Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles

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Summary

1. The future of tropical forest species depends in part on their ability to survive in human-modified landscapes. Forest strips present a priority area for biodiversity research because they are a common feature of many managed landscapes, are often afforded a high level of legal protection, and can provide a cost-effective and politically acceptable conservation strategy.

2. Despite the potential conservation benefits that could be provided by forest strips, ecologists currently lack sufficient evidence to inform policy and guide their design and management.

3. We used a quasi-experimental landscape in the Brazilian Amazon to test the importance of four management-relevant variables (forest type, isolation distance, forest structure, and large mammal activity) on the potential biodiversity conservation value of narrow forest strips for dung beetles.

4. Information-theoretic model selection based on AICc revealed strong support for the influence of large mammal activity and forest type on dung beetle abundance; isolation distance on species richness; and forest structure on the relative abundance of matrix-tolerant species. Multi-dimensional scaling showed a strong influence of forest type and isolation on community composition and structure, with riparian and dry-land strips having complementary sets of species.

5. *Synthesis and applications.* To enhance the conservation value and ecological integrity of forest strips in human-modified landscapes we recommend that strip design considers both isolation distance and whether or not the strips encompass perennial streams. In addition, we identify the maintenance of forest structure and the protection of large mammal populations as being crucially important for conserving forest dung beetle communities.

Key-words: Brazil, fragmentation, isolation, Jari, mammals, Scarabaeinae, tropical forest

Introduction

The future of tropical forest species depends in part on their ability to survive in human-modified landscapes (Gardner *et al.* 2009). Research plays a vital role in informing effective strategies for the design and management of these landscapes, including the spatial arrangement of remnants of native forest and the composition of the wider matrix (Lindenmayer & Hobbs 2007). Historically most work has focussed on habitat fragmentation, and the importance of area and isolation on species persistence in remnant forest patches. However, the simple patch-based dynamics proposed by Island Biogeography Theory are inadequate for understanding fragmented ecosystems (e.g. Laurance 2008) and recent research has highlighted the importance of other factors, including edge effects (Ewers, Thorpe & Didham 2007), matrix properties (Fischer & Lindenmayer 2007), and differences in whole landscape attributes and context (Fahrig 2003; Bennett, Radford & Haslem 2006). Despite these advances, the importance of many landscape features that are likely to influence biodiversity in human-modified landscapes remains poorly understood.

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Narrow forest strips warrant research attention because they are a common feature of many managed landscapes (to delineate land-use boundaries and protect riparian habitat), are often afforded a high level of legal protection, and may provide a particularly cost-effective and politically acceptable biodiversity conservation strategy (compared to changes in production system or set-asides of large blocks of native habitat). Native riparian vegetation is also protected by environmental law in many tropical countries. For example, in Brazil, the Forest Code requires landowners to set aside 30–500 m wide forest buffers alongside perennial streams and rivers, depending on the width of the water course (Código Florestal 2001). *Terra firme* (unflooded) forest strips are less common than these riparian strips, but nevertheless are often used to separate large agricultural and silvicultural blocks, helping prevent soil erosion and the spread of pests, disease and fire (e.g. Zanúncio *et al.* 1998).

Despite the potential conservation benefits of forest strips, there is no strong evidence-base for informing policy and management decisions in modified tropical forest landscapes. Most research on forest strips has focussed on species-specific dispersal (i.e. *passage*) along habitat corridors that connect larger patches of forest, and their positive role in enhancing landscape connectivity (Beier & Noss 1998; Haddad *et al.* 2003). However, narrow forest strips do not necessarily connect larger forest patches, and much less is known about their potential value in providing habitat *per se*. Existing studies on the effectiveness of unconnected forest strips are biassed towards temperate regions (Wiens 2006), while work in the tropics has been mainly limited to vertebrates, including birds (Hawes *et al.* 2008; Lees & Peres 2008), mammals (Lees & Peres 2008), small mammal and leaf-litter frog communities (de Lima & Gascon 1999). To our knowledge information regarding the value of unconnected forest strips for tropical invertebrates is limited to a single study on a small set of beetle species in Australia (Hill 1995). This reflects an important gap in understanding as one of the main conclusions of research on connected strips (i.e. corridors) is that results are often highly taxon-specific (Schmiegelow 2007), and inferences from vertebrate studies may not extend to other taxa (Barlow *et al.* 2007).

We used a quasi-experimental landscape in the Brazilian Amazon to test the importance of four management-relevant variables on the potential biodiversity conservation value of unconnected forest strips. We chose dung beetles (Coleoptera: Scarabaeinae) as an ecological disturbance indicator (*sensu* McGeoch 2007; Gardner 2010) as they are cost-effective indicators of land-use change, both generally (Halffter & Favila 1993; Nichols *et al.* 2007) and for our study region (Gardner *et al.* 2008a, b), and have an important (and relatively well defined) role in ecosystem functioning (Nichols *et al.* 2008). We briefly outline the *a priori* theoretical or empirical support for each of our four hypotheses, which test the extent to which dung beetle abundance, richness and community structure are affected by:

1. Forest type (*terra firme* and riparian): An appreciation of underlying edaphic conditions is essential for determining conservation value (e.g. Brinson & Verhoeven 1999; Franklin & Swanson 2007). Riparian environments are often characterized by distinct vegetation communities, and are likely to present particular challenges to dung beetles as their larval development take place mainly in underground nests (Halffter & Edmonds 1982) and they suffer high mortality rates in waterlogged soils (Brussaard & Slager 1986; Sowig 1995).

2. Strip isolation (landscape structure): Distance along the strip from continuous forest is an important determinant of conservation value for birds and large mammals (Hawes *et al.* 2008; Lees & Peres 2008). In addition, edge effects exert a strong influence on forest biodiversity (Laurance *et al.* 2002; Ewers & Didham 2008), including dung beetles (Klein 1989; Spector & Ayzama 2003), and some generalist invertebrate species may spillover into native forests from neighbouring agricultural or silvicultural areas (e.g. Rand, Tylianakis & Tscharntke 2006).

3. Physical changes to forest structure (reduction in tree basal area): Forest structure is an important determinant of faunal communities in disturbed tropical forests (e.g. Barlow & Peres 2004). Forest strips are especially vulnerable to changes in forest structure such as caused by selective logging because of high accessibility, and because strips may respond to isolation in a similar way to fragments, suffering a 'collapse' in above-ground live biomass through edge-related mortality (e.g. Laurance *et al.* 1997).

4. Resource availability: The distribution of dung beetles is thought to be strongly influenced by the distribution of mammals that provision essential dung resources for feeding and reproduction. However, only one study has yet to explicitly test this relationship without the confounding effect of physical landscape modification (Andresen & Laurance 2007; Nichols *et al.* 2009).

Materials and methods

Sampling was conducted in the 17 000 km^2 landholding of Jari Celulose, located in the north-eastern Brazilian Amazon (0°53S, 52°36W). Approximately 10% of the primary forest in this landholding was converted to exotic tree plantations between 1969 and 1990. At the time of study the landscape consisted of fast growing *Eucalyptus* plantations on 5–7 year rotations, with some large tracts of regenerating secondary forest (14–19 years old), and vast expanses of relatively undisturbed primary forest (Fig. S1, Supporting information). We examined remnant forest strips that extended from primary forest areas into the matrix of commercial *Eucalyptus* plantations. These were on both dry land > 250 m from the nearest stream (called here *terra firme* forest strips = TF) and in the riparian forests along 2–5 m wide perennial streams (called here riparian forest strips = RIP). Primary forests in Jari have a mixed disturbance history that includes hunting of large vertebrates from smallholders (e.g. Parry, Barlow & Peres 2009a, b) and some selective logging that occurred during the implementation of the tree plantations.

We selected eight forest strips in total, including four *terra firme* and four riparian. Three sampling treatments characterized each strip: 'control' sites were located within an area of continuous (> 5000 ha) primary forest adjacent to each of the strips; 'near' sites were located at the start of each forest strip where it connected with the neighbouring continuous forest; while 'far' sites were located

more than 2·5 km along the strip as it extended into the *Eucalyptus* matrix. We therefore sampled a total of 24 sites, with four replicates for each sampling treatment (near, far and control) for both TF and RIP strips. The existing structure of the study landscape constrained our ability to isolate the single causal factor that could explain any observed differences in sampled fauna between TF and RIP strips, because RIP strips were generally wider than TF strips [TF mean width = 115 m (range 95–150 m); RIP mean width = 213 m (125–300 m)], and 'far' sites within riparian remnants were typically further from continuous forest [TF mean distance = 3·4 km (2·5–4·0 km); RIP mean distance = 7·0 km (range 6·0–9·0 km)]. Furthermore, RIP sites were more dispersed geographically than the TF sites (see Fig. S1, Supporting information and Hawes *et al.* 2008 for a map).

FAUNAL SAMPLING

Faunal sampling took place in two periods, from September to December 2005, coinciding with the dry season [mean monthly rainfall (1968–2004) = 70 mm per month over these months], and from January to April 2006, with the wet season [mean monthly rainfall (1968–2004) = 273 mm per month over these months]. Dung beetle and large mammal communities were sampled simultaneously in both seasons, alternating sampling between forest type and isolation classes to minimize the potential influence of seasonality on treatment responses within sample periods. Forest structure was sampled in May–June 2006.

Dung beetles

Dung beetles 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 (see Larsen, Lopera & Forsyth 2006). Five traps each were separated by 200 m along a linear 1-km transect that was located along the middle of each strip (TF), or as close to the middle as possible while avoiding water (RIP). We operated traps for two 24-h periods at each site in both seasons, with the captured individuals removed and bait replaced every 24 h. All captures were later processed in a laboratory and identified to species. Where species names were unknown a series of unidentified species numbers was assigned to each genus, and names were standardized with previous collections made for the same region (Gardner *et al.* 2008b). Voucher specimens have been deposited in three Brazilian collections: Museu Paraense Emílio Goeldi (Belém, Pará), Laboratório de Ecologia e Conservação de Invertebrados, Universidade Federal de Lavras (Lavras, Minas Gerais), and Setor de Entomologia da Coleção Zoológica do Instituto de Biociências da Universidade Federal de Mato Grosso (Cuiabá, Mato Grosso).

Sampling the matrix

We independently sampled dung beetles in 24 plantation blocks distributed across the landscape, using the same trap design and protocol used in the forest strips. Data were collected between September and November 2006, and were used to characterize matrix-tolerant dung beetle species common within the *Eucalyptus* plantations. We classified as matrix-tolerant all species with ≥24 individuals captured in *Eucalyptus*, which was equivalent to the number of sampling sites in this forest type. This definition encompassed 98% of the species that were captured in the plantations (Table S1, Supporting information).

Mammal surveys

We developed a simple index of the total number of independent detections to capture differences in large (> 300 g) mammal activity at each site based upon standardized surveys carried out along 1 km transects. Each transect was surveyed over three consecutive days in each of the seasonal replicates. On day one, a highly experienced observer carried out a line-transect survey along the 1 km transect, between 0630 h and 0730 h, reporting all direct observations (vocalizations within the same strip and visual sightings) and indirect evidence of recent activity (within 48 h) of a species (tracks, scrapes, burrows, and faeces). To standardize the effective strip width, we only included all direct detections that were estimated to be within 50 m from the line-transect (and therefore within the forest strip), and all indirect observations (of faeces, tracks etc.) within 6 m of the line. These initial surveys were complemented with repeat surveys on day two and three, which were carried out at the same time of day and excluding observations recorded on previous surveys.

Forest structure and landscape context

Trees were sampled along a 10 × 250 m section of the faunal transects, measuring all live standing trees > 10 cm DBH if more than 50% of their trunk was within 5 m of the centre of the transect (see Hawes *et al.* 2008). We calculated basal area per plot excluding the largest tree from each sample to remove the potential bias from the stochastic presence of single large trees in relatively small forest plots (although results using all the data remained quantitatively very similar). Landscape context was described by a simple classification according to where it was along each strip (i.e. control, near, and far, see Fig. S1, Supporting information) as these categorical variables captured most of the associated variation in the landscape structure and composition (see Hawes *et al.* 2008).

DATA ANALYSIS

Prior to undertaking analysis, we pooled data from the dry and wet season samples to maximize sample representation at the trap level. This was justified as both the abundance and community structure of dung beetles was positively correlated between the two periods for both TF (Mantel–Relate test R = 0·45; P = 0·002; abundance r = 0·46, n = 24, P = 0·02) and RIP forest plots (Mantel–Relate test R = 0·73, P = 0·002; abundance r = 0·53, n = 24, P = 0·007; see also Gardner *et al.* 2008b for similar results). Unless otherwise stated, all analysis was undertaken in the R statistical environment (R Development Core Team 2009).

The approaches we used for data analysis depended upon the choice of explanatory variables and the response metric (Table 1). First, we examined changes in mammal activity and change in forest structure (basal area) using nonparametric Kruskal–Wallis tests. Generalized Linear Mixed-Effects Models were then used to examine how forest type (TF or RIP), isolation class (control, near or far), forest structure (basal area of live trees) and mammal activity affect patterns of abundance, the proportion of matrix-tolerant species in samples, and species richness (Table 1). We used an information-theoretic approach based on the second-order Akaike's Information Criterion corrected for small sample size (AICc – see Burnham & Anderson 2002). Mixed-effects models were used to account for 'site', entered as a random factor, with five independent samples nested within 24 sites (a total of 120 samples) (Bolker *et al.* 2009). Models were run using the 'glmer' function in the 'lme4' package in the R environment, and fitted using the Laplace approximation and

Table 1. Explanatory variables and dung beetle community response metrics, showing the analyses that were conducted.

Explanatory variables	Abundance[a]	Community response metrics		
		Proportion of matrix-tolerant species[a]	Species richness[a]	Community structure
1) Forest type	**GLMM**	**GLMM**	GLMM SAC	**MDS & ANOSIM** Bio-Env **IndVal**
2) Isolation class	GLMM	GLMM	**GLMM SAC**	**MDS & ANOSIM** Bio-Env **IndVal**
3) Forest structure	GLMM	**GLMM**	GLMM	Bio-Env
4) Mammal activity	**GLMM**	GLMM	GLMM	Bio-Env

[a]Only variables selected in the single best model are shown in bold here, see Table 2 for more details.
Bold font indicates the variables that were given strong support, either through visual assessments of patterns (Species Accumulation Curves, SAC; Multi-dimensional scaling ordination, MDS), significance testing (Indicator Value analysis, IndVal; Analysis of Similarity tests, ANOSIM), model selection (General Linear Mixed-Effects Models, GLMM), or high matching coefficients (Bio-Env)

Poisson errors for count data, and binomial errors for proportion data (R Development Core Team 2009). We used the 'dredge' function from the 'MuMIn' package to test models defined by all possible variable combinations and rank them by their AICc-based model weight (Burnham & Anderson 2002). We did not include any interaction terms in the analysis because of a shortage of sample data, and also because we had no *a priori* ecological justification for their existence.

Species rarefaction curves (calculated in Estimate S v. 7·5, R. K. Colwell, http://purl.oclc.org/estimates) were used to compare species richness across isolation treatments within both TF and RIP forest strips. Non-metric multi-dimensional scaling (MDS) ordination based on the Bray–Curtis similarity indices and analysis of similarity (ANOSIM) tests were used to examine changes in dung beetle community structure (log_{10} transformed and standardized abundance data) and composition (presence-absence) between TF and RIP strips ($n = 24$). In addition, we used Bio-Env analysis to examine the matching coefficient between the four explanatory variables and a similarity matrix based on community structure. We separated TF and RIP data in order to examine the effect of strip type on community structure, and repeated the analysis at the level of transect ($n = 12$), trap ($n = 60$), and at the trap level within each of the eight forest strips ($n = 15$ for each of the eight ordination plots). Multi-dimensional scaling, ANOSIM and Bio-Env analysis was performed using Primer v.5 (Clarke & Gorley 2001).

We used Indicator Value (IndVal) analysis (Dufrene & Legendre 1997) to identify species that were significant indicators of forest strip type, and significant indicators of isolation class separately for TF and RIP forests. This method combines measures of habitat specificity (patterns of relative abundance) and habitat fidelity (patterns of incidence), and uses a randomization procedure to test the significance for each species. Previous work on dung beetles has demonstrated the effectiveness of IndVal for separating species that indicate different habitat types and levels of human-induced degradation (e.g. McGeoch, Van Rensburg & Botes 2002; Gardner et al. 2008b; Gardner 2010).

Results

We captured 89 species in a total sample of 30 565 dung beetles across the 24 forest sites, with 76 species and 20 827 individuals from *terra firme* forests and 78 species and 9738 from riparian forests. In addition, we captured 43 species in a total sample of 6551 individuals in 24 different stands of *Eucalyptus* (at least 500 m from any plantation border), 17 of which were captured ≥24 times and were therefore classified as matrix-tolerant species (Table S1, Supporting information).

MAMMAL ACTIVITY

We recorded 1185 mammal detections split between 26 species and two species groups (Table S2, Supporting information). The majority of observations ($n = 1013$) were indirect (mostly recent tracks, scrapes and holes). Faeces were rarely encountered ($n = 7$), and could not be used as a direct measure of resource abundance. The most frequently recorded species were armadillos, red brocket deer (*Mazama americana*, Erxleben), agoutis (*Dasyprocta leporine*, L.) and tapirs (*Tapirus terrestris*, L.) (Table S2, Supporting information). There was no significant difference in overall mammal encounter rates between *terra firme* and riparian forests ($\chi^2 = 1·6$, d.f. $= 1$, $P = 0·2$). Mammals were recorded significantly more frequently in both near and far forest strips than in continuous forest controls (mean $\pm$ SE in control $= 38·8 \pm 10·8$, near $= 56·9 \pm 16·1$, far $= 56·4 \pm 6·1$, $\chi^2 = 8·4$, d.f. $= 2$, $P = 0·014$), but these differences were NS within each forest type given the small sample sizes (*terra firme*, mean $\pm$ SE in control $= 44·8 \pm 11·4$, near $= 58·5 \pm 18·9$, far $= 58·0 \pm 5·1$, $\chi^2 = 2·8$, d.f. $= 2$, $P = 0·2$; riparian forests, mean $\pm$ SE in control $= 32·8 \pm 6·8$, near $= 49·0 \pm 13·8$, far $= 54·8 \pm 7·4$, $\chi^2 = 5·3$, d.f. $= 2$, $P = 0·07$).

FOREST STRUCTURE

The basal area of live trees was generally lower in the far TF sites than in control plots, but these differences were NS (mean $\pm$ SE: control $= 6·7$ m^2 ha^{-1} $\pm 1·2$, near $= 5·5 \pm 0·8$, and far $= 3·4 \pm 2·4$, $\chi^2 = 4·3$, d.f. $= 2$, $P = 0·12$). Live tree basal area was similar across riparian isolation treatments (mean $\pm$ SD control $= 7·3$ m^2 ha^{-1} $\pm 2·0$ near $= 8·0 \pm 1·6$ and far $= 7·2 \pm 1·8$, $\chi^2 = 0·5$, d.f. $= 2$, $P = 0·79$).

DUNG BEETLE RESPONSE METRICS

Abundance

Model selection revealed strong support for the influence of large mammal activity and forest type on dung beetle abundance (Table 2). An inspection of evidence-ratios between model pairs (calculated as the relative difference in AIC$_c$ model-weights; Burnham & Anderson 2002) suggests that

Table 2. AICc-based model selection for (i) dung beetle abundance, (ii) proportion of total abundance comprised of matrix tolerant species, and (iii) species richness. Generalized Linear Mixed-Effect Models used site as a random factor, and include Basal area (BA), Isolation class (I), Mammal activity (M), and Forest type (FT) as fixed factors. We also show the number of predictor variables (K), AICc differences (Δ) and Akaike weights (ω).

Model ranks Total abundance	Model	K	AICc	Δ	ω	Cumulative ω
1	M + FT	4	1970	0·000	0·497	0·497
2	BA + M + FT	5	1972	1·846	0·197	0·694
3	FT	3	1974	3·670	0·079	0·773
4	I + M + FT	6	1974	3·973	0·068	0·841
5	I + FT	5	1975	4·945	0·042	0·883
6	BA + FT	4	1975	5·468	0·032	0·915
7	BA + M	4	1976	5·991	0·025	0·940
Proportion of total abundance comprised of matrix-tolerant species						
1	FT	4	16·68	0·000	0·243	0·243
2	BA	4	17·24	0·562	0·183	0·426
3	BA + FT	5	17·78	1·104	0·14	0·566
4	M + FT	5	18·84	2·164	0·082	0·648
5	Intercept only	3	18·95	2·273	0·078	0·726
6	BA + M	5	19·24	2·562	0·067	0·793
7	BA + M + FT	6	19·99	3·309	0·046	0·839
8	M	4	20·51	3·83	0·036	0·875
9	BA + I	6	20·83	4·149	0·031	0·906
10	I + FT	6	20·88	4·202	0·03	0·936
Observed species richness						
1	BA + I	5	112·8	0·000	0·260	0·260
2	I + FT	5	114·0	1·232	0·141	0·401
3	BA + I + M	6	114·2	1·408	0·129	0·530
4	BA + I + FT	6	114·3	1·518	0·122	0·652
5	I	4	114·9	2·099	0·091	0·743
6	I + M + FT	6	116·1	3·328	0·049	0·792
7	I + M	5	116·2	3·381	0·048	0·840
8	BA + I + M + FT	7	116·2	3·391	0·048	0·888
9	FT	3	117·3	4·496	0·027	0·915
10	Intercept only	2	117·4	4·663	0·025	0·940

Models are shown up top 95% of cumulative Akaike weights (Cumulative ω). Bivariate relationships are shown in Fig. 2

Model 1 (based on forest type and mammal activity) had the strongest support from the data, although there was also strong evidence for Model 2, which included differences in basal area (ΔAICc was less than two in both cases; Burnham & Anderson 2002). Forest type was present in all of the top ranked models (Table 2), and many more individuals were captured in TF than in RIP sites (Figs 1 and 2). A positive relationship between our index of mammal activity and dung beetle abundance was observed in both TF and RIP forests (Fig. 2), whereas isolation and forest structure appeared to be relatively unimportant (Table 2).

Community composition and structure

Forest type had a strong influence on dung beetle community structure (ANOSIM $R = 0·42$, $P = 0·001$; Fig. S2) and composition (ANOSIM $R = 0·19$, $P = 0·002$), irrespective of isolation treatments. These results were supported by the Bio-Env analysis, as forest type had the highest matching coefficient with the community structure data (0·50), compared with mammal activity (0·40), basal area (0·31), and isolation

($-0·05$). Only one species (*Canthon aff. triangularis 2*) was a consistent indicator of RIP based on the IndVal analysis, and 12 species appeared to avoid RIP and were significant indicators of TF forests (Table 3).

Because of the strong influence of forest type, we examined the effect of isolation on dung beetle community structure separately for TF and RIP forests. Directional change in community structure with isolation can be clearly observed along axis 2 of the MDS ordinations in TF and RIP forests (Fig. 1a, b). Although there was a significant difference between the control and far sites in TF forests when analysed at the site level (Fig. 1a, ANOSIM, $R = 0·50$, $P = 0·03$), there was no significant effect of isolation within riparian strips (Fig. 1b, ANOSIM, $R = 0·06$, $P = 0·3$). However, all isolation treatments were highly significant at the level of trap in both cases (*terra firme*, Fig. 1c, ANOSIM $R = 0·32$, $P = 0·001$, riparian, Fig. 1d – ANOSIM $R = 0·16$, $P = 0·001$) and the differences between treatments were always highly significant when we compared community structure in continuous, near and far traps within each strip separately (Fig. S3, Supporting information).
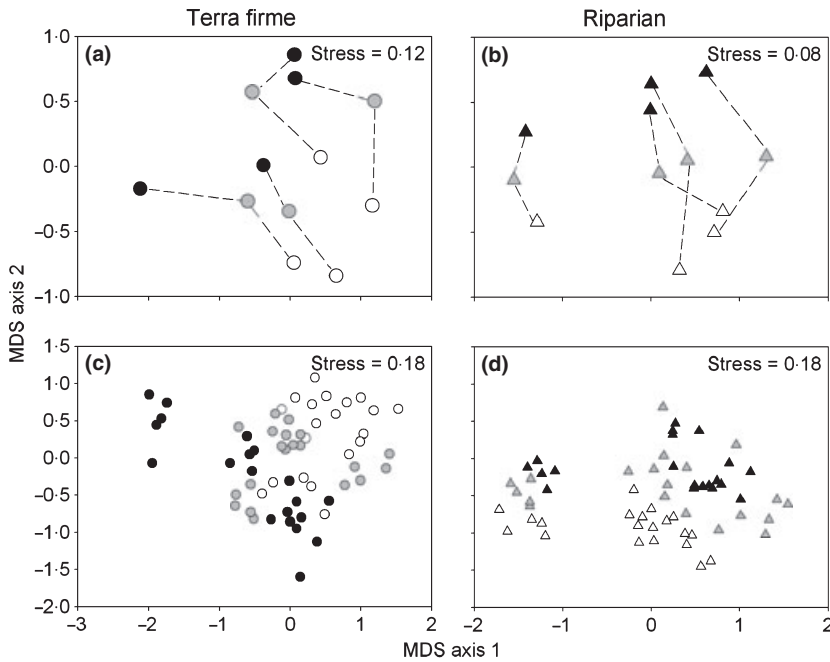
Fig. 1. Non-metric multi-dimensional scaling (NMDS) ordination based on dung beetle community structure for *terra firme* and riparian forests. Black, grey and open symbols denote continuous, near, and far samples, respectively. Dashed lines in panels (a) and (b) link sampling sites from the same area. Panels (c) and (d) present the same data at the level of each pitfall trap.
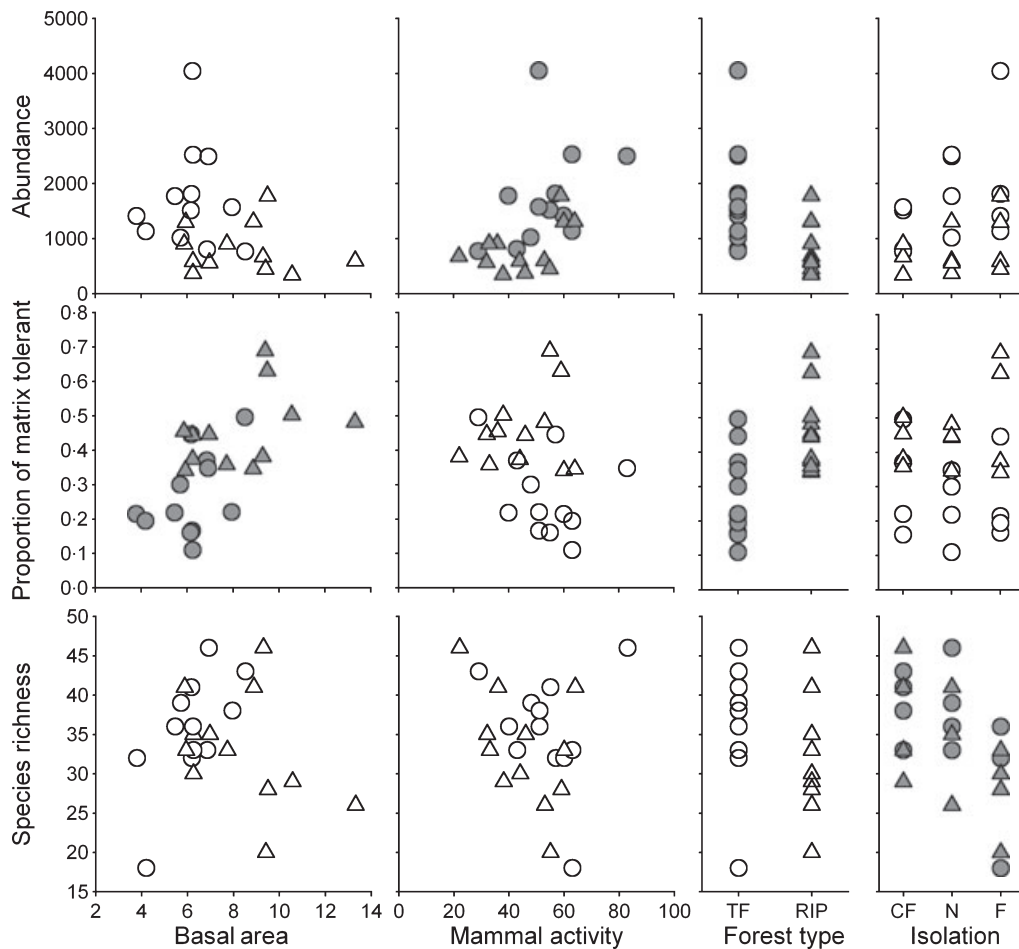

Fig. 2. Bivariate relationships between explanatory variables and dung beetle response metrics. Symbols are shaded for the relationships that were given strong support under model selection (Table 3). Circles = Terra firme (TF) sites, triangles = Riparian (RIP) sites. Isolation treatments are Continuous forest (CF), and forest strips near (N), and far (F) from continuous forest.

Table 3. Mean (± SE) abundance of dung beetle species that were significant indicators of either *terra firme* (TF) or riparian (RIP) forest sites. Species are ranked by the significance of their indicator value

Species	Indicator of:	Mean abundance				
		TF	SE	RIP	SE	Indicator *P*
Trichillum pauliani	TF	31·3	6·5	0·8	0·8	0·0002
Onthophagus haematopus	TF	189·0	47·8	39·6	7·9	0·0004
Canthon aff. triangularis sp. 2	RIP	0·6	0·3	23·6	6·9	0·0004
Canthidium aff. lentum	TF	11·4	2·1	2·0	1·2	0·0008
Dichotomius aff. lucasi	TF	502·8	166·9	65·4	20·5	0·0010
Uroxys sp. B	TF	90·2	33·7	18·3	3·4	0·0012
Ontherus carinifrons	TF	63·8	18·4	5·8	2·9	0·0018
Ateuchus sp. A	TF	117·2	30·0	20·2	9·7	0·0022
Canthidium aff. deyrollei	TF	77·6	30·7	8·0	5·3	0·0034
Ateuchus sp. F	TF	47·8	38·8	1·8	0·8	0·0066
Eurysternus hamaticollis	TF	31·6	15·7	4·3	1·4	0·0076
Canthidium sp. F	TF	7·2	2·7	0·6	0·2	0·0124
Ateuchus pauki	TF	25·8	8·0	5·3	2·0	0·0354

Just three species were significant indicators of isolation distance based on the IndVal analysis (conducted separately for TF and RIP). All of these were significant indicators within riparian forests, with *Ateuchus* sp. A indicating far sites (mean ± SE abundance in control = 3·8 ± 1·7, near = 6·0 ± 1·6, far = 50·8 ± 23·8, IndVal *P* = 0·006), and both *Ateuchus pauki* and *Dichotomius apicalis* indicating continuous forest (*Ateuchus pauki;* mean ± SE in control = 11·8 ± 4·3, near = 2·0 ± 1·2, far = 2·5 ± 1·7, IndVal *P* = 0·04; *Dichotomius apicalis;* mean ± SE in control = 13·3 ± 3·6, near = 1·5 ± 1·6, far = 2·5 ± 1·2, IndVal *P* = 0·007).

Species richness

Rarefaction curves suggest isolation is an important factor determining patterns of species richness, as far sites were consistently less species-rich than control sites in *terra firme* and riparian forests (Fig. 1). The importance of isolation was supported by model selection. Although Akaike model weights were fairly equally distributed across the top four models which included all explanatory variables, isolation class (continuous, near or far) was consistently present in all models where ΔAICc was less than two (Table 2).

Distribution of matrix-tolerant species

Nine thousand five hundred and sixteen of the total 30 565 individuals captured (31%) belonged to species classified as matrix tolerant (Table S1, Supporting information). Forest type and basal area appeared to be the most important factors explaining differences in the relative abundance of these species (Table 2; Fig. 2). It is difficult to separate these two factors, as the evidence ratios suggest that the best model (forest type only) was only 1·3 times more likely than models based on basal area only, and only 1·7 times more likely than the third ranked model which included both variables (Table 2). The influence of forest basal area on the proportion of matrix-toler-

ant individuals was positive (see site-level bivariate plots, Fig. 2). There was no convincing evidence to suggest that the proportion of matrix-tolerant individuals in samples increased with isolation distance or mammal activity, and models containing these variables ranked lower than the null model (Table 2).

Discussion

The Jari forestry landscape provides a unique opportunity to examine how forest strips can help conserve tropical forest biodiversity. Overall, evidence suggests that all four of the factors we measured play a role in determining the dung beetle community found in a given forest strip, although different response metrics were more strongly influenced by different sets of explanatory variables (Tables 1 and 2; Fig. 2). We consider the implications of these findings for the design and management of forest strips for biodiversity conservation.

FOREST TYPE

The comparison between dry-land and riparian forests is complicated by the constraints imposed by the existing structure of the study landscape, including differences in mean strip width and length (see Materials and methods), historical origin, and the greater dispersion of riparian strips across the landscape (Fig. S1, Supporting information). Nonetheless, our results suggest that proximity to perennial streams can play an important role in structuring dung beetle communities in tropical forests: forest type had a strong influence on all of our response metrics except species richness (e.g. Table 1), and most dung beetle species were more abundant in TF forest strips and appeared to avoid RIP areas (Table 3). This makes biological sense, as flooding or peak high soil moisture can increase larval mortality (Brussaard & Slager 1986; Sowig 1995) and (with the exception of *Eurysternus hamaticollis* and *Trichillum pauliani*) the species preferring TF are paracoprids (burrowers),

requiring soil free from flooding for nesting (FZVM pers. obs.). In contrast, the only indicator species of RIP sites, *Canthon aff. triangularis* sp. 2, is a telecoprid (roller) which may allow for selection of more suitable nesting conditions. Given the suite of differences between TF and RIP sites, our results support calls to include underlying topographical or edaphic conditions when managing or designing landscapes for conservation (e.g. Brinson & Verhoeven 1999; Franklin & Swanson 2007).

STRIP ISOLATION

Sites furthest from primary forest were not invaded by *Eucalyptus* matrix-tolerant species, suggesting the silvilcultural matrix added little to the conservation value of these strips. However, the distance along the strip from continuous forest does seem to be an important determinant of conservation value as far sample sites (>2.5 km from continuous forest) had a lower species richness (Fig. 3) as well as a distinct community structure (Fig. 1, Fig. S3) compared to either nearer sites and continuous forest (see also Hawes *et al.* 2008; Lees & Peres 2008). The recolonisation of far sites by populations in continuous forest is unlikely as most species would require successive generations to disperse distances greater than 1 km during their adult phase (Arellano, Leon-Cortes & Ovaskainen 2008). Given these findings, it is logical to recommend focusing conservation efforts on strips close to continuous forest, and minimizing the distance to continuous forest when designing landscapes with forest strips as conservation features. However, we do not propose any hard and fast rules on minimum acceptable distances, as these are likely to be both context and taxon-specific (Schmiegelow 2007; Gardner *et al.* 2009).

FOREST STRUCTURE

Sites with a low tree basal area have tended to have a higher proportion of matrix-tolerant species (Table 2), with results consistent across different forest types (Fig. 2). This has important implications for the conservation of forest dung beetles, as the proportion of matrix-tolerant species in a sample can be taken as an inverse measure of conservation value (species that are unable to utilize the matrix are typically forest specialists and therefore afforded the highest level of conservation concern). Maintaining forest structure to closely resemble undisturbed continuous forest (i.e. by prohibiting selective logging

and protecting areas from fire and livestock disturbance) could therefore be one of the most effective ways of helping to maintain forest biodiversity in these strips. Conservation strategies that emphasize the landscape configuration of forest remnants will fail unless they also work to retain the structural integrity of those remnants. Furthermore, it is often likely to be easier to protect or restore the structural integrity of existing forest remnants than alter the configuration of the landscape itself.

Our results regarding forest structure should be viewed as a best-case scenario when compared to forest strips in other human-modified tropical forest landscapes. We did not observe the consistent collapse of above-ground live biomass in these forest strips that has been documented in fragmented Amazonian forests near Manaus (see Laurance *et al.* 1997), and most of our study sites have not been subject to the high levels of disturbance and degradation commonly associated with forest fragments in agro-pastoral landscapes elsewhere in Amazonia, including browsing and trampling from livestock in cattle-dominated areas (see Lees & Peres 2008).

MAMMAL ACTIVITY

Our results strongly support the notion that large mammal activity is an important determinant of dung beetle abundance. This finding contributes to a growing body of correlative evidence linking the distribution of mammals and dung beetles across land-use intensity gradients (Estrada *et al.* 1998; Estrada, Anzures & Coates-Estrada 1999) and gradients of hunting pressure (Andresen & Laurance 2007) elsewhere in the tropics (Nichols *et al.* 2009). Our data are particularly convincing as a strong positive relationship was observed in both riparian and *terra firme* forest strips and, in contrast to two of the previous studies (Estrada *et al.* 1998; Estrada *et al.* 1999), was not potentially confounded by collinearity with isolation (see Nichols *et al.* 2009).

Our results lend weight to claims that mammal-dependent invertebrates such as dung beetles may be indirectly affected by mammal hunting (Andresen & Laurance 2007; Nichols *et al.* 2009). However, it is likely that patterns of mammal activity within forest strips in Jari are more closely related to the management of the *Eucalyptus* matrix rather than any spatially explicit gradient in hunting pressure. Although forest strips may occasionally be used by subsistence hunters (Parry *et al.* 2009a, b), overall large mammal activity was actually higher in forest strips than in the continuous forest controls. Moreover,
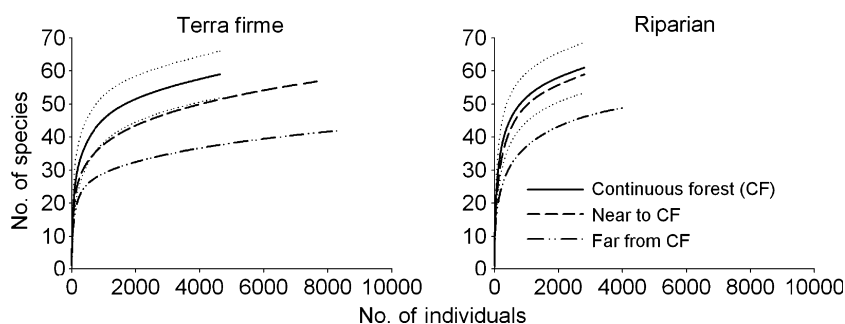

Fig. 3. Individual-based species accumulation curves for dung beetles in three isolation treatments (continuous, near and far) in *terra firme* and riparian forests. The dotted lines show 95% confidence intervals for the continuous forest.

discussions with local hunters and our own observations suggest that forest strips were used as shelter belts for ungulates such as collared peccaries (*Pecari tajacu* L.) and brocket deer, which browse and forage on the rich understorey in the *Eucalyptus* plantations at night and remain in the strips during the day. Our results may therefore be more favourable than those in forest strips in landscapes dominated by agriculture, as the matrix habitat in Jari (tree plantations) is used by many forest vertebrates (see Barlow *et al.* 2007).

Our index of large mammal activity was intended to reflect total dung resource availability rather than precise estimates of the density, total biomass, or relative abundance of individual mammal species, or the quality and quantity of the dung they produce. Future research is necessary to understand how the spatial distribution of dung resources influences the distribution of resource-dependent beetles, and how differences in species-specific life history strategies can help explain different dung beetle responses (Nichols *et al.* 2009).

CONCLUSIONS AND CONSERVATION IMPLICATIONS

The conservation of forest strips in tropical forest landscapes dominated by agriculture or silviculture is generally motivated by legal requirements to protect remnant forests, especially along water courses, as well as by the benefits that buffer strips provide in demarking landholdings and land-uses, and providing protection from wind damage and crop diseases. Consequently, forest strips may often present a cost-effective and politically viable mechanism for biodiversity conservation within human-use areas. Our results demonstrate that 95–150 m wide *terra firme* forest strips and 125–300 m wide riparian strips both contain an appreciable component of the native forest dung beetle fauna, yet are not sufficient for the conservation of many primary forest specialists as neither retained a full complement of species at distances beyond 2·5 km from continuous primary forest. We highlight the importance of the local management of forest strips, and the need to maintain both the original structure of intact forest and protect native large mammal populations.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Map of study area showing the 24 sampling sites and areas of *Eucalyptus* plantation (dark grey), secondary forest (light grey) and primary forest (white). Symbols show continuous forest (circles), 'near' sites (squares) and 'far' sites (triangles) in terra firme (black) and riparian (white) forest strips. Inset shows detail of the three sample treatments in forest strips.

Fig. S2. Multi-dimensional scaling ordination (MDS) based on dung beetle community structure across 24 sample points, showing ordination of *terra firme* (circles) and riparian forests (triangles). Black, grey and open symbols denote continuous, near and far samples, respectively.

Fig. S3. Multi-dimensional scaling ordination (MDS) based on dung beetle community structure within each forest strip [near (grey) and far (white) sites] and the continuous forest control. Statistics are the stress for the MDS ordination and the Global R and P-values for ANOSIM tests. In every case, the community structure was significantly different between isolation treatments at $P = 0.008$. For comparative purposes the x-axis has been reversed in some cases so that continuous forest is always shown on the left.

Table S1. Rank abundance of matrix-tolerant dung beetles species that were frequently caught in *Eucalyptus* plantations (i.e. species caught ≥ total number of sampling sites -24).

Table S2. Mammals detected during faunal surveys, ranked by the number of detection events (both direct and indirect) for each species or species group.

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