

Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles

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Summary

1. Secondary and plantation forests are becoming increasingly widespread in the tropics. A recent meta-analysis on the impacts of land-use change on tropical forest dung beetles concluded that regenerating forests can be effective in helping to offset species loss following deforestation. However, our understanding of the extent to which these results can be generalized to new locations remains very poor.

2. We attempted to overcome many of the design limitations that characterize previous studies by collecting spatially independent dung beetle samples from primary, secondary and *Eucalyptus* plantation forests in north-east Brazilian Amazonia across a large quasi-experimental landscape that minimized confounding edge and fragmentation effects.

3. We recorded 9203 dung beetles, comprising 85 species. Species richness was significantly higher in primary forest and the majority of species were more abundant there than elsewhere, whereas secondary and plantation sites harboured an impoverished subset of primary forest species.

4. Our data illustrate the low value of tropical secondary and plantation forests for dung beetles in our study area, and our conclusions are more pessimistic than those of earlier studies.

5. Because of differences in the order of species rank-abundance and rank-biomass patterns, re-coding community data from abundance to biomass significantly altered the analytical weight of individual species in determining community patterns. Larger bodied beetles were more prone to local extinctions and abundance declines and this effect was consistent both within and between genera.

6. *Synthesis and applications.* Our study demonstrates that secondary and plantation forests in a large neotropical landscape host exceptionally impoverished dung beetle communities. Furthermore, the depletion of beetle abundance combined with a reduction in average body mass in converted forests is likely to have detrimental consequences for the maintenance of dung beetle-mediated ecosystem services in these habitats. Differences in biogeographical and landscape context, and the influence of common limitations in sampling design, may explain why many other studies have painted a more optimistic picture of the conservation value of anthropogenic habitats. In the absence of further evidence we caution strongly against the claim that forest regeneration schemes on degraded land can effectively offset the loss of species following deforestation, and urge that conservation strategies prioritize the protection of remaining areas of primary forest.

Key-words: Scarabaeinae, tropical forests, habitat change, habitat value, deforestation, Brazil, sampling bias, biomass

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Introduction

The survival of many tropical forest species is dependent on conservation management in human-dominated landscapes as a consequence of the rapid rate of tropical deforestation and the inadequacy of existing protected areas (Daily 2001). While the conversion of primary forest for intensive agriculture inevitably leads to dramatic losses in biodiversity, conservation biologists are far less certain about the conservation value of more structurally complex secondary and planted forests (Dunn 2004; Wright & Muller-Landau 2006; Gardner *et al.* 2007a; Laurance 2007). This lack of consensus is illustrated in a series of recent reviews on a variety of taxa, including birds (Barlow *et al.* 2007a), amphibians and reptiles (Gardner, Barlow & Peres 2007) and butterflies (Barlow *et al.* 2007b; Koh 2007). This uncertainty, coupled with the rapid expansion of secondary (Wright 2005) and plantation forests (FAO 2006) across the tropics, highlights the need for more biodiversity research in human-dominated landscapes.

Dung beetles (Coleoptera: Scarabaeinae) form an important component of the tropical forest insect fauna (Peck & Forsyth 1982), contributing to several key functional roles, such as secondary seed dispersal, nutrient recycling, soil aeration and control of vertebrate parasites (Andresen & Feer 2005). Dung beetles can also be sampled more cost-effectively than many other rainforest taxa, and have been proposed as effective indicators of landscape change (Gardner *et al.* 2008). A recent meta-analysis on the consequences of landscape change for tropical forest dung beetles showed that, while clear-felling and intensive agriculture led to significant reductions in diversity, land uses that maintained a high degree of forest cover and relatively high vegetation complexity (such as secondary forests) held species-rich dung beetle communities similar to those found in intact areas (Nichols *et al.* 2007; cf. Vulinec 2002; Quintero & Roslin 2005; Vulinec, Lambert & Mellow 2006). Although these preliminary results demonstrate the potential biodiversity value of forest regeneration following deforestation, there are some important reasons to cast doubt on these conclusions.

First, Nichols *et al.*'s (2007) meta-analysis is based upon a relatively small number of studies. For example, only seven studies on late secondary forests (> 15 year) and six studies on tree plantations were available for analysis across the tropics (Nichols *et al.* 2007), and there were marked between-study differences in the habitat types sampled (e.g. plantation forests comprised of different tree species and different types of understorey vegetation). Secondly, almost all of the studies were confounded by the methodological problems that are present in many tropical biodiversity studies (Barlow *et al.* 2007c; Gardner *et al.* 2007a) and often result in a near best-case scenario of the value of converted forest for biodiversity (Dunn 2004). Finally, very few studies have evaluated patterns of biomass when detailing the response of dung beetle communities to habitat change (Nichols *et al.* 2007). However, species abundance often provides a poor predictor of biomass in arthropod community data (Saint-Germain *et al.* 2007), such that analyses employing either abundance or biomass data alone may

produce very different results, subject to potentially different ecological interpretations (Vulinec 2002).

The primary aim of this study was to contribute to our understanding of the value of primary, secondary and plantation forests for tropical dung beetles. Working within a large quasi-experimental forestry landscape allowed us to overcome many design limitations, including access to extensive primary forest controls, minimizing the confounding influence of edge effects and habitat fragmentation and maximizing the spatial independence among sites of each forest type. We compared patterns of species richness, abundance and diversity with the results of a recent meta-analysis on the consequences of tropical forest modification for dung beetles (Nichols *et al.* 2007), and hypothesize that the conclusions reached by Nichols *et al.* (2007) paint an overly optimistic picture of the conservation value of these habitats. Finally, we evaluated the potential implications of converting abundance data into biomass data when examining the structure of dung beetle communities in response to landscape change.

Methods

STUDY AREA AND SITE SELECTION

The project was conducted within a 1.7-Mha landholding located in the state of Pará in north-eastern Brazilian Amazonia (00°27'00"–01°30'00" S, 51°40'00"–53°20'00" W), containing 53 000 ha of *Eucalyptus* plantations and a similar area of regenerating native vegetation, embedded within a large and virtually undisturbed primary forest matrix (> 500 000 ha). Fifteen study sites were established, with five replicates each in primary rainforest, 'mature' *Eucalyptus* plantations (4–5 years old) and even-aged secondary forest (14–19 years since abandonment) (for a map and more detailed habitat descriptions see Barlow *et al.* 2007a). The scale of the landscape allowed us to select sites that were both spatially independent [mean distance between primary, secondary and *Eucalyptus* sites was 30 km (range 14–67), 9 km (4–44) and 11 km (7–50), respectively] and of sufficient size [mean size of *Eucalyptus* and secondary forest blocks was 1687 ha (range 574–3910) and 2682 ha (1079–3508), respectively] to minimize problems of spatial pseudoreplication and edge effects. Moreover, *Eucalyptus* and secondary forest sites were located at similar mean distances from the nearest areas of continuous primary forest [1124 m (range 550–2300) and 1316 m (650–2800), respectively].

DUNG BEETLE SAMPLING

Dung beetles (Coleoptera: Scarabaeinae) were sampled using pitfall traps (20 cm diameter, 15 cm depth) buried flush with the ground and baited with c. ~20 g of fresh human dung, the most effective bait for dung beetle studies in the neotropics (for a similar design see Larsen & Forsyth 2005). Five traps were placed at each site, separated by 200 m along a linear 1-km transect.

Trapping was conducted twice at each site, coinciding with the early dry (July–August 2004) and mid-wet (April–May 2005) seasons. Traps were operated for 2 × 24-h periods at each site in both seasons, with the captured individuals removed and bait being replaced every 24 h. All captures were later processed in a laboratory and separated to species. Where species names were unknown a series of morphospecies numbers was assigned to each genus. To obtain body mass estimates for each species, a sample of between 1 and 31 individuals (median

= 12, mode = 30) was dried in a constant-temperature oven at 60 °C for 1 week prior to weighing on a balance accurate to 0.0001 g (see Table S1 in the supplementary material).

DATA ANALYSIS

Patterns of species richness and abundance

Comparisons of species richness among habitat types were made by visual assessment of overlapping 95% confidence intervals on individual-based rarefaction curves (Gotelli & Colwell 2001) implemented in EstimateS v.7.5 (Colwell 2005). Species richness, total abundance and species-rank abundance distributions varied little between seasons (see Appendix S1 in the Supplementary material) and data were therefore pooled across all samples for each analysis.

To describe patterns of beta diversity across the landscape, we calculated the average number of species absent in each site defined as $\beta = \gamma - \alpha$, where γ is the number of species sampled in the entire landscape (gamma diversity) and α is the average number of species present at a given site (alpha diversity). This approach is used as a measure of additive partitioning of diversity and allows for a direct comparison between alpha and beta diversities in terms of numbers (or percentage) of species (Gardner *et al.* 2007b).

We compared the relative abundance of 'common' (> 15 captures) primary forest species in each of the three habitat types by scaling species' abundances in each site by the average abundance for that species across all sites in the landscape. The average scaled abundances for all species were then plotted for each habitat in turn. Deviation from the expected abundance (i.e. if all individuals of a species were randomly distributed across all 15 sites of the three habitats) was evaluated by comparing the mean and 95% bias-corrected bootstrap confidence interval (Efron 1987) for each species with the scale factor of 1. If the confidence interval fell above or below 1 then the abundance of that species in a given habitat was significantly different from that expected by chance ($P = 0.05$).

Comparison with a recent meta-analysis

We compared our data with the results of the meta-analysis by Nichols *et al.* (2007) by visually comparing the 95% bootstrapped confidence intervals for standardized community parameters reported in the meta-analysis with the single value for the same parameters calculated using our data. The six parameter values examined were: total number of species and individuals, total number of primary forest species and individuals, community similarity (Morista–Horn similarity index) and community evenness (Pielou's evenness index). Parameter values in Nichols *et al.* (2007) were standardized relative to values calculated for intact forest sites in each study (Dunn 2004).

Comparing dung beetle communities with both abundance and biomass data

The biomass of each species in each site was calculated by multiplying the mean body mass by the total abundance for that species, such that the pooled species biomass was the sum of all species products (Peck & Howden 1984). The interspecific relationship between body mass and abundance was examined using linear regression on log-transformed data (Saint-Germain *et al.* 2007).

We evaluated patterns of community turnover between the three forest types by constructing two separate community matrices,

based separately on abundance and biomass data (Saint-Germain *et al.* 2007). We used non-metric multidimensional scaling (MDS) to define the overall differences in community structure within and between habitats based on each matrix type, implemented in PRIMER v.5 (PRIMER-E, Plymouth Marine Laboratory, UK). Ordinations were conducted using site-standardized and square-root transformed data and the Bray–Curtis similarity index, although patterns were qualitatively similar when using either untransformed or presence–absence data. We used analysis of similarities (ANOSIM; Clarke & Warwick 2001) to test for significant differences in multivariate community structure between forests for each data type, and a non-parametric Mantel test (RELATE; Clarke & Warwick 2001) to compare directly the abundance and biomass-based similarity matrices.

Finally, to detect differences in the analytical weight of individual species in discriminating patterns of community turnover when using abundance vs. biomass data, we calculated the similarity percentage contribution (SIMPER; Clarke & Warwick 2001) of each species, and plotted the percentage values for abundance vs. biomass data for both pairwise habitat dissimilarities and within-habitat community similarities.

Evaluating the effects of habitat change on dung beetle body mass and biomass

Overall differences between habitat types in the average body mass per species (irrespective of individuals) and per individual (irrespective of species), as well total biomass (body mass \times individuals summed across species), were compared using non-parametric Kruskal–Wallis tests. To control for the impact of changes in the abundance of species of a particular size on observed habitat differences in body mass, we examined relationships within individual genera in cases where multiple representatives of a given genus occurred across different habitat types. As well as providing a proxy correction for phylogenetic differences (the true phylogeny for all species being unknown), comparisons within genera also provide a proxy for gross differences in beetle size and functional behaviour (Vulinec 2002). Comparisons were only made in cases where there were more than 10 individuals (and ≥ 2 species) of a given genus in each between-habitat pairwise comparison. Average species body sizes (and pooled biomass values) for each genus in secondary and plantation forest sites were scaled against the average values obtained for primary forest sites.

Results

PATTERNS OF SPECIES RICHNESS AND ABUNDANCE

We captured totals of 9203 individuals and 85 species of dung beetle, with 5208 individuals and 72 species in primary forest, 2077 individuals and 48 species in secondary forests, and 1918 individuals and 43 species in *Eucalyptus* plantations (see Table S1 in the supplementary material). Sample representation (of beetles attracted to human faeces) was estimated to be $\geq 83\%$ in each habitat type (see Table S2 in the supplementary material).

We captured significantly more species and individuals in primary forest than in secondary forests or *Eucalyptus* plantations, which were indistinguishable from each other in terms of both species richness and abundance (Fig. 1).

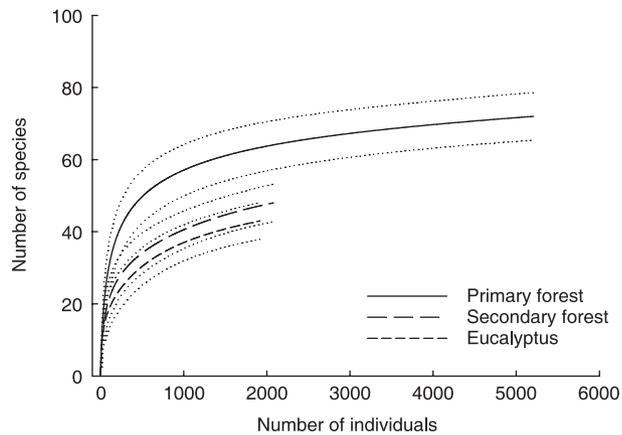


Fig. 1. Individual-based rarefaction curves for dung beetles in primary, secondary and *Eucalyptus* plantation forests. Fitted dotted lines indicate 95% confidence intervals.

Seventy-nine per cent of species were recorded in primary forest and 31% of all species were unique to this habitat (see Table S2 in the supplementary material). In contrast, only 56% and 50% of all species were recorded in secondary and *Eucalyptus* forest, respectively (see Table S2 in the supplementary material). Discounting occasional species whose distribution may represent sampling artefacts (i.e. those that were captured less than five times), 99% and 86% of species captured in secondary and plantation forests, respectively, were also found in primary forest. The gamma diversity of the entire landscape can be expressed in an additive form as: $85 [\gamma] = 28 [\alpha] + 57 [\beta]$. Beta diversity contributed 39%, 49% and 62% of the total gamma diversity for primary, secondary and *Eucalyptus* forests, respectively.

Species-abundance distributions were also strongly nested across the three habitats, and the majority of species recorded in both primary and converted habitats had markedly higher abundances in primary forest sites (Fig. 2). Eighty-three per cent of these species had a greater average abundance in primary forest than was expected by chance, and the difference was significant for 28%. This pattern was consistent irrespective of whether species were relatively common or rare in our samples (Fig. 2).

COMPARISON WITH A RECENT META-ANALYSIS

Compared with primary forest controls, the total species richness and abundance of dung beetles in secondary forests was significantly, or nearly significantly, lower than the conclusions from the recent meta-analysis by Nichols *et al.* (2007) (Fig. 3). This result was consistent when compared with the results of other studies that sampled both young (< 10 years) and old (> 15 years) secondary forest sites. Although our study was in broad agreement with the findings of Nichols *et al.* (2007) that plantation forests have greatly reduced species richness, we found a large decrease rather than an increase in dung beetle abundance. Community evenness in our study was similar to that found in other studies of secondary forest, and greater than the evenness recorded in most

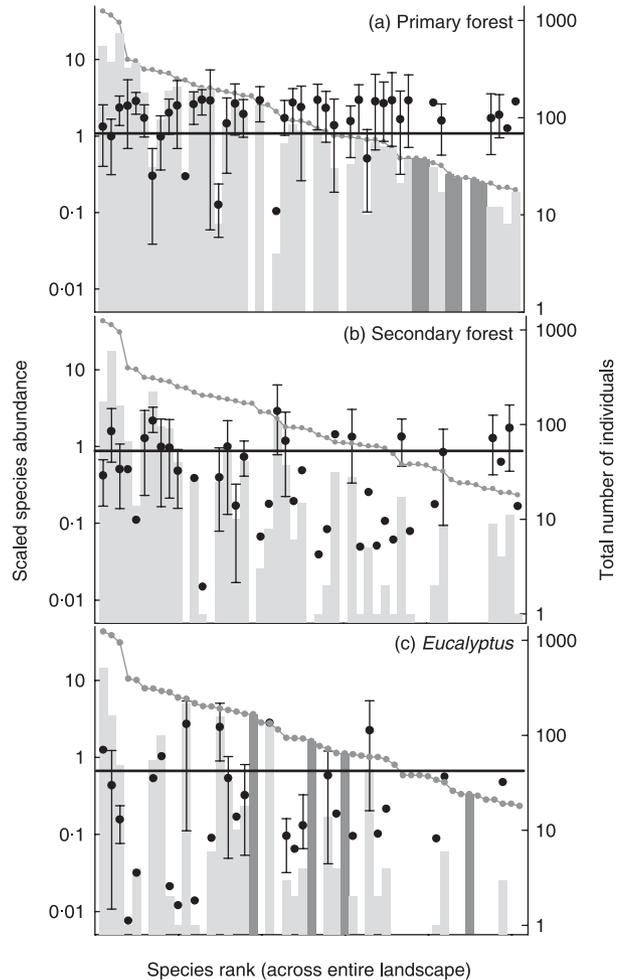


Fig. 2. Scaled mean abundances (solid circles) for primary forest dung beetle species in (a) primary, (b) secondary and (c) plantation forests. Species that fall above the average value for the entire landscape (scale parameter = 1) are more likely to occur in that forest type than would be expected by chance; (a) clearly demonstrates that most individuals of more and less abundant species were found in primary forest. Bias-corrected 95% bootstrap confidence intervals are presented where data were sufficient. The secondary axis (shaded bars) complements the pattern of average abundances, and illustrates the total number of captures of each species in each forest type, compared with the rank abundance across all samples (the grey line and dots). Darker bars identify species that were confined to a single habitat.

plantation studies (Fig. 3). The standardized difference in community composition of plantation samples from primary forest controls was similar to that found for other studies, while our secondary forest samples were more distinct from (but within the confidence intervals of) the results of the meta-analysis (Fig. 3).

COMPARING ABUNDANCE AND BIOMASS DATA

There was no relationship between species body mass and abundance ($R^2 = 0.001$, $P = 0.82$, $n = 76$), and this pattern was consistent when comparing among species for each genus in turn ($n = 7$ genera with > 3 species, mean $R^2 = 0.11$,

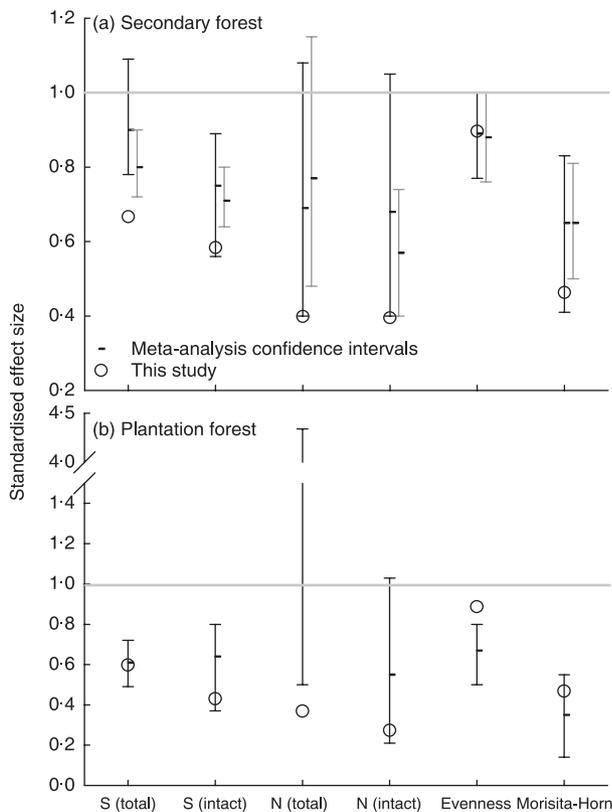


Fig. 3. Comparison of standardized community parameters in (a) secondary and (b) *Eucalyptus* forests (scaled by average values from intact forest; grey bar) between this study (circles) and similar studies elsewhere, presented in a recent meta-analysis by Nichols *et al.* (2007), illustrated by bias-corrected 95% bootstrap confidence intervals. For secondary forest, grey and black confidence intervals describe the findings of studies in young (< 10 years) and old (> 15 years) secondary forests, respectively. Plantation forests in Nichols *et al.* (2007) included other timber and crop species. Values for species richness and abundance in our study are consistently lower than those reported in other studies.

SE = 0.069, $P > 0.12$ in all cases). In contrast, there was a positive relationship between species abundance and total biomass for all sites combined and for each individual forest type (Fig. 4; with consistent within-genus patterns, mean $R^2 = 0.68$, SE = 0.1 and $P < 0.05$ in all cases, except *Deltochilum* which showed no relationship). However, there was considerable variance in the abundance–biomass relationship across all species, with marked discrepancies in the rank-abundance and rank-biomass of individual species (overall $R^2 < 0.40$ in all forest types; Fig. 4).

Despite the relatively weak relationship between species abundance and biomass distributions, patterns of turnover in overall community structure among sites were similar when analysed using either data type (Fig. 5; RELATE, $Rho = 0.9$, $P < 0.001$) and both the abundance and biomass matrices were equally effective at discriminating among habitats (Fig. 5; ANOSIM; abundance data, global $R = 0.56$, $P < 0.001$, all pairwise comparisons $P < 0.032$; biomass data, global $R = 0.61$, $P < 0.001$, all pairwise comparisons $P < 0.008$). However, discrepancies in abundance–biomass relationships (Fig. 4)

meant that individual species often contributed a very different weight to each analysis (Fig. 6). In particular, when transforming abundance to biomass data, the analytical weight of larger bodied species invariably increased, while the weight of smaller bodied species either decreased or remained similar (Fig. 6). Consequently, in almost all cases less than half of the top 10 weighted species were the same for abundance and biomass-based analyses (see Tables S3 and S4 in the supplementary material).

EVALUATING THE EFFECTS OF HABITAT CHANGE ON BODY MASS AND BIOMASS

A significantly greater mean site biomass of dung beetles was recorded in primary forest sites (mean 102 g, SE 15.6) than either secondary (mean 26.7 g, SE 8.5) or plantation (mean 20.2 g, SE 6.9) forests (Kruskal–Wallis; $\chi^2 = 9.5$, $P = 0.009$, d.f. = 2). In addition to diminished abundances (Figs 1 and 2), this difference could be attributed to the fact that the average body mass of both species (mean 0.011 g, SE 0.0017, $n = 5$) and individuals, irrespective of species (mean 0.083 g, SE 0.065) in primary forest, was greater than that in either secondary (mean 0.0029 g and 0.045 g for species and individuals, respectively) or plantation forests (mean 0.0022 g and 0.031 g) (Kruskal–Wallis; species body mass $\chi^2 = 9.5$, $P = 0.009$, individual body mass $\chi^2 = 6.7$, $P = 0.035$, d.f. = 2).

The community-level pattern of reduced species body size and pooled biomass outside primary forest was consistent within different genera, irrespective of the huge variation in mean body size of species between the largest (*Coprophaneus*; 0.96 g) and smallest genera (*Uroxys*; 0.003 g; Fig. 7). In some cases, primary forest species were larger because the largest representatives of any given genus were wholly confined to primary forest samples (e.g. *Onthophagus onthochromus*, *Canthidium* sp. 2, *Ateuchus* sp. 2 and *Uroxys* sp. 3), while in others it was more simply a function of larger species being more likely to occur in a primary forest site (e.g. *Coprophaneus lancifer*, *Eurysternus hamaticollis* and *Oxysternon festivum*; see Table S1 in the supplementary material).

Discussion

VALUE OF PRIMARY, SECONDARY AND PLANTATION FORESTS FOR DUNG BEETLES

The overall conclusion from our study is that dung beetle communities in both secondary forest and *Eucalyptus* plantations in our study area are severely impoverished compared with neighbouring areas of primary forest. Although plantation areas were not ‘green deserts’, both *Eucalyptus* and secondary forests in Jari harbour a depleted subset of primary forest species. The prediction that human impacts in managed landscapes can have a negative effect on site (alpha)-level patterns of species richness, but promote higher gamma diversity at the landscape scale (Halffter, Favila & Halffter 1992; Arellano & Halffter 2003) was only very weakly supported as few open-area species colonized areas outside primary forest.

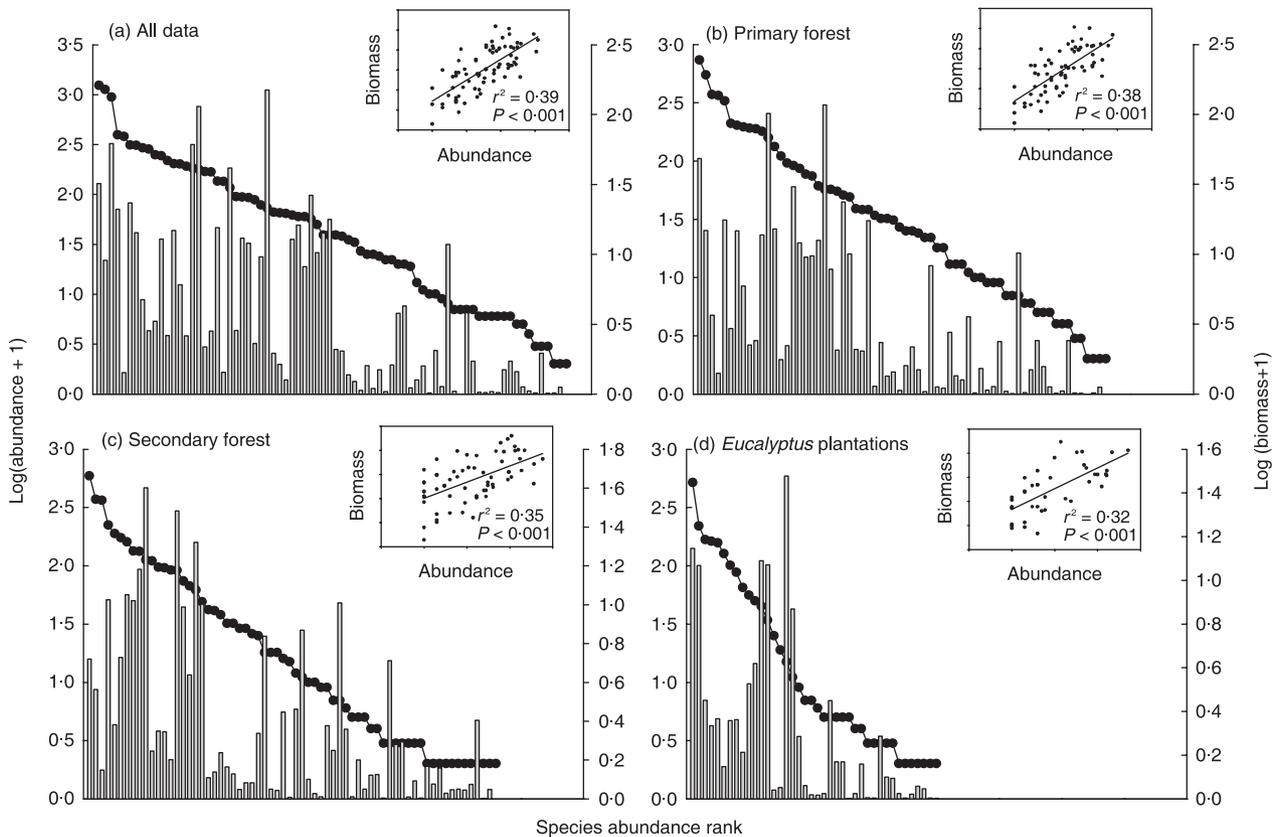


Fig. 4. Species rank-abundance curves (lines) for dung beetles sampled across the entire Jari landscape, and separately for primary, secondary and plantation forests, with biomass values superimposed (bars). Linear regressions between species abundance and species biomass are presented as insets. All data are \log_{10} transformed.

Furthermore, we found no evidence of density compensation by habitat generalists or open-area specialists, and species-poor habitats consistently held fewer individuals of both relatively rare and relatively common species, highlighting the fact that the relationship between rarity and local extinction risk remains poorly understood (Gaston 1994).

The restructuring of dung beetle communities following habitat change is frequently explained by two non-exclusive hypotheses: changes in vegetation structure and changes in the availability of mammalian dung resources. It is well known that dung beetle communities that are closely associated with tropical forest habitats are greatly influenced by differences in vegetation structure (Halffter & Matthews 1966; Halffter, Favila & Halffter 1992; Halffter & Arellano 2002), with individual species often having specific affinities for certain structural habitat properties (Davis *et al.* 2001). Furthermore, secondary forests and *Eucalyptus* plantations in Jari, like elsewhere, are typically characterized by low, relatively open canopies with hot and dry understorey environments. These microclimatic differences could help explain the observed impoverishment of dung beetle communities through a physiological intolerance to high temperatures (Chown 2001), the influence of solar radiation on adult activity patterns (Lobo, Lumaret & Jay-Robert 1998) or the influence of decreased soil moisture content on larval survival

(Sowig 1995). Numerous observational and experimental studies have demonstrated the strength of interspecific competition for ephemeral dung resources in dung beetles (reviewed in Horgan & Fuentes 2005). Three lines of indirect evidence indicate that the availability of mammalian dung resources is markedly lower outside primary forest in our study landscape. (i) Primates are known to be keystone resource providers for many dung beetles (Estrada, Anzures & Coates-Estrada 1999) and their biomass was reduced by an order of magnitude in *Eucalyptus* sites and by about half in secondary forest (C. A. Peres, unpublished data). (ii) High ambient temperatures outside primary forest can rapidly desiccate dung piles, making them inaccessible to many beetles (Peck & Forsyth 1982). (iii) Scavenger flies were more abundant in plantation and secondary forests than in primary forest (Barlow *et al.* 2007c), potentially increasing competition within the wider dung insect community. Although it is difficult to ascertain the relative importance of vegetation structure and resource availability for structuring dung beetle communities, we predict that the latter is likely to have a weaker influence in Jari, as few tropical forest dung beetles are resource specialists (Peck & Forsyth 1982; Larsen, Lopera & Forsyth 2006) and the biomass of small-bodied primates, large rodents and ungulates remains relatively high outside primary forest (C. A. Peres, unpublished data).

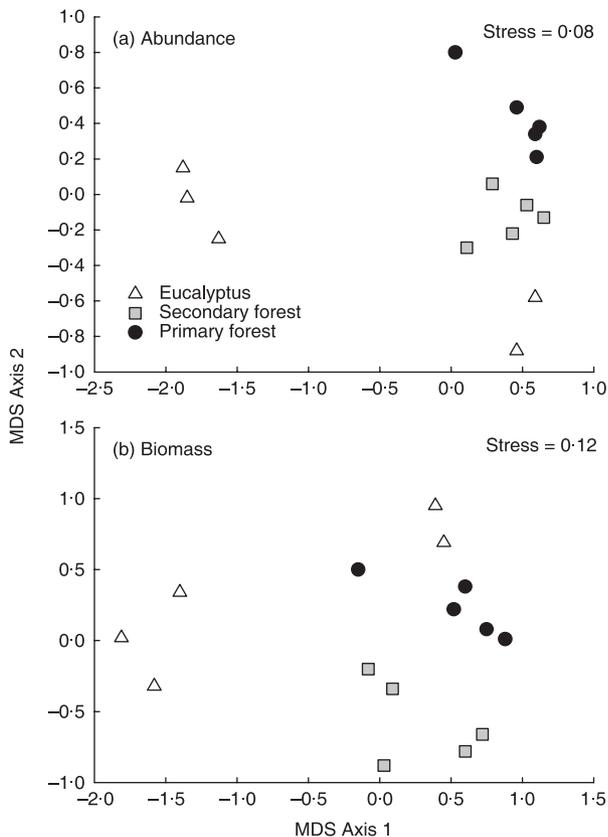


Fig. 5. Multidimensional scaling (MDS) ordination of dung beetle community structure across primary, secondary and plantation forests based on the abundance (a) and biomass (b) data. The three habitats host largely distinct dung beetle communities and converting abundance data into biomass data gives a superficially very similar pattern. Patterns were similar using both transformed (presented) and untransformed data.

COMPARISON WITH A RECENT META-ANALYSIS

Our results contrast markedly with the consensus reported by Nichols *et al.* (2007), which suggests that regenerating secondary forests may be effective in mitigating future losses in dung beetle diversity following continued deforestation (Nichols *et al.* 2007; Shahabuddin, Schulze & Tscharnkte 2004; Quintero & Roslin 2005; Vulinec, Lambert & Mellow 2006). In further contrast, Nichols *et al.* (2007) concluded that dung beetle abundance was a poor metric for distinguishing community responses across habitat modification gradients because of the large numbers of beetles often found in degraded forests, whereas we found low levels of abundance in both secondary and plantation forests.

We have examined three potential explanations for these significant discrepancies. First, it is possible that there is something unique about the types of habitats we sampled or the Jari landscape in general. However, our secondary forest sites were older than many in the meta-analysis by Nichols *et al.* (2007) and, although there are no previous studies of *Eucalyptus* plantations, other studies have encompassed a wide variety of perennial crops, including coffee (*Coffea* spp.),

cacao (*Theobroma cacao*) and oil palm (*Elaeis guineensis*). Furthermore, while it is possible that conditions of relatively poor soil quality and low productivity in the geologically older (> 300 million years) central and eastern Amazon region could lead to a more generally impoverished native biota (including dung beetles; Radtke, da Fonseca & Williamson 2007), the fact that our primary forest sites contained highly abundant and diverse samples suggests that this is unlikely to explain the observed patterns.

Secondly, it is likely that community-level consequences of habitat change are strongly influenced by differences in biogeographical context and the available pool of regional colonists (Nichols *et al.* 2007). The vast majority of neotropical dung beetles are forest dwellers, unable to persist in artificially open and more xeric environments (Howden & Nealis 1975; Klein 1989). This situation may be exacerbated in lowland areas, where species may have lower physiological tolerances to microclimatic change (Janzen 1967). As a result, continually forested lowland sites often exhibit highly nested patterns of species distribution, with few open-habitat specialists (this study but see also Vulinec 2002; Escobar 2004). In contrast, forested areas adjacent to open habitats (most notably large natural savanna regions such as west Africa; Davis & Philips 2005; but also areas that have been heavily deforested historically, such as central America; Halffter, Favila & Halffter 1992; and the Andes; Medina, Escobar & Kattan 2002) are characterized by a much stronger turnover in species composition, with open habitat specialists elevating the alpha diversity of disturbed forests and increasing overall landscape diversity (Arellano & Halffter 2003).

Finally, many existing studies on habitat change suffer from methodological limitations that can dilute the perceived effect of forest conversion on biodiversity (Gardner *et al.* 2007a). Such sampling problems are increasingly recognized as widespread in biodiversity studies in general (Hamer & Hill 2000; Hill & Hamer 2004; Barlow *et al.* 2007a, b, c; Gardner *et al.* 2007b; Gardner, Barlow & Peres 2007; Koh 2007). Key issues include the following. (i) The size and matrix context of secondary and plantation sites. Many studies are subject to edge and spill-over effects (of dung beetles and also the mammal species upon which they depend; Medina, Escobar & Kattan 2002; Vulinec 2002; Shahabuddin, Schulze & Tscharnkte 2004; Avendaño-Mendoza *et al.* 2005; Quintero & Roslin 2005). Also, small modified forest patches that are surrounded by primary forest may have a more humid microclimate than larger and more isolated areas of converted forest (Avendaño-Mendoza *et al.* 2005). (ii) The size and quality of control sites. Many studies, particularly those in Mesoamerica (Avendaño-Mendoza *et al.* 2005), Andean countries (Medina, Escobar & Kattan 2002; Escobar 2004) and parts of south-east Asia (Boonrotpong, Sotthibandhu & Pholpunthin 2004), have access only to relatively small and isolated fragments of semi-degraded primary forest, which are unlikely to be representative of pre-disturbance conditions. (iii) The spatial extent of study landscapes. Although it is often logistically challenging (or impossible) to secure spatially independent samples of both treatment and control forests, the fact that we

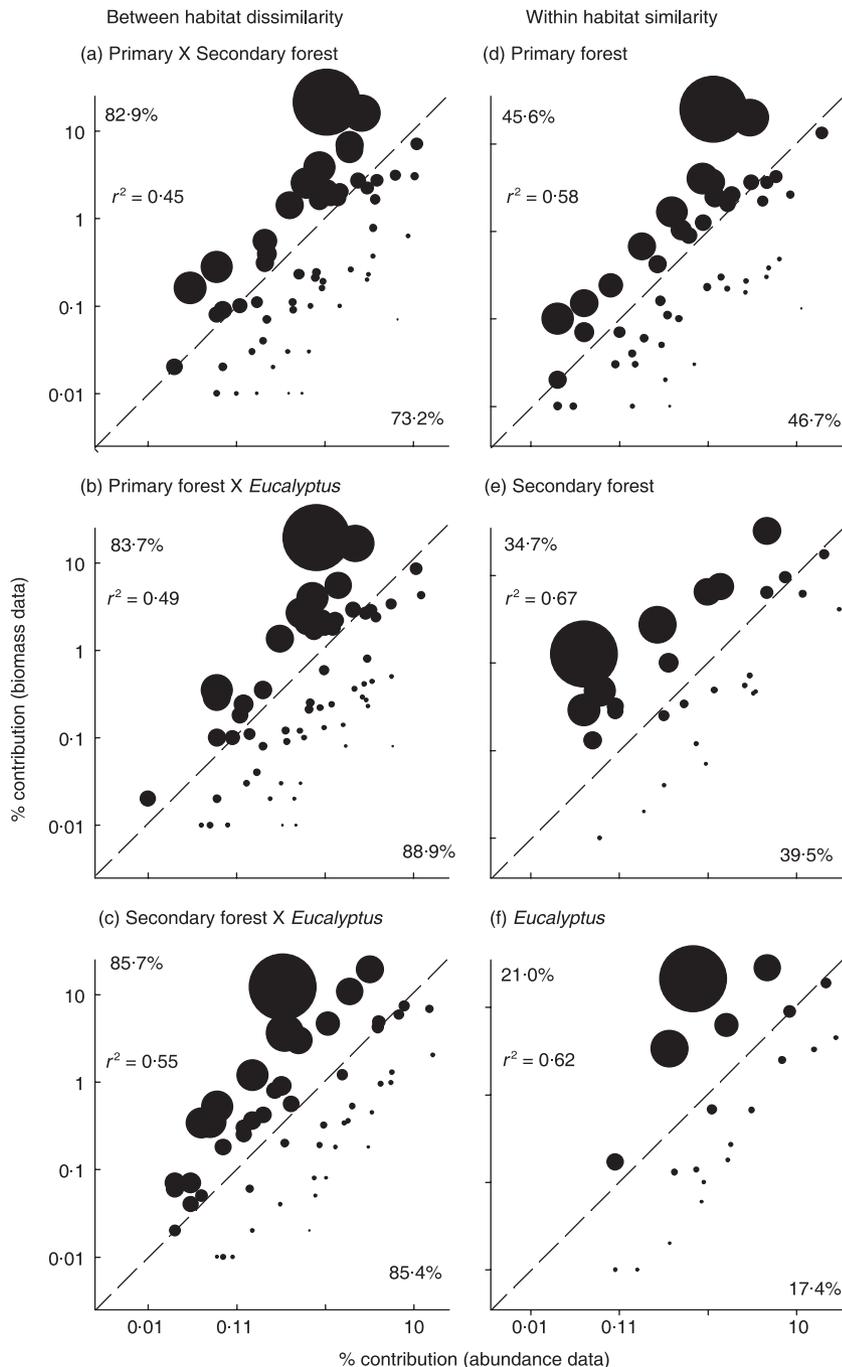


Fig. 6. Percentage contributions, based separately on abundance and biomass data, of individual species towards patterns of community structure between (a–c) and within (d–f) habitats. Species are represented by black circles, which are scaled by differences in average body mass. Both axes are logged so the species in the top right corner of each panel contribute the most towards the patterns (see Tables S3 and S4 in the supplementary material for identities of top-ranked species). The diagonal dashed line identifies the position of species that contribute equal weights to analyses based on both data sets, so that large-bodied species clearly contributed the most to patterns based on biomass data. Total percentage dissimilarity and similarity values are displayed next to each axis, and are almost identical for each data type.

found a high (33–62%) turnover in species composition across sites in all three habitats illustrates the importance of conducting studies at a landscape scale (Arellano & Halffter 2003).

In conclusion, we believe that one of the most probable explanations for the differences between our results and those of the studies reviewed by Nichols *et al.* (2007) relates to the large spatial scale and experimental design of our study. While our study area may not be typical of a highly fragmented landscape, it does present an almost unique opportunity for understanding the value of large secondary and plantation forest blocks for tropical forest dung beetles. We

believe that our findings are therefore vital in moderating optimistic generalizations about the conservation value of these habitats elsewhere (Wright & Muller-Landau 2006).

COMMUNITY-WIDE EROSION OF DUNG BEETLE BODY MASS AND BIOMASS

Although community analyses based upon species abundance and species biomass data may produce superficially similar patterns, these may be driven by distinct sets of species (Fig. 6) that are potentially associated with distinct ecological mechanisms (Peck & Forsyth 1982; Saint-Germain *et al.*

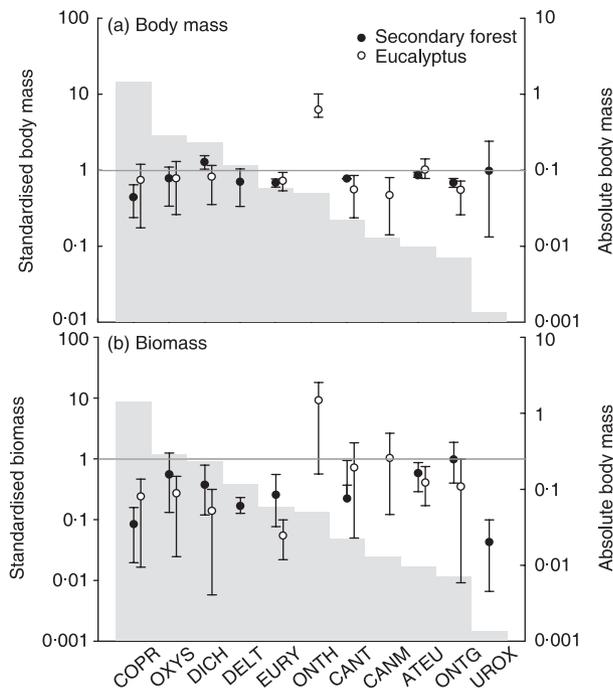


Fig. 7. Standardized changes from primary forest in (a) average species body mass and (b) average pooled biomass for 11 dung beetle genera sampled in secondary and plantation forest sites. Average values with bias-corrected 95% bootstrap confidence intervals are compared against the respective average for that genus in primary forest samples (horizontal line), demonstrating that genera in secondary and plantation forest are consistently represented by smaller species and lower levels of biomass than in intact habitat. Genera are arrayed left to right by rank-order of absolute size (the absolute body mass, shown by grey bars). All data are \log_{10} transformed. Genus codes are: COPR, *Coprophanaeus*; OXYS, *Oxysternon*; DICH, *Dichotomius*; DELT, *Deltochilum*; EURY, *Eurysternus*; ONTH, *Ontherus*; CANT, *Canthon*; CANM, *Canthidium*; ATEU, *Ateuchus*; ONTG, *Onthophagus*; UROX, *Uroxys*.

2007). Consequently, analyses based on both abundance and biomass data can provide complementary information that is vital in achieving a robust understanding of the ecological consequences of habitat change for tropical forest dung beetles (Peck & Forsyth 1982). Our data suggest that larger bodied dung beetles are more susceptible than smaller bodied species to abundance declines, if not local extinctions, following conversion of primary rainforest to secondary or plantation forest. Large body size is one of the most commonly cited traits promoting extinction over ecological time scales, and has been reported in both vertebrates and invertebrates, including dung beetle studies on the effects of fragmentation (Klein 1989; Larsen, Williams & Kremen 2005) and forest clearance (Scheffler 2005). Interpreting the ecological mechanisms responsible for this reduction in mean body size in converted forests is confounded by the fact that body size is often correlated with other variables that are themselves positively and negatively associated with extinction risk (Gaston 1994). Nevertheless, changes in the physiological tolerance to thermal stress, and alterations in the supply of dung resources, indicate why size-dependent effects may be important.

Cooling rates in dung beetles are inversely related to body mass (Bartholomew & Heinrich 1978) and, while elevated body temperatures provide a competitive advantage in the cool, humid environment of tropical forests, an inability to dissipate excess heat in more open environments may incur severe physiological costs (Chown 2001). In addition, larger beetles require higher soil humidity content for digging deeper galleries (Anduaga 2004), and therefore these species may be disadvantaged when exposed to drier conditions. Larger dung beetles also use a disproportionately larger share of resources (Doube 1990) and therefore may be negatively affected by reductions in resource availability outside primary forest. Finally, there is some evidence to suggest that larger beetles are attracted to larger dung piles (Peck & Howden 1984) and that a reduction in the mean body size of resident mammal species may deplete the resources available to larger beetle species (Cambefort 1991). In support of this hypothesis we observed a marked decrease in the mean body size of all primate species encountered during standardized line transect surveys in secondary forest (1.3 kg individual⁻¹) compared with that of primary forest (3.6 kg), and the largest primate species in Jari (spider monkey, *Ateles paniscus*) was restricted to primary forest (C. A. Peres, unpublished data).

One of the most striking and novel results from this study is that the decline of dung beetle body size observed across the whole community was largely consistent within individual genera. Similar results have been found in other analyses, controlling for higher level phylogenetic differences, on patterns of body size and extinction risk in birds (Gaston & Blackburn 1995) and beetles (Cunningham & Murray 2007). However, it is not immediately clear why this should be the case across a much finer (i.e. genus level) taxonomic scale of functionally similar species. It seems unlikely that the same physiological or resource-based mechanisms responsible for driving community-wide changes in body mass are also responsible for driving patterns within genera that vary in mass by orders of magnitude. Nevertheless, non-random species co-occurrence patterns are common in nature and, if our observation reflects a more general phenomenon, it is possible that a combination of internal species' constraints (e.g. taxon-dependent competitive advantages or dispersal ability) and external environmental filters (e.g. phylogenetically constrained thresholds of physiological tolerance; Chown 2001) serve to determine a set of assembly rules that selects against large bodied congeners outside primary forest. However, understanding the nature of any such set of rules is hampered by our almost complete lack of ecological information on most tropical forest dung beetles, especially small-bodied genera.

CONCLUSIONS

We have demonstrated that secondary and plantation forests in a large neotropical landscape host exceptionally depauperate dung beetle communities. That secondary and plantation forests harboured smaller populations of most primary forest species and tended to lack larger bodied species has worrying implications for the maintenance of dung beetle-mediated

services outside primary forests, such as secondary seed dispersal and dung burial (Andresen & Feer 2005).

The discrepancy between our results and those of studies elsewhere in the tropics is most probably explained by the importance of differences in biogeographical and landscape context, together with the influence of systematic sampling biases. These factors confound our ability to draw general patterns, and highlight the importance of developing quantitative meta-analyses (Nichols *et al.* 2007) that can provide an objective basis for evaluating future empirical studies.

In accounting for many of these confounding factors, our results indicate that we are in danger of understating the tropical forest biodiversity crisis (Laurance 2007). Specifically, we caution strongly against optimistic views that forest regeneration schemes in highly degraded landscapes can effectively offset the loss of species following the loss of primary forest habitat (Wright & Muller-Landau 2006). To be effective, management strategies for production landscapes need to emphasize the importance of protecting remaining areas of primary forest. In areas where this is not possible, it is vital that the key methodological and ecological considerations highlighted in our study are given priority when assessing the conservation value of human-dominated forest lands.

Acknowledgements

We thank the Brazilian Ministério de Ciências e Tecnologia (CNPq) and Ministério do Meio Ambiente (MMA-IBAMA) for permission to conduct this research. We thank Grupo Orsa and the staff of Orsa Florestal and Jari Celulose at Jari for permissions and logistic support. We are very grateful to Fernando Z. Vaz-de-Mello for help in the identification of specimen material. The project was funded by a Natural Environment Research Council (NERC) Studentship to T. A. Gardner, the UK Government Darwin Initiative, National Geographic Society, Conservation Food and Health Foundation, and Conservation International. We thank Liz Nichols and Sacha Spector for discussions, and Liz Nichols, Julio Louzada and three anonymous referees for valuable comments on earlier versions of this manuscript. This is publication number 15 of the Land-Use Change and Amazonian Biodiversity Project (see www.tropicalforestresearch.org).

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Received 5 August 2007; accepted 5 December 2007

Handling Editor: Julia Jones

Supplementary material

The following supplementary material is available for this article.

Appendix S1. The influence of seasonality on patterns of observed species richness and relative abundance in primary, secondary and *Eucalyptus* plantation forests in Jari, north-east Brazilian Amazonia

Table S1. Species, numbers of captures and average body masses of Scarabaeinae dung beetles sampled in primary, secondary and *Eucalyptus* plantation forests

Table S2. Species richness, sample coverage and completeness, and diversity of dung beetles sampled in primary, secondary and *Eucalyptus* plantation forests

Table S3. Species percentage contributions towards pairwise dissimilarities in dung beetle community structure across primary, secondary and *Eucalyptus* plantation forests

Table S4. Species percentage contributions towards within habitat similarities in dung beetle community structure for primary, secondary and *Eucalyptus* plantation forests

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