $p < 0.01$) and *Pouteria* ($\chi^2 = 28.54$, $DF = 3$, $p < 0.001$): a higher proportion of seedlings established from buried seeds, than from seeds that remained on the surface (Fig. 4). For *Pourouma* seeds the effect of burial treatment showed the same trend, but was not significant ($F_{3,6} = 0.750$, $p > 0.05$).

When sites were compared in terms of the proportions of seeds preyed (all seeds pooled), a significantly lower percentage of seed predation was found in the continuous forest than in the fragments (all fragments pooled) for the three species (*Micropholis*: $\chi^2 = 14.96$, $DF = 1$, $p < 0.01$; *Pouteria*: $\chi^2 = 49.84$, $DF = 2$, $p < 0.01$; *Pourouma*: $\chi^2 = 8.67$, $DF = 2$, $p = 0.01$).

Discussion

Dung beetle communities, dung removal and seed burial

The same number of dung beetle species was captured in 10-ha fragments and continuous forest, but only half that number was captured in 1-ha fragments. Mean size of beetles increased with increasing forest area. The same number of individuals was captured in 1-ha fragments and continuous forest, but more than twice that amount was captured in 10-ha fragments. These results are only partially in accord with the study conducted by Klein (1989) in the same study area. In the continuous forest, Klein captured more species, more individuals, and larger beetles than in both 10-ha and 1-ha fragments. The differences from the present study could partly be due to Klein's method of analysis, in which he pooled beetles captured with carrion and beetles captured with dung. Furthermore, Klein captured beetles at each site only once (a 4-d sampling period), making his sampling method susceptible to temporal and spatial fluctuations of the dung beetle assemblage (Andresen 2000). Finally, when Klein conducted his study the fragments had been isolated for 2–6 yr, while during my study, fragments had been isolated for 13–18 yr. It is probable that with time more beetle species disappeared from the 1-ha fragments due to diminishing dung availability, while the numbers of individuals started increasing in the 10-ha fragments due to increased dung availability per unit area (see below). This would be consistent with the emerging realization that biotic and abiotic conditions in forest fragments exhibit much temporal variation (Didham 1997b, Kapos et al. 1997, Restrepo et al. 1999).

But why is the abundance of dung beetles in 10-ha fragments so high? The composition and structure of dung beetle communities is highly correlated with the availability of fresh dung (Hanski and Cambefort

1991). In several Neotropical forests, it has been proposed that dung beetle communities are largely supported by howler monkey dung (Howden and Young 1981, Peck and Forsyth 1982, Gill 1991). Howler monkeys are able to survive in 10-ha fragments in Central Amazonia (Rylands and Keuroghlian 1988). However, the home range of a howler monkey troop in the continuous forest is ca 30 ha (Neves and Rylands 1991). Since the size of monkey troops is similar in fragments and continuous forest (personal observation), a monkey troop confined to a 10-ha fragment represents a much higher monkey density, and consequently higher dung availability per unit of area, than a troop in continuous forest.

The rate of dung removal in the present study was similar in continuous forest sites and in 10-ha fragments, but was significantly lower in 1-ha fragments. These results coincide with Klein's findings for the study area in 1986 (Klein 1989). The fact that dung removal was similar in continuous forest and 10-ha fragments, regardless of the much higher number of beetles captured in 10-ha fragments, could be a consequence of the time elapsed before assessing dung removal. It is possible that if dung removal rates were measured after shorter periods of time (e.g., 6 h instead of 24 h), a faster removal rate would be detected in the 10-ha fragments.

Alternatively, it could be that the larger mean size of beetles in continuous forest is responsible for a removal rate similar to that of the 10-ha fragments. Both amount of dung consumed and dung-burial rate are positively correlated with dung beetle size (Lee and Peng 1981, Doube 1990). Small mean beetle size is most likely also responsible for the low dung removal in 1-ha fragments, even though the number of beetles captured was similar to the number captured in continuous forest.

Larger dung beetles also bury more of the seeds present in dung than do smaller beetles (Feer 1999, Andresen 2000). The importance of large beetles in secondary seed dispersal, particularly of large seeds, was confirmed by the results of Experiment 2, in which lower proportions of *Pouteria* seeds were buried when large beetles were excluded in the continuous forest. Similarly, fewer seeds of the two larger species (*Micropholis* and *Pouteria*) were buried in the fragments, where beetles are of mean smaller size, than in continuous forest. This again stresses the particularly important role of large beetles as secondary dispersers of large seeds.

In terms of burial depth, the data show a tendency towards shallower depths in forest fragments than in continuous forest. However, most of the differences were not significant, due to small sample sizes and large variation. Burial depth is an important factor in determining seed fate. While seed detection by rodents decreases with increasing depth (Estrada and Coates-Estrada 1991, Shepherd and Chapman 1998, Andresen 1999, Feer 1999), non-emergence of germinating seeds increases with increasing depth (Shepherd and Chapman 1998, Feer 1999, Andresen 2000, 2001). It would be relevant to conduct additional experiments to test whether differences in burial depth between continuous forest and forest fragments are biologically important.

Long-term seed fates

Predation on *Micropholis*, *Pourouma*, and *Pouteria* seeds was higher in forest fragments than in continuous forest. This result is consistent with Malcolm's (1997) findings for the BDFFP reserves of increased rodent populations in forest fragments compared to continuous forest. Other studies have also reported increased densities of rodents and other kinds of seed predators (e.g., insects, granivorous birds) in forest fragments and/or around forest edges (Laurance 1997, Pizo 1997).

For the three seed species studied, and in all sites, the proportion of seedlings establishing from seeds with dung and from seeds without dung was the same. This is consistent with the result found in a similar study

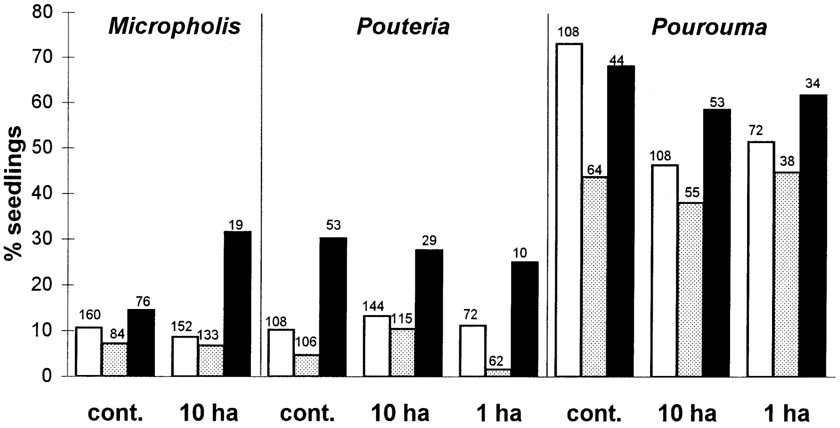

Fig. 4. Percentage of seedlings of three species establishing from seeds without dung (white bars), seeds placed with dung but not buried by beetles (gray bars) and seeds placed with dung and buried by beetles (black bars), in continuous forest (cont.), 10-ha fragments and 1-ha fragments. Numbers of seeds are given above each bar.

conducted with eight additional seed species in continuous forest (Andresen 2000), and indicates that the long-term fates of seeds dispersed through defecation by mammals will be the same as those of seeds dispersed through other means (e.g., regurgitated by birds).

However, when comparing seeds that remained on the forest floor (either with or without dung) with seeds buried by dung beetles, a higher percentage of *Micropholis* and *Pouteria* seedlings established from buried seeds than from surface seeds. This is consistent with the results of an experiment conducted in continuous forest with eight additional seed species (Andresen 2000). Also, at least for *Micropholis* seeds, the advantage of buried vs surface seeds was much more pronounced in the forest fragments than in the continuous forest (Fig. 4). This is probably due to the higher seed predation observed in the fragments. In addition, microclimatic conditions are often altered in forest fragments, fluctuating more than in the continuous forest (Kapos et al. 1997). Reduced germination for surface seeds, independently of predation, has been observed for seeds in fragments vs continuous forest (Bruna 1999). Consequently, buried seeds in fragments may encounter a much more homogeneous environment than surface seeds, relative to seeds buried in continuous forest.

Finally, it is important to note that while it is possible to generalize these results to some extent, the degree to which seed burial by dung beetles is advantageous for seed survival and seedling establishment, may greatly vary with seed species (Andresen 2000). For example, in this study, seeds of *Micropholis* and *Pouteria*, seemed to benefit more from seed burial than, *Pourouma* seeds. This was due to the former species suffering higher predation rates, either due to their larger size, or because they are exposed longer periods of time to seed predators, due to their longer germination times. Also, *Micropholis* and *Pouteria* seeds might benefit more than other seed species from burial by dung beetles as it allows them to avoid seed desiccation, and it has been shown that seed viability of some Sapotaceae species is very sensitive to water loss (Benítez-Malvido 1995).

Concluding remarks

In many regions the most important source of food for dung beetles is the dung of mammalian herbivores (Hanski 1991). In forest fragments ≤10-ha in Central Amazonia all large mammals, except howler monkeys, typically disappear (Rylands and Keuroghlian 1988, Schwarzkopf and Rylands 1989), and consequently the availability of dung may be greatly altered (Klein 1989). However, in several Neotropical sites, it has been argued that dung beetle communities are largely supported by howler monkey dung (Howden and Young 1981, Peck and Forsyth 1982, Gill 1991). In Mexico, researchers found that the number and biomass of beetles captured in forest fragments was positively related to howler monkey densities in those fragments (Estrada et al. 1999). Also, howler monkeys are probably one of the main seed dispersers in many forest fragments in Central Amazonia (Neves and Rylands 1991) as well as in other Neotropical forests (Galetti et al. 1994, Ferrari and Diego 1995, Estrada and Coates-Estrada 1996). Therefore, howler monkeys in forest fragments are both acting as seed dispersers and they are helping to maintain a healthy dung beetle community. A healthy dung beetle community will in turn play an important role in secondary seed dispersal, as well as provide other ecosystem services such as facilitating soil aeration, speeding up nutrient cycling, promoting mycorrhizal associations, and reducing parasite populations (Klein 1989, Mittal 1993, Hill 1995, Vulinec 2000).

The threat of having forests in which ecological processes are not functioning normally, and which are likely to change drastically in the composition of their communities on the long-term, might be overlooked by studies that focus on the effects of fragmentation on a single species or group of species. Although it has been argued that studies on higher-order interactions are extremely demanding and have a low probability of success (Harrington et al. 1997), it is necessary to start linking focal species to others with which they interact, and to ecosystem processes in which they are involved (Didham 1996, Turner 1996, Didham 1997a, Laurance and Bierregaard 1997, Debinski and Holt 2000).

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Appendix 1. Total number of dung beetles captured in five trapping periods in continuous forest sites (cont-E and cont-W), in five trapping periods in 10-ha forest fragments (10-CO and 10-PA), and in three trapping periods in 1-ha forest fragments (1-CO and 1-PA). Mean body length of dung beetle species, standard error, and number of beetles used to calculate mean body length (N) are also given.

Species	Body length (mm)			# individuals captured					
	mean	SE	N	cont-E	cont-W	10-CO	10-PA	1-CO	1-PA
Aphodius sp. 1	3.5	0.13	8	37	65	52	151	2	7
Aphodius sp. 2	2.4	0.12	7	35	56	114	137	117	4
Ateuchus sp. 2	4.3	0.12	9	221	347	707	733	83	32
Ateuchus sp. 3	2.9	0.11	5	9	24	24	28	1	2
Ateuchus sp. 4	4.4	0.08	6	9	0	1	1	0	0
Ateuchus sp. 5	6.5	0.10	10	16	33	12	18	3	0
Ateuchus sp. 6	6.7	0.09	8	41	40	14	212	7	6
Ateuchus sp. 7	4.4	0.10	6	12	3	0	12	0	0
Canthidium sp. 1	3.2	0.06	10	4	38	31	30	8	1
Canthidium sp. 2	6.4	0.24	8	1	1	1	1	0	0
Canthidium sp. 3	3.6	0.08	6	2	5	0	0	0	0
Canthidium sp. 4	4.6	0.11	6	142	290	793	589	57	1
Canthidium sp. 5	3.4	0.10	7	0	1	1	0	0	0
Canthidium sp. 6	5.5	0.14	10	1	0	0	0	0	0
Canthidium sp. 7	4.8	0.12	10	157	88	298	187	63	50
Canthidhtm sp. 8	7.4	0.26	10	48	73	63	109	3	42
Canthidium sp. 9	7.7	0.22	9	4	9	6	11	0	1
Canthon sordidum (Har.)	6.2	0.14	10	0	2	1	23	0	0
Canthon sp. 2	5.1	0.15	9	1	3	12	3	0	0
Canthon sp. 3	6.6	0.19	10	0	2	2	6	0	0
Canthon triangularis (Drury)	9.5	0.21	10	34	6	215	59	4	8
Coprophanaeus lancifer (L.)	38.4	0.91	10	0	1	2	2	1	0
Coprophanaeus sp. 1	30.8		1	0	0	1	0	0	0
Cryptocanthon peckorum (Howden)	2.3	0.10	5	0	9	1	0	0	0

Appendix 1. (Continued).

Species	Body length (mm)			# individuals captured					
	mean	SE	N	cont-E	cont-W	10-CO	10-PA	1-CO	1-PA
Deltochilum carinatum Westwood	7.7	0.15	9	0	3	9	25	4	0
Deltochilum guyanensis Paulian	12.4	0.19	10	18	23	0	2	1	0
Deltochilum orbiculare Lansberge	24.8	0.61	10	19	6	0	4	0	0
Deltochilum pseudoicarus Balthasar	24.3	0.55	9	4	2	1	1	0	0
Dichotomius boreus (Oliv.)	24.7	0.50	10	72	43	18	85	3	6
Diehotomius lucasi (Luederwaldt)	12.1	0.24	9	126	78	8	35	1	1
Dichotomius sp. 1	16.1	0.34	7	12	10	20	28	0	0
Dichotomius sp. 2	15.3	0.24	8	15	8	32	17	1	0
Dichotomius subaeneus (Laporte)	16.6	0.50	10	9	15	41	47	4	0
Eurysternus caribaeus (Herbst)	14.1	0.44	10	32	26	6	44	4	0
Eurysternus hirtellus Dalman	6.1	0.29	10	1	4	0	8	2	0
Eurysternus velutinus Bates	16.9	0.30	10	6	14	2	5	0	0
Neocanthidium atricolle (Preudh.)	8.9	0.30	10	2	1	1	0	0	0
Neocanthidium auricolle (Har.)	8.1	0.17	10	3	0	0	1	0	0
Ontherus carinifrons Luederwaldt	12.4	0.45	10	1	1	6	0	0	0
Onthophagus bidentatus Drapiez	5.3	0.20	10	29	78	925	827	974	97
Onthophagus sp. 2	5.0		1	0	0	15	0	0	0
Oxysternon durantoni Arnaud	14.6	0.35	8	6	2	1	0	0	0
Oxysternon prox. *silenum*	15.2	0.45	10	3	0	3	1	0	0
Phanaeus chalcomelas Perty	13.5	0.27	8	1	0	1	4	0	0
Scybalocanthon pygidialis (Schmidt)	8.4	0.11	10	33	15	25	13	0	0
Uroxys pigmaeus Har.	2.7	0.10	10	507	392	568	908	179	746
sp. CC	2.5		1	0	0	0	1	0	0
sp. DD	10.2	0.21	5	0	1	2	11	3	0
sp. FF	14.3	0.39	6	5	1	0	0	0	0
sp. GG	6.3	0.12	10	1	4	0	0	0	1
sp. H	3.5	0.32	4	1	3	12	3	0	0
sp. HH	4.3	0.10	2	0	0	0	1	0	0
sp. JJ	9.8		1	0	1	0	0	0	0
sp.O	2.0		1	3	3	0	0	0	0
sp. P	1.6	0.10	2	3	12	22	1	2	2
sp. R	6.2	0.22	6	0	1	1	1	0	0
sp. W	2.7	0.10	10	12	6	30	8	2	1
sp. Y	1.5		1	0	2	13	9	7	0
Total				1698	1851	4113	4402	1536	1008