RAPID RECOVERY OF DUNG BEETLE COMMUNITIES FOLLOWING HABITAT FRAGMENTATION IN CENTRAL AMAZONIA

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Abstract. Few studies have directly assessed how rapidly functionally important insect communities recover following rain forest loss and fragmentation. In 1986, B. Klein compared the dung and carrion beetle assemblages of clearcuts, fragmented, and non-fragmented forests in central Amazonia, reporting drastic short-term changes in community composition. Fifteen years later, we resampled the same sites using identical techniques and found that, with the regrowth of secondary vegetation between forest fragments, the initial differences had largely disappeared. As the secondary vegetation itself supports dung beetle assemblages similar to those of continuous forest, we conclude that, from the perspective of the dung beetles, the experimentally fragmented area had returned to a continuous state within approximately one decade. These results offer some good news for the conservation of tropical ecosystems, since they suggest that conditions favorable for functionally important arthropods may be quickly restored by secondary regrowth. They also suggest that the preservation of forest fragments and secondary vegetation may provide an important complement to the conservation of intact mature forest.

Key words: Amazonas; Brazil; dung beetle; forest fragmentation; matrix habitat; rain forest; recovery; secondary vegetation.

INTRODUCTION

Around the world, human activities are shredding the original forest cover into smaller fragments of variable size. Insects are demonstrably susceptible to the adverse effects of deforestation and forest fragmentation (Aizen and Feinsinger 1994, Didham et al. 1996, Didham 1997, Andresen 2003). As these organisms maintain many important ecosystem processes, such as pollination, seed dispersal, and nutrient recycling, the changes ultimately imperil ecosystem functioning (Didham et al. 1996). Insects also form integral parts of many food webs, and the effects of their loss may cascade through larger communities, causing unexpected changes at higher and lower trophic levels (Terborgh 1976, Gibbs and Santon 2001, Koh et al. 2004).

While it is now beyond any doubt that habitat modification and fragmentation may induce short-term changes in the abundance and distribution of many insect groups (Lovejoy et al. 1986, Powell and Powell 1987, Didham et al. 1996, 1998, Didham 1997), the duration of such changes has been much less explored. Of particular interest is the rapidity with which functionally important insect groups recover after disturbance. As mature forests are cleared throughout the tropics, much of the deforested land is later abandoned and allowed to regrow (Nepstad et al. 1991). Hence, to conserve local biodiversity, the protection of forest fragments and secondary vegetation may offer an important complement to reserves established in the few remaining tracts of continuous mature forest (Vandermeer and Perfecto 1997, Gascon et al. 1999, Dunn 2004). Nevertheless, the effectiveness of this approach will depend on the rate at which animal communities recover after disturbance. If it is rapid, the conservation of fragments and secondary vegetation provides an effective investment. If it is slow, the conservation of mature forest remains the only tenable alternative.

Yet, few earlier studies have rigorously assessed the rate at which insect communities recover following rain forest fragmentation. In a recent review of the literature on faunal recovery with tropical forest regeneration, Dunn (2004) predicted that the complete recovery of species richness in an important insect group—the ants—would typically take approximately 40 years after deforestation and the recovery of species composition “substantially longer.” These rates would then be comparable to those observed in birds (Dunn 2004) and plants (Uhl et al. 1988, Guariguata and Ostertag...
published data sets on the recovery of insects, and the literature turned out to suffer both from a general lack of accurate sampling design and from a taxonomic bias. In fact, half of the studies were unreplicated, and 11 of the 17 data sets on insects concerned ants. Hence, there is clearly an urgent need for rigorously designed studies addressing the rate of recovery in less known but functionally important taxa.

This study builds on the sampling and resampling of dung beetle communities at a replicate set of sites. Dung beetles are functionally important taxa playing a crucial role in tropical and subtropical forests by recycling nutrients (Halffter and Matthews 1966, Mittal 1993, Estrada et al. 1998), aerating soil (Mittal 1993), controlling vertebrate parasites (Fincher 1973, Bryan 1976), and dispersing seeds (as recently reviewed by Andresen and Feer [2005]). In some instances, dung beetles may even act as plant pollinators (Sakai and Inoue 1999).

The first sampling was conducted by Bert Klein in 1986. In his comparison of dung beetle assemblages between three experimentally isolated 1-ha forest fragments, three 10-ha fragments, and three continuous forest areas, Klein (1989) found that forest fragments had fewer and smaller beetle species and lower population densities than intact forest. These differences were clearly reflected in ecosystem functioning: dung decomposed at a slower rate in 1-ha fragments than in larger forest tracts.

The second sampling was conducted by Ellen Andresen in 1996–1997. Andresen (2003) focused on two of Klein’s (1989) original forest fragments (a 1-ha and a 10-ha fragment), two additional forest fragments, and two sites in continuous forest. At this stage, despite some general differences in sampling techniques, Andresen could still discern differences in the species richness, general abundance, and size of dung beetles among forest fragments of different size, 10 years after Klein’s (1989) initial study was conducted. In addition, she also detected another consequence of forest fragmentation on ecosystem functioning: dung beetles were quicker to bury seeds in continuous forest than in forest fragments, with potential implications for plant regeneration.

The third sampling was conducted by ourselves in 2000, 15 years after Klein performed his original study and three years after Andresen revisited the sites. We used Klein’s original methods to sample the local dung beetle communities and assessed the changes that had taken place in intervening years. More specifically, we asked: (1) How has the relative abundance of individual species within forest fragments changed over time? (2) How have the beetle assemblages of the matrix habitat between the fragments changed over time? (3) Can the structure of beetle assemblages supported by small forest fragments still be distinguished from that of the matrix and that of the continuous forests?

**METHODS**

**Study area**

Our study was conducted 80 km north of Manaus, Brazil, at the site of the Biological Dynamics of Forest Fragments Project (BDFPP, formerly the Minimum Critical Size of Ecosystems Project; Lovejoy et al. 1986, Bierregaard et al. 1992, Bierregaard and Gascon 2001). This system is one of a very few tropical sites where habitat fragmentation has been experimentally induced: the fragments were created by scheduled logging in 1979–1990 (Bierregaard et al. 1992). Subsequently, the management of the vegetation surrounding the forest fragments has varied substantially in both time and space, with secondary vegetation repeatedly invading the clear-cut areas, only to be cut back and abandoned again. Given the exceptional knowledge about both the dung beetle fauna and fragmentation history of these Brazilian sites, the system offers a unique opportunity to assess the manner in which the assemblage structure develops through time after experimental disturbance.

**Sampling sites**

At each of three different sites (Cidade Powell, Colosso, and Dimona), four habitats were sampled: a 1-ha forest fragment, a 10-ha forest fragment, the matrix habitat between the fragments, and a continuous forest tract (for a map, see Klein [1989]). General conditions at the study site as well as details of each forest fragment are described by Klein (1989), Lovejoy et al. (1986), and Bierregaard et al. (1992). More recently, it has been shown that the sizes of the forest fragments slightly differ from their nominal values, with the true size of 1-ha fragments ranging from 1.56 to 2.8 ha and that of 10-ha fragments ranging from 10.7 to 13 ha (M. Santamaría-Gomez, personal communication).

**Successional change**

The forest fragments were originally created by scheduled logging in 1980 (Colosso), 1983 (Cidade Powell), and 1984 (Dimona). However, the vegetation around fragments rapidly regenerates (Bierregaard et al. 1992, 2001), and when Klein sampled the sites in 1986, scattered secondary vegetation had begun to appear. At Cidade Powell, the forest canopy had already closed at a height of 2.5 m. In 1997–1998, when Andresen (2003) resampled the two sites at Colosso, the vegetation at this site had recently been burnt and cleared (in 1994–1995), and the fragments were surrounded by pasture and/or low (2–4 m) secondary growth composed mostly of *Vismia* spp. (Clusiaceae) and *Cecropia* spp. (Cecropiaceae; Andresen 2003). When we returned to the sites in 2000, successional change had progressed substantially at all sites. At Cidade Powell, the vegetation between the forest fragments had not been cleared in the intervening years and now formed a tall (25 m) closed-canopy forest.
dominated by *Cecropia*. At Dimona and Colosso, the matrix habitat had been cut and burned at intervals of 2–10 yr. At Dimona, the secondary vegetation had now reached an age of 10 yr and was relatively tall (20 m) and dominated by *Cecropia*; at Colosso, the vegetation was younger (ca. 5 yr), lower (5–6 m), and dominated by *Vismia* sp.

**Data collection**

When resampling the sites in 2000, we took every effort to repeat the original methods of Klein (1989). In brief, the sampling was conducted during the dry season, between June and July 2000 (compared to May–July in 1986). Each individual sample was based on a transect of six pitfall traps (14 cm in diameter × 5 cm in depth) spaced 17 m apart and alternately baited with human dung and decaying beef. The traps were run for 4 d, with the baits replaced every 24 h and the beetles collected every 48 h. All transects in continuous forest were placed at least 350 m from the nearest forest edge. The exact trapping locations were selected based on the maps of Klein (1989), with the aid of experienced field assistants who knew the original sites. To minimize sampling error and obtain as good coverage of local dung beetle assemblages as possible in 2000, we repeated the complete sampling program of Klein three times, trapping each site during each of three consecutive sampling rounds. Hence, the number of trap days per site was three times higher in 2000 than in 1986.

In sampling the matrix habitat between forest fragments, we adhered to the original locations used by Klein in 1986 and placed the traps within the secondary vegetation. To include the open habitat originally sampled by Klein, we placed three of the six traps at Dimona in secondary growth, and three traps in a small open pasture. Samples from these two habitats were then treated separately, and trap-specific counts of beetles were multiplied by a factor of two to allow comparison with samples based on six traps.

The outer dimensions of the forest fragments had remained largely unchanged since the sampling of Klein (1989), with one important exception: at Dimona, the continuous forest tract had now been turned into a 100-ha forest fragment. At this site, we sampled both the original site of Klein and a new area of continuous forest located 2.5 km to the west. As our results remained qualitatively unchanged whether we used data from this new site or from the original site sampled by Klein, we will only present data including the latter.

Beetles were identified to genera based on the keys given by Halffter and Martinez (1977), Howden and Young (1981), and Medina and Lopera (2000) and to species based on comparison with the collection deposited at Brazil’s National Institute for Amazon Research (INPA) at Manaus, Brazil, by Brett Ratcliffe. Voucher specimens of each species collected in 2000 were brought to the Florida State Collection of Arthropods (FSCA) in Gainesville, Florida, USA, for direct comparison with the synoptic collection of Klein (1989). Species identifications were confirmed by expert taxonomists Bruce Gill (Quarantine Section, Canadian Agriculture Department) and Robert Woodruff (FSCA). After the identification work was completed, both Klein’s original material and the material from the present study were repatriated to Brazil and deposited in the invertebrate collection at INPA.

**Statistical methods**

Klein (1987, 1989) did not publish his site-specific observations; instead, he reports species-specific counts as pooled across all sites of a given size. This limits the scope for direct statistical comparisons among years. Therefore, we have taken an indirect approach: we analyze our own material by the original methods of Klein (1989) and assess whether the patterns discovered in 1986 were still qualitatively present in 2000.

Based on this rationale, we replicated the exact statistical methods of Klein (1989). Hence, we used analyses of variance (ANOVA) to compare community parameters among forest fragments of different size. Data on total species richness were log-transformed, whereas data on species-specific counts were \( \sqrt{(x + 0.5)} \)-transformed. To test for differences in the weighted mean length of individuals per site, we first determined the mean length of each species by measuring 10 individuals (less if <10 individuals were captured) without discriminating among sexes. We then used the Mann-Whitney \( U \) test, multiplying the species-specific mean length by the total number of individuals captured per 1 ha, 10 ha, or continuous forest site. Species diversity was calculated with the Shannon-Wiener information index (Lloyd et al. 1968) and compared among sites by ANOVA. These comparisons of species diversity were supplemented by visual inspection of log abundance curves (Whittaker 1965, Magurran 1988). Following Klein (1989), the similarity of dung beetle communities among different habitats was also visualized by detrended correspondence analysis (DCA) (Hill and Gauch 1980). Here, the sample from the open clear-cut area at Dimona was a strong outlier, obscuring patterns between the other areas. Following Klein (1989), we therefore excluded this site from the analysis. Finally, we used \( \chi^2 \) tests to assess the independence between years and fragment size in determining local dung beetle diversity at the level of individuals, species, and genera (cf. Table 1 with one test for each taxonomic level) and the independence between habitat and site in determining local dung beetle abundances in 2000 (cf. Appendix A with one test per species-specific table of four habitats × three sites, the clearcut excluded). All ANOVAs and \( \chi^2 \) tests were implemented in Systat 8.0 (SPSS, Chicago, Illinois, USA), whereas the DCA analysis was conducted with the Vegan library of R (Ihaka and Gentleman 1996, R
Table 1. Dung beetle diversity at different hierarchical levels in two different years, 2000 (current study) and 1986 (based on Klein [1989]), and in four different habitats, clearcuts invaded by secondary growth (SG), forest fragments of different size (1 ha and 10 ha), and continuous forest (CF) in the Biological Dynamics of Forest Fragments Project 80 km north of Manaus, Brazil.

<table>
<thead>
<tr>
<th>Diversity measure, by year</th>
<th>SG 1 ha</th>
<th>10 ha</th>
<th>CF</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total no. genera observed</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1986</td>
<td>7</td>
<td>14</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>2000</td>
<td>17</td>
<td>17</td>
<td>16</td>
<td>17</td>
</tr>
<tr>
<td>Total no. species observed</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1986</td>
<td>12</td>
<td>38</td>
<td>39</td>
<td>44</td>
</tr>
<tr>
<td>2000</td>
<td>53</td>
<td>56</td>
<td>54</td>
<td>53</td>
</tr>
<tr>
<td>Total no. individuals observed</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1986</td>
<td>717</td>
<td>935</td>
<td>749</td>
<td>1381</td>
</tr>
<tr>
<td>2000</td>
<td>2584</td>
<td>3983</td>
<td>4002</td>
<td>3047</td>
</tr>
</tbody>
</table>

Note: The sampling effort implemented in 2000 was three times higher than that of 1986. Hence, absolute numbers are not directly comparable across years, and tests presented in the text are specifically aimed at evaluating the independence between year and habitat.

Results

Fifteen years after Klein’s (1989) seminal study, a three-fold increase in the sampling effort yielded a roughly proportional increase in the number of dung beetle individuals captured: overall, we caught 3.9 times more individuals than Klein (Appendix A, Table 1). Nevertheless, the species diversity of different habitats had not changed in like proportion between 1986 and 2000 (Table 1; $\chi^2 = 353.5, P < 0.0001$ for individuals; $\chi^2 = 13.6, P = 0.004$ for species), resulting in a much more even distribution of both species and individuals among habitats in 2000 than in 1986. At the level of genera, there was also some equalization among habitats, but this change was not statistically significant ($\chi^2 = 2.0, P = 0.56$).

Shifts in the general species diversity of different habitats were associated with substantial changes in the species-specific distribution of individuals among habitats. In 1986, six of the 19 most frequently captured species significantly differed in abundance among 1-ha, 10-ha, and continuous forest, and five of them were found in significantly higher numbers in continuous forest than in forest fragments (Klein 1989). In 2000, the pattern had changed substantially, as shown by the much clearer separation of species-specific abundances relative to standard errors in 1986 than in 2000 (Fig. 1). In fact, none of the species observed in 2000 differed significantly in abundance among forest fragments of different size (Fig. 1; species-specific ANOVAs, $P > 0.07$ for all 61 species). Nevertheless, we found some differences in the distribution of individual species among habitats at individual sites, e.g., in Deltochilum septemstriatum ($\chi^2 = 108.0, P < 0.0001$), Deltochilum guyanensis ($\chi^2 = 119.2, P < 0.0001$), and Phanaeus lancifer ($\chi^2 = 15.8, P = 0.01$). In these species, the abundance of individuals seemed more evenly distributed across habitats at Cidade Powell, the site with the most advanced regrowth of secondary vegetation, than at Dimona and Colosso (Appendix A).

In 1986, several species were caught in only one of the four habitats: two in the clearcuts, four in the 1-ha sites, three in the 10-ha sites, and six in continuous forest. In 2000, the figures were much lower (one, zero, one, and two, respectively), suggesting an expansion of species’ distributions among habitats. Onthophagus rubrescens, the only frequently captured species (i.e., species with over six individuals captured; Klein 1989) to be found exclusively in continuous forest in 1986, was now encountered in all habitats, including the smallest and most isolated forest fragments and secondary growth. The one taxon to maintain a highly uneven distribution among habitats between years were the four open-area specialist species in the genus Glaphyrocanthon. Klein (1989) encountered this taxon only in the clear-cut areas, with a few stray individuals in 1-ha fragments. In 2000, the distribution of Glaphyrocanthon was still unchanged: all four species were highly abundant within the small open area at Dimona, and the species did not penetrate into the forest proper.

At the level of individual habitats, the most drastic changes were observed within the matrix habitat between forest fragments. While Klein (1989) found the matrix habitat to be dominated by four species in the genus Glaphyrocanthon, supplemented by eight species at very low abundances (3% of all individuals), we captured 54 different species. Hence, 42 species had expanded their distribution into the matrix habitat since 1986, now accounting for 99.7% of all individuals. The increase in dung beetle diversity was clearly linked to the invasion of the areas by secondary growth. At Dimona, where three traps had been placed in a small remaining area of open pasture, the local community still resembled that described by Klein (1989): the four Glaphyrocanthon species were found in high numbers, along with five forest species caught at low abundances. At Cidade Powell, the area with the highest and oldest secondary vegetation in the matrix habitat, we caught 43 different species.

Temporal changes in the abundance and distribution of individual species were accompanied by changes in species richness (Table 2). While Klein (1989) reported differences in total species richness between forest fragments of different size, we detected no such pattern (ANOVA, $P = 0.86$). Moreover, while Klein (1989)
Figure 1. Abundance (means ± se, log scale) of individual dung beetle species in open clearcuts (CC), in clearcuts invaded by secondary growth (SG), in continuous forest (CF), and in forest fragments of different size (1 ha and 10 ha) at the Biological Dynamics of Forest Fragments Project 80 km north of Manaus, Brazil. Solid vertical lines identify species; stippled vertical lines separate observations from two different time periods: 1986 (Klein 1989) and 2000 (current study). Shown are the 19 species analyzed in detail by Klein (1989); for the six species indicated with asterisks, Klein observed significant differences in mean abundance across forest fragments of different area. Since site-specific counts for 1986 are no longer available, we have only included the standard errors explicitly published by Klein (1989). For the year 2000, we include standard errors for all species and all fragment sizes except clearcuts (for which $n = 1$). Species names were matched among materials as indicated in Appendix A, and a constant of 1 was added to each value to allow the plotting of zero counts.
Table 2. Dung beetle abundance and diversity in three replicates of each of four habitats: clearcuts (CC), previous clearcuts invaded by secondary growth in 2000 (SG), forest fragments of different size (1 ha and 10 ha), and continuous forest (CF).

<table>
<thead>
<tr>
<th>Characteristic, by year</th>
<th>CC Mean</th>
<th>CC SE</th>
<th>SG Mean</th>
<th>SG SE</th>
<th>1 ha Mean</th>
<th>1 ha SE</th>
<th>10 ha Mean</th>
<th>10 ha SE</th>
<th>CF Mean</th>
<th>CF SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance</td>
<td>1986</td>
<td>239.00</td>
<td>42.03</td>
<td></td>
<td>311.70</td>
<td>75.33</td>
<td>249.70</td>
<td>8.13</td>
<td>460.30</td>
<td>204.40</td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>1041.00</td>
<td>106.00</td>
<td></td>
<td>1328.00</td>
<td>77.53</td>
<td>1334.00</td>
<td>464.50</td>
<td>1016.00</td>
<td>127.67</td>
</tr>
<tr>
<td>Richness</td>
<td>1986</td>
<td>4.00</td>
<td>0.33</td>
<td></td>
<td>13.00</td>
<td>1.33</td>
<td>5.03</td>
<td>1.50</td>
<td>24.70</td>
<td>1.83</td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>9.00</td>
<td>0.88</td>
<td></td>
<td>43.33</td>
<td>1.20</td>
<td>45.33</td>
<td>3.48</td>
<td>44.33</td>
<td>2.02</td>
</tr>
<tr>
<td>Diversity (H')</td>
<td>1986</td>
<td>0.91</td>
<td>0.44</td>
<td></td>
<td>1.97</td>
<td>0.14</td>
<td>2.10</td>
<td>0.24</td>
<td>2.63</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>1.11</td>
<td>0.31</td>
<td></td>
<td>2.53</td>
<td>0.28</td>
<td>2.65</td>
<td>0.21</td>
<td>3.05</td>
<td>0.02</td>
</tr>
<tr>
<td>Equitability (J')</td>
<td>1986</td>
<td>0.22</td>
<td>0.10</td>
<td></td>
<td>0.46</td>
<td>0.03</td>
<td>0.50</td>
<td>0.01</td>
<td>0.63</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>0.52</td>
<td>0.08</td>
<td></td>
<td>0.62</td>
<td>0.08</td>
<td>0.69</td>
<td>0.05</td>
<td>0.81</td>
<td>0.01</td>
</tr>
</tbody>
</table>

**Notes:** In 2000, we sampled a single clearcut kept free from secondary vegetation; hence, the corresponding standard errors are lacking. Figures for 1986 are from Klein (1989). The sampling effort implemented in 2000 was three times higher than that of 1986, and absolute numbers are therefore not directly comparable across years.

found beetles from continuous forests to be significantly larger than beetles from 1-ha and 10-ha fragments, this difference had disappeared over time (Mann-Whitney U tests, P > 0.9). Neither could we detect any difference in species-specific abundances between 1-ha and 10-ha sites on the one hand and continuous forest on the other (Wilcoxon matched-pairs test, P > 0.2), although such a difference had been observed by Klein (1989).

Dominance-diversity plots for the year 2000 provide further support for a striking similarity between the dung beetles communities of continuous forest, forest fragments, and even areas of secondary growth (Appendix B). This pattern is very different from the one observed in 1986, when Klein (1989) found an increase in species richness (indicated by the endpoints of the curves on the abscissa) and equitability (shown by the slope of the curves) from the matrix habitat towards 1-ha fragments, 10-ha fragments, and continuous forest. Only within the small remaining area of open pasture at Dimona was the distribution more geometric, showing the dominance of a few species characteristic of this habitat (Appendix B). The same similarity among dung beetle communities from different habitats is also shown by the DCA ordination: where Klein (1989) found a distinct grouping of communities from individual habitat types in 1986, the groups had more or less merged in 2000 (Fig. 2). Only the analyses of diversity and equitability indices suggested some persistent discrepancies in community structure among habitats over time: the value of the Shannon-Wiener information index (H') consistently increased with decreasing disturbance, from secondary vegetation to continuous forest, whereas equitability (J') increased (Table 2). However, these differences were not statistically significant (ANOVA, P = 0.21 for H' and P = 0.20 for J', respectively).

**Discussion**

This study demonstrates rapid changes in the community structure of a functionally important group of insects. Fifteen years after Bert Klein (1989) reported drastic effects of fragmentation on the dung beetle assemblages of central Amazonia, we could no longer distinguish general differences either in the attributes of full dung beetle communities or in the abundance of individual species between secondary vegetation, forest fragments, and continuous forest. Hence, our results suggest a real homogenization of dung beetle communities among habitats less than two decades after the experimental fragmentation of a continuous rain forest tract. To our knowledge, this is one of the first studies to rigorously sample, then resample a replicate set of sites by identical methods to directly assess the rate at which tropical forest insects recover from habitat modification (but see Eggleton et al. [1995], Davies et al. [1999]). It also dates recovery to a much shorter time period than that suggested for another functionally important group of insects—the ants—when recovering from deforestation. While Dunn (2004) predicted that ant communities would completely recover from the consequences of deforestation with approximately four decades of secondary regrowth, fragmented dung beetle communities appear to recover more than twice as fast. Moreover, while Dunn (2004) expected recovery at the level of species composition to lag far behind recovery in terms of species numbers, we detected recovery at both levels. Not only were most species present in fragments of any size, but even present at similar abundances in all habitats.

A comparison with recent results by Andresen (2003) allows us to date the recovery rather precisely and suggests that for a large fraction of dung beetle species, recovery may have taken place in very recent years.
Figure 2. Detrended correspondence analysis ordination of dung beetle samples from (a) 1986 (modified from Klein [1989]) and (b) 2000. Individual samples emanate from three clearcuts invaded by secondary vegetation in 2000 (SGC, SGP, SGD, corresponding to sites Colosso, Cidade Powell, and Dimona, respectively), three 1-ha forest fragments (labeled 4, 5, and 6; sites Colosso, Cidade Powell, and Dimona, respectively), three 10-ha forest fragments (labeled 7, 8, and 9; sites Colosso, Cidade Powell, and Dimona, respectively), and three continuous forest areas (labeled 10, 11, and 12; sites Colosso, Cidade Powell, and Dimona, respectively). In 1996–1997, Andresen conducted an independent study of the dung beetle communities of the Biological Dynamics of Forest Fragments Project, including the 1-ha and the 10-ha fragments at Colosso. At this stage, the matrix habitat had recently been cut and burnt (in 1994 around the 10-ha fragment, in 1995 around the 1-ha fragment; M. Santamaria-Gomez, personal communication), and the fragmentation effects were correspondingly drastic: the 1-ha fragments had only 51% and 44% of the number of species captured in 10-ha fragments and continuous forest, respectively (Andersen 2003: Fig. 1b). These differences among forest fragments of different size were no longer discernible in 2000, suggesting very quick changes in local assemblage structure. Nevertheless, in a few species, individuals seemed more evenly distributed across habitats at Cidade Powell, the site with the most advanced regrowth of secondary vegetation, than at Dimona and Colosso. The persistence of patterns suggests that the most sensitive species may still respond to habitat modification and fragmentation over five years and that species may differ in their rate of recovery. The time needed for complete recovery of dung beetle assemblages could then be dated to between 2–6 yr and 17 yr. Here, the minimum estimate of 2 yr corresponds to the time interval between cutting and burning at Colosso and Dimona and the sampling by Andresen in 1996–1997 (when differences were still discernible) and 6 yr corresponds to the time elapsed between the cutting and burning of these sites and our sampling in 2000 (when the differences had largely disappeared). The maximum estimate of 17 yr corresponds to the time available for secondary regrowth at Cidade Powell, the site where most or all species were evenly distributed among habitats in 2000.

From a conservation perspective, our results are clearly encouraging, as they suggest that successional dynamics in the matrix habitat can rapidly restore conditions favorable for functionally important arthropods. This view is also supported by earlier findings from dung beetles and from another group of functionally important insects: euglossine bees. Working on dung beetles in remnants of tropical montane cloud forest, Pineda et al. (2005) recently demonstrated that a matrix habitat with a structure partly similar to the original vegetation may help sustain diverse dung beetle assemblages in the fragments and even within the matrix itself (see also Arellano and Halffter [2003]). Focusing on euglossine bees, Becker et al. (1991) found that short-term effects of forest fragmentation (Powell and Powell 1987) were transient and that the recovery of bee assemblages was facilitated by only a few years of secondary regrowth. Notably, the latter observations derive from some of our own study sites, suggesting that the current findings may extend to several different taxa. Nevertheless, results from our particular study system should not be uncritically generalized to other taxa or regions, for two principal reasons. First, taxa may differ in their rate of recovery (Dunn 2004), and dung beetles may recover more quickly than other arthropod assemblages (see also Pineda et al. [2005]), since they are likely to be good dispersers (Peck and Forsyth 1982, Kolhmann 1994, Montes de Oca and Halffter 1998, Roslin 2000) and not particularly specialized with respect to resource quality (Halffter and Matthews 1966, Gill 1991). Both features may allow them to reinvade a disturbed area quicker than, for instance, herbivorous taxa waiting for particular host plant species to spread. Second, the observed response may depend on the specific type and distribution of habitats examined. At the experimental sites, populations of both dung beetles and dung-producing mammals remain in continuous forest at comparatively short distances from the forest fragments, allowing efficient recolonization of the area as soon as the vegetation reverts to a favorable state (Malcolm 1997, Gilbert and Setz 2001, Gilbert 2003; M. Santamaria-Gomez, per-
In more fragmented landscapes, clear-cut areas may extend over larger areas and remain over longer time periods. Studies of dung beetles inhabiting other habitats illustrate the contingency of the observed patterns on the spatial configuration of the system and on relatively small differences in land use history; patterns vary from indistinguishable communities to substantial differences in assemblage structure (e.g., Nummelin and Hanski 1989, Estrada et al. 1998, Davis et al. 2001, Halffter and Arellano 2002, Vulinec 2002).

In conclusion, this study provides a first demonstration of how quickly matrix succession may restore the structure of fragmented dung beetle communities. If the vegetation of deforested areas is allowed to regrow, it may stop the loss of species from remaining rain forest fragments and rapidly reconnect remnant populations. Hence, our study supports the view of Dunn (2004) that the conservation of secondary forest may be an important investment in future biodiversity. Our study also identifies a clear priority for future research: to examine the manner in which the recovery of target taxa is reflected in the recovery of ecosystem functioning. In the current case, nearly all dung beetle species have returned to each habitat at the BDFFP sites. As a result of restored species richness, we expect that ecosystem functioning has been restored across the landscape (cf. Didham et al. 1996:258), but this prediction remains to be tested in a future study.

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APPENDIX A
A table presenting the total number of each dung beetle species captured in 2000 at three different sites in four different habitats is available in ESA’s Electronic Data Archive: Ecological Archives E086-181-A1.

APPENDIX B
A figure presenting habitat-specific dominance-diversity curves for dung beetle communities in 1986 and 2000 is available in ESA’s Electronic Data Archive: Ecological Archives E086-181-A2.