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Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis

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Abstract

Although insects are crucial for maintaining ecosystem function, our understanding of their overall response to human activity remains limited. This is no less true of dung-burying beetles (Coleoptera: Scarabaeidae: Scarabaeinae), which provide a suite of critical ecosystem functions and services, yet but face multiple conservation threats, particularly from landscape conversion. Here we use a review and meta-analysis to synthesize the current knowledge concerning response to tropical forest modification and fragmentation of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). For every modified habitat type and individual forest fragment across 33 studies, we calculated six dung beetle community parameters, standardized relative to intact tropical forest. We organized modified habitats along an approximate disturbance gradient ranging from selectively logged, late and early secondary forest, through agroforestry, tree plantations, to annual crops, cattle pastures and clear-cuts. Secondary forests, selectively logged forest and agroforests supported rich communities with many intact forest species, while cattle pastures and clear-cuts contained fewer species overall with few forest-dwelling species. Abundance generally declined with increasing modification, but was quite variable. Communities in open habitats were often characterized by hyper-abundance of a small number of small-bodied species, leading to low evenness. Across fragmentation studies, dung beetle species richness, abundance and evenness declined in smaller forest fragments. Richness and abundance sometimes declined in more isolated fragments, although this response appeared to depend on matrix quality. Across both habitat modification and fragmentation studies, geographic location and landscape context appeared to modify dung beetle response by influencing the available pool of colonists. We discuss potential underlying mechanisms and conclude with recommendations for management and conservation and for future research.

Article Outline

Appendix B. Appendix

References

1. Introduction

The alteration of natural landscapes by humans is the primary cause of global biodiversity loss across all major taxonomic groups (Reid et al., 2005) and is expected to increase in severity over the coming decades as human populations continue to grow exponentially (Sala et al., 2000). Understanding the response of biotic communities to the modification of natural habitat is essential for predicting and mitigating further biodiversity loss. Yet the rate at which this required knowledge is accumulated is being vastly outpaced by even more rapid rates of biodiversity decline (Balmford and Bond, 2005).

Habitat modification and fragmentation comprise two of the most common types of landscape conversion. The former involves the direct alteration of a habitat as a result of human activities whereas the latter involves the reconfiguration of a habitat into smaller, isolated patches within a matrix of modified habitat. Developing theoretical and empirical frameworks for evaluating the impacts of habitat modification and fragmentation on biological diversity has long been a focus of ecology and conservation biology (Tilman, 1999 and Fahrig, 2003). The many published studies on the subject have created a deep, but highly uncoordinated foundation of data on the response of many taxonomic groups to these drivers at local to regional scales. Recent efforts to unite the growing body of empirical studies within comprehensive summaries of the growing corpus of empirical studies have begun to yield generalizable, global understanding of the dynamics of biodiversity in human dominated landscapes (IUCN et al., 2004, Reed, 2004 and Balmford and Bond, 2005).

Invertebrates are often affected strongly and more rapidly than other taxa by landscape changes, though they are often overlooked in disturbance studies (Samways, 1993 and Dunn, 2004a). As an abundant and diverse component of most ecosystems, insects are key players in many ecosystem processes and their loss can have negative cascading effects throughout entire communities (Coleman and Hendrix, 2000). Despite this, our knowledge of the response of insects to human activity continues to lag far behind that of other taxa. A strong, synthetic understanding of insect response to human activity is necessary to both support conservation policy decisions and assess the functional consequences of human disturbance (Balmford and Bond, 2005).

Scarabaeine dung beetles are an excellent focal taxon for examining interactions between anthropogenic disturbance and community structure (Favila and Halffter, 1997 and Spector and Forsyth, 1998). They have a wide global distribution and are a diverse and abundant group in both tropical and warm temperate ecosystems. They also have well understood ecological roles (Hanski and Cambefort, 1991) and a relatively stable taxonomy (Philips et al., 2004). By using dung as a food and nesting resource, they are key providers of several ecological services such as waste removal, secondary seed dispersal and vertebrate parasite suppression (Mathison and Ditrich, 1999, Andresen and Feer, 2005 and Horgan, 2005). Dung beetles exhibit a wide variety of morphological and behavioral traits (Hanski and Cambefort, 1991 and Feer and Pincebourde, 2005) and display rapid, graded responses to many kinds of natural and anthropogenic disturbance (Spector and Ayzama, 2003 and Horgan, 2005). Because of their dependence on vertebrate dung, beetle communities are likely to be influenced by changes in mammal communities (Estrada et al., 1999), which are often themselves affected by the synergistic effects of forest modification, fragmentation and elevated hunting pressure that can accompany increased forest access. Importantly, dung beetle community structure can be rapidly determined using simple, standardized trapping methods (Larsen and Forsyth, 2005), this permits efficient comparative evaluation of human impacts around the world. Here we provide the first global synthesis of dung beetle response to landscape conversion in tropical forests through a summary of the effects of tropical forest modification and fragmentation on dung beetle community structure across 33 studies from Central and South America, Southeast Asia and Africa. The analyses include data from several common types of modified forest (e.g. selectively logged forest, secondary growth, agroforestry, tree plantation annual crops, cattle pasture and clear-cuts) and for three commonly investigated forest fragment characteristics (size, degree of isolation and resource availability) on dung beetle species richness, abundance, evenness and composition. We discuss potential causal factors underlying beetles' response to landscape alteration and conclude with a discussion of priorities for conservation and for future research.

2. Methods

We performed a literature search in 2005 using the Science Citation Index Expanded with the following keywords: Scarabaeinae, dung beetle, tropical forest, anthropogenic, deforestation, modification and fragmentation for the years 1990–2005. In addition, we pursued publications cited by these works that were not retrieved by the keyword search, resulting in 43 publications. We also requested unpublished datasets from members of the Scarabaeinae Research Network, which resulted in six unpublished studies contributed by Trond Larsen, Sacha Spector, Kevina Vulinec and Federico Escobar. These published and unpublished works address the response of tropical Scarabaeine dung beetles to the modification ($n = 22$ published, four unpublished) and fragmentation ($n = 18$ published, two unpublished) of predominantly moist tropical forest. To understand the influence of these factors on dung beetle community structure, a subset of 33 of these studies was quantitatively reviewed. We employed the following selection criteria (Roberts et al., 2006); we selected only one publication to include if an author published upon identical data multiple times (e.g. in different languages). However we incorporated all useable studies when multiple publications based on independent sampling events were conducted within a single landscape. We selected only those studies which used internally consistent sampling methods across all sites and treatments, had minimal elevation differences across sites with a study and sampled dung beetles with standardized dung-baited pitfall traps.

Further selection within the 'modification' subset was conducted by selecting only studies which sampled both one or more modified habitat types and intact forest within the same system, defining 'intact' forests as those defined by individual authors as 'contiguous' or 'primary' forest. While sampling efforts and the species richness of the sampled beetle communities sometimes ranged widely, we made no restrictions on a minimum sampling effort. For those studies that sampled multiple replicates of a single modified habitat type, we incorporated an average value across all replicates, but did not weight studies on the basis of the number of replicates sampled.

For these ‘modification’ studies, we compared dung beetle communities in intact forest with those sampled from a series of common tropical land-uses. We defined land-use categories with the original published definitions and ordered them in a qualitative gradient of increasing habitat modification relative to intact forest (Glor et al., 2001, Beck et al., 2002 and Jones et al., 2003). Land-uses included: selectively logged forest (abbreviated SL; 14–168 m^3 wood extracted/ha; $n = 4$) late secondary forest (LS; >15 yr; $n = 7$), early secondary forest ($\leqslant$10 yr; $n = 8$), agroforests (AF; coffee or cacao under native forest cover; $n = 4$), tree plantations (TP; monoculture timber, sun coffee or cacao; $n = 6$), annual crops (AC; predominantly corn fields; $n = 3$), cattle pastures (PAS; grass monocultures with no tree cover; $n = 9$) and clear-cuts (CC; small clearings, often embedded within forest; $n = 7$). The lack of detailed site descriptions from the majority of studies prevented a more quantitative ordering of increasing habitat modification. Further detail on the authors’ descriptions of each modified habitat and sampling efforts can be found in Appendix A.

For the ‘fragmentation’ studies, we additionally removed those studies that sampled within a single fragment. The remaining 12 studies related beetle response to fragment characteristics such as fragment area, distance from potential source populations, resource (dung) availability and, occasionally, vegetative composition. As no study was conducted using landscapes rather than individual fragments as the unit of replication, we can only make inferences about the role played by factors which generally must be comparatively sampled at the landscape level, such as matrix composition or fragment age (Fahrig, 2003). Of the 12 studies, seven were comparatively sampled in both intact forest and forest fragments (109 fragments in total). As with the modification studies, we made no restrictions on a minimum sampling effort, which ranged across studies.

Several approaches may be taken to aggregate existing small-scale data sets to assess broader ecological patterns of change or response (Côte et al., 2005). We used two methods to summarize trends in dung beetle community response to tropical forest modification and fragmentation. The first was a quantitative literature review based on individual studies and the second was a formal meta-analysis, which incorporated modification and fragmentation studies into separate pooled analyses.

To translate the results of these 33 studies into a single data set, for both analytical strategies we created a set of standardized community parameters from each individual study. These were calculated from the reported per-trap individual abundance of each species in every intact forest, modified habitat type and individual forest fragment sampled. When a study simply reported a total number of individuals captured per habitat type or fragment, we divided that total by the total number of traps.

Community parameters include:

1. Total species richness (S_{total}): the total number of species recorded in a modified habitat or forest fragment. Ranges from 0 to ∞.
2. Intact species richness (S_{intact}): the proportion of species recorded in a modified habitat type or forest fragment that were also captured in that study's intact forest. This metric tracks the response of 'forest species' defined broadly as all those species captured in intact forest. Ranges from 0 to 1.
3. Total abundance (N_{total}): the total abundance in a modified habitat type or forest fragment. Ranges from 0 to ∞.
4. Abundance of the intact forest species assemblage (N_{intact}): the abundance of those species present in a modified habitat type or forest fragment that were also captured in that study's intact forest. Ranges from 0 to N_{total}.
5. Community similarity (C_{MH}): the abundance-weighted similarity of species composition of a modified habitat type or forest fragment relative to intact forest, measured by the Morisita-Horn similarity index (Magurran, 1988). Ranges from 0 to 1.

6. Community evenness (E_H): the evenness of species' abundance distributions in a modified habitat type or forest fragment, measured by the Shannon evenness index (Magurran, 1988). Ranges from 0 to ∞.

For each study, community parameters calculated for each modified habitat type and individual fragment were then standardized relative to values calculated for that study's intact forest, such that the intact forest value was scaled to 1.0, and every modified habitat type or fragment supported some proportion that intact forest value (Dunn, 2004b).

2.1. Quantitative literature review

To review the findings of individual habitat modification studies, we calculated the proportion of studies that found an increase or decrease in standardized community parameters in each modified habitat type relative to the intact forest value of 1.0 within each study. To determine the magnitude of this response, we used a simple averaging method to calculate the mean change in community parameters in response to each type of habitat modification.

To review the individual fragmentation studies, we used partial and bivariate Pearson correlations to determine the proportion of studies finding a positive, negative or non-significant relationship between dung beetle community parameters and published values of three commonly reported fragment characteristics: fragment size, distance from intact forest and mammal density (a commonly sampled proxy for resource availability). Distance was reported across these studies as straight-line distance between a fragment and the nearest intact forest or large fragment, rather than a metric of 'effective' distance (Winfree et al., 2005). Information on dung availability (mammal density) is often collected in dung beetle studies due to the strong resource dependency of Scarabaeine beetles on mammal dung for food and nesting resources (Hanski and Cambefort, 1991; Nichols et al., unpublished). Across four fragmentation studies, food availability was assessed as primate density, reported as total primate individuals/fragment (Estrada et al., 1999, Chapman et al., 2003a and Chapman et al., 2003b; Larsen, unpublished) or primate density classes (Feer and Hingrat, 2005). For those studies that reported insufficient data for us to conduct correlations we report the original findings of the authors. We also present the findings of the few studies that examined the effects of habitat structure in forest fragments and surrounding matrix.

2.2. Meta-analysis

2.2.1. Modification meta-analysis

To test which modified habitats deviated from intact forest values for a given community parameter, we incorporated standardized community parameters as unweighted effect sizes in a fixed-effect categorical model with resampling (5000 iterations) (Hedges and Olkin, 1985 and Rosenberg et al., 2000). For each parameter in each modification type, we determined the cumulative effect size and bias corrected bootstrap 95% confidence intervals. Bias corrected confidence intervals were used to correct for small sample size (Efron, 1987). In these meta-analyses, we considered the cumulative effect size to be significant when its confidence intervals did not include the standardized intact forest value of 1.0. However, as S_{intact} and C_{MH} cannot vary above the intact forest value of 1.0, we present the observed values for these parameters and refer to those values of S_{intact} and C_{MH} below 0.85 as demonstrative of a biologically relevant decline. This cut-off value is arbitrary. It represents either the point at which 85% or fewer members of the intact-forest species assemblage are present, or a reduction in community similarity below 85%. By presenting the full range of observed values, we invite the reader to assess where a biologically significant difference occurs.

To determine if dung beetle community structure differed between types of modified habitat, we partitioned the total heterogeneity (Q_{T}) of each standardized community parameter into between-group (Q_{M}) and within-group (Q_{E}) heterogeneity, in a manner analogous to a parametric analysis of variance. The significance of Q_{M} was then tested against a null distribution generated by randomly assigning each community parameter value to a different habitat type and recalculating Q_{M} across 5000 iterations. This approach estimates significance as the proportion of randomly generated statistics more extreme than the observed Q_{M} (Adams et al., 1997). This method potentially offers more conservative conclusions than results based on parametric tests (Rosenberg et al., 2000), while accommodating effect sizes for which no standard error estimates are available (Gurevitch et al., 1992).

We then identified those modified habitats with similar magnitudes of dung beetle response by assessing homogeneity in community parameters between habitat types in a step-wise fashion, analogous to a post-hoc test. We began testing for homogeneity at the intact forest end of the modification gradient, sequentially adding the effect size of the next habitat type along the gradient until Q_M reached a ‘break point’ and significantly deviated from a randomly generated distribution (i.e. the effect size of the last habitat type was not drawn from the same population as the habitat types included previously). We considered the last habitat type added before the break point to be the last member of the group and began the step-wise process again from the break point. Homogeneity and randomization tests were conducted with MetaWin 2 (Rosenberg et al., 2000).

2.2.2. Fragmentation meta-analysis

The scarcity and heterogeneity of studies addressing dung beetle response to fragmentation precluded a similar meta-analysis of response to fragment characteristics. Instead, we correlated beetle response parameters with fragment characteristics (fragment size, isolation and mammal density) across a pooled dataset composed of the seven studies that sampled both intact and fragmented forest (n = 109 fragments). We used partial Pearson correlations because of related independent variables, although we also provide linear regressions to illustrate patterns using scatterplots. N_{total}, N_{intact}, fragment area and distance to intact forest were log-transformed to achieve normality. SPSS 11.0 was used for all correlations and figures (SPSS, 2004).

3. Results

3.1. Habitat modification

Total species richness (S_{total}) declined relative to intact forest levels in every type of modified habitat investigated, based on the proportion of studies finding each response and on the average change across studies (Table 1; Fig. 1a). Meta-analysis results indicated that S_{total} significantly declined from intact forest levels in all habitats more modified than selectively logged and late secondary forest (Table 1). Stepwise post-hoc tests detected three distinct homogeneous response groups across the modification gradient (Table 2). Intact forest supported the highest dung beetle species richness, clear-cuts the lowest and all other habitats (SL, LS, ES, AF, TP, AC and PAS) supported an intermediate level of species richness.

Table 1.

Summary of quantitative literature review and meta-analysis of the response of dung beetle communities to habitat modification

Standardized community parameter	**Modified habitat type**	**Literature review**			**Average across studies**		**Formal meta-analysis**		
		N	**N+**	**N−**	**Mean**	**SE**	E_j	**Upper CI**	**Lower CI**
S_{total}	Selective logging	4	2	2	0.90	0.11	0.92	1.09	0.78
	Late secondary forest	7	2	5	0.87	0.06	0.90	1.04	0.75
	Early secondary forest	**8**	**1**	**7**	**0.81**	**0.05**	**0.80**	**0.90**	**0.72**
	Agroforestry	**4**	**1**	**3**	**0.82**	**0.10**	**0.81**	**0.94**	**0.58**
	Tree plantation	**6**	**0**	**6**	**0.60**	**0.08**	**0.61**	**0.72**	**0.49**
	Annual crops	**3**	**0**	**3**	**0.68**	**0.13**	**0.80**	**0.93**	**0.55**
	Cattle pasture	**9**	**1**	**8**	**0.43**	**0.10**	**0.51**	**0.72**	**0.33**
	Clear-cuts	**7**	**0**	**7**	**0.22**	**0.05**	**0.25**	**0.40**	**0.14**
S_{intact}	Selective logging	4	0	4	0.73	0.07	0.74	0.85	0.60
	Late secondary forest	7	1	6	0.74	0.06	0.75	0.89	0.56
	Early secondary forest	**8**	**0**	**8**	**0.67**	**0.05**	**0.71**	**0.80**	**0.64**
	Agroforestry	**4**	**0**	**4**	**0.68**	**0.11**	**0.44**	**0.53**	**0.26**

Standardized community parameter	**Modified habitat type**	**Literature review**			**Average across studies**		**Formal meta-analysis**		
		N	**N+**	**N−**	**Mean**	**SE**	**E_j**	**Upper CI**	**Lower CI**
	Tree plantation	**6**	**0**	**6**	**0.40**	**0.09**	**0.64**	**0.80**	**0.37**
	Annual crops	**3**	**0**	**3**	**0.43**	**0.20**	**0.50**	**0.77**	**0.34**
	Cattle pasture	**9**	**0**	**9**	**0.22**	**0.08**	**0.25**	**0.42**	**0.11**
	Clear-cuts	**6**	**0**	**6**	**0.12**	**0.05**	**0.13**	**0.23**	**0.06**
N_{total}	Selective logging	4	2	2	1.23	0.32	1.06	1.53	0.64
	Late secondary forest	7	1	6	0.66	0.16	0.69	1.08	0.40
	Early secondary forest	8	2	6	0.77	0.18	0.77	1.15	0.48
	Agroforestry	4	1	3	0.81	0.40	0.86	1.66	0.43
	Tree plantation	6	2	4	1.99	1.13	1.93	4.34	0.50
	Annual crops	**3**	**1**	**2**	**0.68**	**0.43**	0.66	1.12	0.17
	Cattle pasture	9	3	6	1.03	0.52	1.04	2.19	0.22
	Clear-cuts	**6**	**0**	**6**	**0.30**	**0.15**	**0.31**	**0.62**	**0.08**
N_{intact}	Selective logging	4	1	3	0.88	0.19	0.88	1.19	0.59
	Late secondary forest	7	1	6	0.68	0.18	0.68	1.05	0.40
	Early secondary forest	**8**	**0**	**8**	**0.55**	**0.11**	**0.57**	**0.74**	**0.40**
	Agroforestry	4	1	3	0.75	0.41	0.75	1.60	0.27
	Tree plantation	6	1	5	0.55	0.23	0.55	1.03	0.21
	Annual crops	**3**	**0**	**3**	**0.17**	**0.08**	**0.17**	**0.25**	**0.00**
	Cattle pasture	9	2	7	0.74	0.44	0.74	1.75	0.07
	Clear-cuts	**5**	**0**	**5**	**0.09**	**0.06**	**0.09**	**0.21**	**0.02**

Standardized community parameter	**Modified habitat type**	**Literature review**			**Average across studies**		**Formal meta-analysis**		
		N	**N+**	**N−**	**Mean**	**SE**	$\mathbf{E_j}$	**Upper CI**	**Lower CI**
E_H	Selective logging	4	1	3	0.89	0.07	0.86	1.00	0.68
	Late secondary forest	7	2	5	0.92	0.06	0.89	1.00	0.77
	Early secondary forest	8	1	7	0.81	0.07	0.88	1.00	0.76
	Agroforestry	4	1	3	0.82	0.22	0.95	1.11	0.79
	Tree plantation	**6**	**0**	**6**	**0.59**	**0.08**	**0.67**	**0.80**	**0.50**
	Annual crops	3	1	2	0.79	0.20	0.79	1.18	0.58
	Cattle pasture	**9**	**0**	**9**	**0.56**	**0.10**	**0.56**	**0.74**	**0.38**
	Clear-cuts	**5**	**0**	**5**	**0.48**	**0.13**	**0.48**	**0.66**	**0.22**
C_{MH}	Selective logging	4	0	4	0.79	0.07	0.62	0.90	0.29
	Late secondary forest	**7**	**0**	**7**	**0.71**	**0.08**	**0.65**	**0.83**	**0.41**
	Early secondary forest	**8**	**0**	**8**	**0.67**	**0.09**	**0.65**	**0.81**	**0.50**
	Agroforestry	**4**	**0**	**4**	**0.78**	**0.05**	**0.59**	**0.82**	**0.27**
	Tree plantation	**6**	**0**	**6**	**0.32**	**0.10**	**0.35**	**0.55**	**0.14**
	Annually cropped fields	**3**	**0**	**3**	**0.28**	**0.26**	**0.28**	**0.79**	**0.01**
	Cattle pasture	**9**	**0**	**9**	**0.23**	**0.10**	**0.16**	**0.30**	**0.05**
	Clear-cuts	**5**	**0**	**5**	**0.03**	**0.01**	**0.04**	**0.06**	**0.01**

Review columns summarize the total number of studies (n) showing a positive (n+) or negative (n−) value for each community parameter relative to each study's intact forest. Meta-analysis columns summarize the effect size (E_j) and 95% confidence interval within each modified habitat type. Standardized community parameters significantly different from the intact forest value of 1.0 via meta-analysis are in bold. Abbreviations include:

S_{total} (total species richness), S_{intact} (richness of the intact forest species), N_{total} (total abundance), N_{intact} (abundance of the intact forest species), E_{H} (Shannon evenness index) and C_{MH} (Morisita Horn index of community similarity, relative to intact forest).

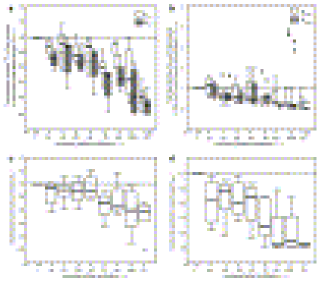

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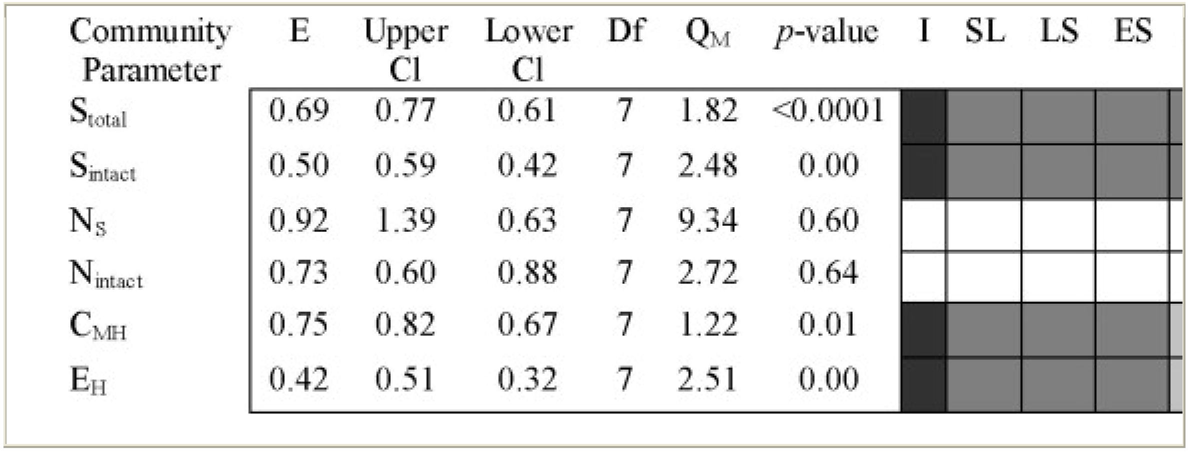
Fig. 1. (a–d) Influence of habitat modification on standardized dung beetle community parameters in tropical forest. Habitat abbreviations are: selectively logged forest (SL), late secondary forest (LS), early secondary forest (ES), agroforests (AF), tree plantations (TP), annually cropped fields (AC), cattle pastures (PAS) and clear-cuts (CC). (a) S_{total} (total species richness) and S_{intact} (richness of the intact forest species), (b) N_{total} (total abundance) and N_{intact} (abundance of the intact forest species), (c) E_{H} (Shannon evenness index) and (d) C_{MH} (Morisita Horn Index of community similarity, relative to intact forest). N_{total} in tree plantations from **Davis and Philips (2005)** was removed from (b) as an outlier ($N = 7.5$).

Table 2.

Cumulative effect size (E), 95% confidence intervals and between (Q_M) group heterogeneity values calculated across intact tropical forest and eight modified habitat types



Community Parameter	E	Upper Cl	Lower Cl	Df	Q_M	*p*-value	I	SL	LS	ES
S_{total}	0.69	0.77	0.61	7	1.82	<0.0001	■	▨	▨	▨
S_{intact}	0.50	0.59	0.42	7	2.48	0.00	■	▨	▨	▨
N_S	0.92	1.39	0.63	7	9.34	0.60				
N_{intact}	0.73	0.60	0.88	7	2.72	0.64				
C_{MH}	0.75	0.82	0.67	7	1.22	0.01	■	▨	▨	▨
E_H	0.42	0.51	0.32	7	2.51	0.00	■	▨	▨	▨

p-Values < 0.05 indicate significant difference in the magnitude of standardized community parameters across modified habitats. Shading indicates significantly homogenously groups of dung beetle community change from the intact forest state, as defined by post-hoc step-wise analysis. Abbreviations include: S_{total} (total species richness), S_{intact} (richness of the intact forest species), N_{total} (total abundance), N_{intact} (abundance of the intact forest species), E_H (Shannon evenness index) and C_{MH} (Morisita Horn index of community similarity, relative to intact forest), I (intact forest), SL (selectively logged forest), LS (late secondary forest), ES (early secondary forest), AF (agroforests), TP (tree plantations), AC (annually cropped fields), PAS (cattle pastures) and CC (clear-cuts).

Richness of the dung beetle species found in intact forest (S_{intact}) declined below 0.85 in the majority of modified habitats across all studies (Table 1; Fig. 1a). Meta-analysis revealed significant declines in S_{intact} from intact forest levels in all modified habitats along the gradient, beginning with early secondary forest (Table 1). This decline formed four response groups, distinguishing communities in intact forest from selectively logged forest, secondary forest and agroforests, to tree plantations, annual crops and pasture and finally clear-cuts (Table 2). The richness of intact forest species found in clear-cut areas averaged less than 25% of that found in intact forest.

While the majority of studies found a decline in total abundance (N_{total}) in each modified habitat type, the average change in abundance was associated with high variance across the gradient (Table 1, Fig. 1b). Meta-analysis revealed that only dung beetle communities in clear-cut areas significantly declined in N_{total} relative to intact forest (Table 1). Generally, total abundance was a poor metric to distinguish dung beetle community response across the modification gradient (Table 2). In cases in which abundance either did not change or increased in response to habitat modification, beetle communities were often characterized by a hyper-abundance of a few, small-bodied species, particularly in cattle pastures. Scheffler, 2005, Vulinec, 2000 and Vulinec et al., 2006 all found little change in beetle biomass between intact and selectively logged forests and Shahabuddin et al. (2005) reported no overall difference in biomass between early secondary and intact forest. Scheffler (2005) found significantly reduced total dung beetle biomass in clear-cut areas relative to intact forest

Abundance of the intact forest dung beetle species (N_{intact}) declined more strongly and less variably than N_{total} in most modified habitats across all studies (Table 1; Fig. 1b). Abundance of these intact forest species significantly declined in early secondary forest, annually cropped fields and clear-cut areas (Table 1). Selectively logged forests retained the highest levels of N_{intact} across the gradient and clear-cuts the lowest, where N_{intact} declined by an average of 91%.

Dung beetle community evenness declined relative to intact forest levels across most modified habitat types and studies (Table 1, Fig. 1c). Meta-analysis demonstrated a significant decline in evenness in tree plantations, cattle pastures and clear-cuts relative to intact forest (Table 1). This decline distinguished four distinct community response groups in intact forest, closed canopy habitats (SL, LS and ES), partially open-to open canopy habitats (AF, TP, AC and PAS) and clear-cut areas (Table 2).

Dung beetle community similarity relative to intact forest (C_{MH}) declined below 0.85 in most modified habitats and reached nearly zero in tree-less habitats such as maize fields, cattle pastures and clear-cuts (Table 1, Fig. 1d). Meta-analysis revealed a significant difference in the composition of dung beetle communities between intact forest and every modified habitat type, except selectively logged forest (Table 1). This overall decline formed the same response groups as dung beetle community evenness, in intact forest, natural closed canopy habitats (SL, LS and ES), partially open-to open canopy habitats (AF, TP, AC and PAS) and clear-cut areas (Table 2).

3.2. Habitat fragmentation

Several correlations occurred between the independent variables of isolation distance, fragment area and mammal density across the pooled dataset. Isolation distance and fragment area were negatively associated ($r_{81} = -0.35$, $p = 0.001$) while a positive relationship existed between isolation distance and mammal density ($r_{81} = 0.46$, $p < 0.001$). Across all fragments, many dung beetle community parameters were associated with fragment size and isolation, but none were related with primate density after controlling for isolation distance or fragment area.

The majority of studies found higher dung beetle species richness in larger fragments (Table 3). Meta-analysis showed a positive correlation between S_{total} and fragment size across all fragments ($r_{87} = 0.52$, $p < 0.001$) (Fig. 2a). Total species richness declined with increasing fragment isolation in half of the studies, but was unrelated to isolation distance in the other half (Table 3). Overall, meta-analysis indicated no relationship between total species richness and isolation distance ($r_{81} = -0.06$, $p > 0.05$; Fig. 2b). One of the two studies that related vegetation structure within fragments to dung beetle species richness found no relationship between richness and the number of felled or standing tree density (Chapman et al., 2003a). The other study reported a positive correlation between beetle species richness and plant diversity (H') and vegetation complexity, although there were no controls for other fragment characteristics (e.g. area and isolation) (Estrada et al., 1998).

Table 3.

Summary and results of 12 studies assessing impacts of tropical forest fragmentation on dung beetle community structure

Reference	**Landscape components reported**					
	Intact forest	**Matrix composition**	**Fragment isolation**	**Fragment area**	**Fragment vegetation**	**Mammal density**
Andresen (2003)	–			–		
Chapman et al. (2003a)	–		–	–	–	–
Hingrat and Feer (2002)/Feer and Hingrat (2005)	–		–	–		–
Klein (1989)	–	–		–		
Larsen et al. (2005)	–		–	–		

Reference	**Landscape components reported**					
	Intact forest	**Matrix composition**	**Fragment isolation**	**Fragment area**	**Fragment vegetation**	**Mammal density**
Quintero and Roslin (2005)	–	–		–		
Vulinec (in review)				–	–	
Amezquita et al. (1999)				–		
Escobar (unpublished)				–		–
Estrada et al. (1999)	–		–	–	–	–
Pineda et al. (2005)				–		

Reference	**Landscape components reported**					
	Intact forest	**Matrix composition**	**Fragment isolation**	**Fragment area**	**Fragment vegetation**	**Mammal density**

	Fragment area (ha)									**Fragment isolation (km to intact forest)**								**Data**
	S_{total}	**S**	S_{intact}	N_{total}	N_{intact}	**N**	C_{MH}	E_{H}	E	S_{total}	**S**	S_{intact}	N_{total}	N_{intact}	**N**	C_{MH}	E_{H}	
Andresen (2003)	+		+	+	+		+	=										**ET**
Chapman et al. (2003a)	=		=	=	=		=	=		=		=	=	=		=	=	**PC**
Hingrat and Feer (2002)/Feer and Hingrat (2005)	+			+						–			–					**R**
Klein (1989)	+		+	–	=		+	+										**ET**
Larsen et al.	+		+	+	=		=	=		–		–	–	–		=	=	**PC**

Reference	**Landscape components reported**																	
	Intact forest	**Matrix composition**	**Fragment isolation**	**Fragment area**	**Fragment vegetation**	**Mammal density**												
(2005)																		
Quintero and Roslin (2005)	=		=	=	=		=	=										**PC**
Vulinec (in review)		=				=			=									BCU
Amezquita et al. (1999)	+					+												ET
Escobar (unpublished)	=					+												BCU
Estrada et al. (1999)	+					+					=				=			PC
Pineda et al.		=				=			+									ET

Reference	**Landscape components reported**																	
	Intact forest	**Matrix composition**	**Fragment isolation**	**Fragment area**	**Fragment vegetation**	**Mammal density**												
(2005)																		

Studies in bold were incorporated into the meta-analysis. The following notation summarizes direction of study results: + (positive association), = (no association), – (negative association). Data for study results were obtained by: estimating trends in published tables (ET), partial correlation analysis using reported data (PC), bivariate correlation using reported unstandardized community parameters (BC) or results reported in publication (R). Standardized community parameters include: S_{total} (total species richness), S_{intact} (richness of the intact forest species), N_{total} (total abundance), C_{MH} (Morisita Horn Index of community similarity relative to intact forest) and E_{H} (Shannon evenness index), unstandardized community parameters include S (total species richness), N (total abundance) and E (community evenness).

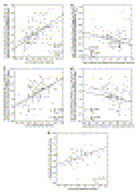


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Fig. 2. (a–e) Influence of fragment characteristics on standardized dung beetle community parameters. (a) S_{total} (total species richness) and S_{intact} (richness of the intact forest species assemblage) vs. fragment area (ha), (b) S_{total} and S_{intact} vs. fragment distance from nearest intact forest (m), (c) N_{total} (total abundance) and N_{intact} (abundance of the intact forest species assemblage) vs. fragment area (ha), (d) N_{total} and N_{intact} vs. fragment distance from nearest intact forest (m), (e) E_{H} (Shannon evenness index) vs. fragment area (ha). Linear regressions are shown for visual purposes and partial correlation statistics are provided in the text.

As with S_{total}, larger fragments supported higher levels of S_{intact} within the majority of individual studies (Table 3) and in comparisons across fragments ($r_{47} = 0.56$, $p < 0.001$) (Fig. 2a). Richness of intact forest dung beetle species was negatively associated with isolation distance in one study (Larsen et al., 2005), but demonstrated no association in a second (Chapman et al., 2003a and Chapman et al., 2003b), or across the pooled dataset ($r_{40} = -0.21$, $p > 0.05$) (Fig. 2b).

Total abundance of dung beetle was positively associated with larger fragments, both in the majority of individual studies (Table 3) and in comparisons across all fragments ($r_{87} = 0.493$, $p < 0.001$) (Fig. 2c and b). N_{total} declined in more isolated fragments in half of the studies and was unrelated to isolation in the other half (Table 3). Across all fragments, N_{total} diminished with increasing distance from intact forest ($r_{81} = -0.303$, $p = 0.005$; Fig. 2d). Chapman et al. (2003a) found no relationship between dung beetle abundance and felled or standing tree density in forest fragments. In contrast, Vulinec et al. (submitted for publication) found an inverse relationship between tree density and the abundance of one dominant species. Estrada et al. (1998) found dung beetle abundance to positively correlate with plant diversity (H') and vegetation complexity, without controlling for other fragment characteristics.

As with N_{total}, abundance of intact forest species was positively correlated with fragment size in most individual studies (Table 3) as well as across all fragments ($r_{87} = 0.52$, $p < 0.001$; Fig. 2c). N_{intact} declined with increasing isolation in half of the studies (Table 3), but demonstrated no significant response in pooled comparisons across all fragments ($r_{39} = -0.09$, $p > 0.05$; Fig. 2d).
Dung beetle community evenness was higher in larger fragments in two studies, but was unrelated to fragment area for five studies (Table 3). Across all fragments, community evenness positively correlated with fragment size ($r_{49} = 0.44$, $p = 0.001$; Fig. 2e). Community evenness was unassociated with isolation distance within individual studies (Table 3) and across all fragments ($r_{46} = -0.037$, $p > 0.05$).

Dung beetle community similarity relative to intact forest was positively related to fragment size in two studies, and unrelated in another three studies (Table 3) and across the entire pooled dataset ($r_{47} = 0.13$, $p > 0.05$). Across and within the two studies for which it could be calculated, community similarity was not associated with isolation distance ($r_{40} = -0.096$, $p > 0.05$; Table 3).

Although no studies explicitly contrasted dung beetle communities in fragments with differing matrix types, a series of three studies conducted over 20 years at the same site in Brazil indicate that matrix quality influences dung beetle response to fragmentation (Klein, 1989, Andresen, 2003 and Quintero and Roslin, 2005). The earliest study found beetle species richness, abundance and community similarity to intact forest strongly reduced by fragmentation. Vegetation in the matrix regenerated during the time between studies and recently Quintero and Roslin (2005) found the negative influence of fragmentation to have all but vanished. They attribute their findings to the increasing similarity in vegetation physiognomy between the forest fragments, contiguous forest and regenerating secondary forest in the matrix.

4. Discussion

A globally coherent picture of dung beetle community response to human modification of tropical forest emerges across these studies. Land-uses with a high degree of forest cover such as selectively logged forest, secondary and agro-forests support dung beetle communities with similar community attributes to those found in intact tropical forest (Pineda et al., 2005 and Vulinec et al., 2006). As the extent of primary tropical forests continues to decline at a global scale, the proportion of these secondary and managed forest types increases (Wright, 2005). This review suggests that these habitats can provide important habitat services that may mitigate future dung beetle diversity losses from continued deforestation (Dunn, 2004b and Vulinec et al., 2006).

In contrast, heavily modified habitats with little or no tree cover support species-poor dung beetle communities with high rates of species turnover, dramatically altered abundance distributions and smaller over-all body size from those found in intact forest. Several beetle communities from highly modified habitats were characterized by a hyper-abundance of a few small-bodied species, including species in the genera *Trichillium* (Scheffler, 2005; Spector, unpublished) and *Tiniocellus* (Davis and Philips, 2005). It is unlikely that this elevated abundance translates into increased functional capacity. The functional contribution of smaller species (even in high abundance) is greatly reduced relative to large-bodied species, which bury disproportionately more dung and secondarily disperse more plant seeds (Andresen, 2003 and Larsen et al., 2005). The few studies that reported biomass demonstrated that beetle abundance and biomass can respond very differently to disturbance. The negative impacts of habitat modification may be more clearly reflected by changes in the latter (Vulinec, 2002 and Scheffler, 2005). Habitat modification also has been shown to differentially affect different functional guilds (Escobar, 2004), which in turn has strong implications for continued ecological functioning.

The decline in intact species richness and abundance with increasing habitat modification was often complemented by an increase in the abundance and richness of species characteristic of more open habitats. The magnitude of this phenomenon was greatest in open, managed fields (annually cropped fields and cattle pastures) and appeared to depend on landscape context (Howden and Nealis, 1975, Davis et al., 2000a and Vulinec, 2002). For example, Shahabuddin et al., 2005 and Avendaño-Mendoza et al., 2005 found both maize fields in close proximity to secondary forest and small clear-cuts embedded within primary forest to contain surprisingly robust dung beetle communities. Similar patterns of species loss and replacement with increasing modification of tropical forest have been documented for multiple taxa (Liow et al., 2001 and Scott et al., 2006). The studies reviewed here encompassed a range of elevations that may have increased variability in community responses across the meta-analysis. Relative to higher-elevation dung beetle communities, lowland communities are more species rich, composed of species with smaller geographic distributions (Escobar et al., 2005) and potentially lower physiological tolerance to changes in microclimate (Janzen, 1967 and Ghalambor et al., 2006). This may confer a different magnitude of response to microclimatic changes that accompany habitat modification. While dung beetle communities are simultaneously affected by changing dung resource availability and habitat loss in modified forests, the absence of explicit assessment of resource availability into general studies of community-level response to tropical forest modification was striking.

Nearly every tropical forest fragment supported dung beetle communities with reduced richness, abundance, community similarity and evenness relative to intact forest. Changes in these community parameters were primarily related to changing fragment size, and though we could not explicitly include matrix composition into these analyses, it appeared to play an important role in determining patterns of response. While larger fragments generally retained higher species richness and abundance, studies without a statistically detectable relationship between fragment size and beetle richness or abundance occurred in landscapes with substantially vegetated matrices such as mixed smallholder agriculture (Chapman et al., 2003a and Chapman et al., 2003b) or early secondary forest growth (Quintero and Roslin, 2005). These land-uses likely mitigated the impacts of fragmentation by permitting dung beetle dispersal between fragments or supporting viable communities within the matrix itself, though we encountered no published mark-recapture studies from which to empirically validate this idea. In contrast, positive species-area and abundance-area relationships were often demonstrated in systems where the matrix and fragment habitat types contrasted strongly, such as the artificially inundated islands of (Feer and Hingrat, 2005 and Larsen et al., 2005) or cattle pastures (Estrada et al., 1998).

As in other recent studies, we also found the effects of fragment isolation shifted according to matrix characteristics (Bender and Fahrig, 2005 and Ewers and Didham, 2005). The contrast between the negative effect of isolation on forest-dwelling dung beetle richness and abundance in systems with presumably poor matrix habitat (such as open water or cattle pastures) and the lack of discernable influence of isolation in systems with structurally diverse, vegetated matrices, suggest that sharp contrasts between the fragment and matrix habitat prevent the otherwise moderating effects of dispersal on isolation distance. When combined with the observation of rapid recovery of dung beetle species richness and community structure with increasing forest regeneration (Klein, 1989, Andresen, 2003 and Quintero and Roslin, 2005), these results indicate the significant role played by the matrix in mediating observed species responses in habitat patches.

Other fragment variables such as dung availability, time since isolation (fragment age), and changes in vegetation structure are very likely to play a role in determining dung beetle community structure in fragmented landscapes. However, so few studies measured these variables that only primate density could be included in the meta-analysis, as a proxy for general mammal/food availability. We caution against extrapolating generalities of the influence of dung availability on dung beetles from these forest fragmentation studies alone for several reasons. First, the use of primate dung availability inadequately represents the overall food availability in a fragment, which realistically encompasses the entire mammal community as well as the spectra of non-mammalian dung food resources utilized by many dung beetle species (e.g. bird, insect and reptile feces, carrion, fungi and rotting fruits (Young, 1981 and Gill, 1991)). Second, mammal populations in fragmented forest demonstrate a variety of responses from extirpation (Chapman et al., 2003b) to crowding (Feeley and Terborgh, 2006), which could lead to changes in dung beetle assemblage structure due to increases or decreases in dung density or particular dung types. As for time since isolation, it is known to affect species' persistence in forest fragments (Tilman et al., 1994 and Brooks et al., 1999), but it was excluded from analysis here because most of the studies sampled within single landscapes where forest fragments were of similar ages.

We acknowledge several limitations in the dataset used in this review. Several studies reported raw (unrarefied) species abundances, others reported results from contrasting habitats without identical sampling effort. While both of these features potentially bias estimates of species richness (Gotelli and Colwell, 2001), we were unable to rarefy these values across every study; instead we attempted to minimize the influence of this bias by presenting data on a per-trap basis, and with the use of internally standardized values (Dunn, 2004a). Given the general paucity of fragmentation studies comparatively sampling in both forest fragments and intact forest, the studies available for review were conducted in a variety of matrix compositions, which may have affected the general comparability across studies. While we acknowledge that these matrix effects may have clouded the effect of isolation distance on dung beetle community parameters within fragments, the results as they stand are reflective of the current published consensus of the diverse and contrasting effects of isolation distance in fragmented systems.

The multiple biotic and abiotic mechanisms that ultimately underlie these community responses to habitat modification or fragmentation cannot be covered extensively here, but are key to a full understanding of the dynamics of community change. Alterations in vegetative structure change microclimatic factors such as radiant heat (Halffter et al., 1992), light intensity and air and soil temperature and humidity (Davis et al., 2002). Given the narrow abiotic tolerances of many dung beetle species, local extirpation following disturbance that alter microclimate factors are probable, yet poorly known (Osberg et al., 1993, Osberg et al., 1994, Sowig, 1995, Davis et al., 2000b and Duncan and Byrne, 2000). Habitat disturbances also frequently alter trophic dynamics, and could result in changes in the natural enemies of dung beetles, though we did not find any studies examining this.

5. Conclusions and recommendations

This review has demonstrated a strong and negative response of by tropical forest dwelling dung beetle communities to increasing modification of tropical forest and declining fragment size. However the overall picture of community response within a fragmented landscape remains complex and requires further, more comprehensive study. Several suggestions for future work emanate from this review. Investigators should report the habitat and biogeographic affinities of species when possible, as this information is invaluable for both interpreting and predicting species' response to landscape conversion (Davis et al., 2000a). Studies should calculate beetle biomass as well as abundance, since biomass is indicative of the total available resource base and may decline with disturbance even as abundance increases (Horgan, 2005 and Larsen et al., 2005). More explicit inclusion and reporting of study scale and landscape configuration would facilitate future comparison between studies. Although logistically challenging, future studies that sample beetle response to fragment characteristics across multiple landscapes would greatly improve our ability to generalize their results (Fahrig, 2003 and Ewers and Didham, 2005).

This review additionally provides a baseline from which to calibrate dung beetle community level responses to a variety of anthropogenic disturbances in tropical forests and supports the utility of Scarabaeine dung beetles as focal taxa. The composition and structure of dung beetles communities have the capacity to transmit information about the health or conservation status of their environment at various scales of organization (Davis et al., 2001 and McGeoch et al., 2002). Rapid surveys and long-term monitoring of dung beetle communities can reliably inform successful conservation and management practices (Halffter and Favila, 1993 and Spector and Forsyth, 1998) in a cost efficient manner (T.A. Gardner et al., unpublished data), as well as contribute to global conservation mechanisms such as the Convention on Biological Diversity's 2010 goals (Butchart et al., 2005).Together with a suite of other invertebrate focal groups, dung beetles can provide a broader, taxonomic representation in the development of conservation practice and policies.

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Appendix A.

Summary of 26 reviewed studies of dung beetle response to tropical forest modification

Study information				Description given in publication			Trapping information				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
I	Avendaño-Mendoza et al. (2005)	Guatemala	Low	Moist tropical forest, cardamon in understory	3000	Rainy 5–10 dry 12–4	12	5	15 m Octagon	24	3–8
AC	Avendaño-Mendoza et al. (2005)	Guatemala	Low	Average of two continuous corn fields	3000	Rainy 5–10 dry 12–4	12	5	15 m Octagon	24	3–8
ES	Avendaño-Mendoza et al. (2005)	Guatemala	Low	Average of four continuous patches of secondary growth	3000	Rainy 5–10 dry 12–4	12	5	15 m Octagon	24	3–8
I	Boonrotpong et al. (2004)	Thailand	Low	Primary tropical rainforest	2000	Rainy 7–9 dry 1–6	60	6	50 m Linear	72	Entire year
ES	Boonrotpong et	Thailand	Low	10 yr Re-growth from	2000	Rainy 7–9 dry	60	6	50 m	72	Entire

Study information				Description given in publication			Trapping information				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
	al. (2004)			rubber plantation		1–6			Linear		year
I	Davis et al. (2001)	Borneo	Low	Primary evergreen, dipterocarp rainforest. 1000 m from river	2744	Predominantly aseasonal	30	3	20 m Linear	72	Entire year
SL	Davis et al. (2001)	Borneo	Low	Average of three selectively logged sites; A: logged at 75.9 m^3 ha^{-1}, B: 97.5 m^3 ha^{-1}, D: 145.2 m^3 ha^{-1}	2744	Predominantly aseasonal	30	3	20 m Linear	72	Entire year
TP	Davis et al. (2001)	Borneo	Low	Adjacent acacia and mahogany plantations; surrounded by selectively logged forest	2744	Predominantly aseasonal	27	3	20 m Linear	72	Entire year
AF	Davis et al.	Borneo	Low	Cocoa plantation	2744	Predominantly	30	3	20 m	72	Entire

Study information				**Description given in publication**			**Trapping information**				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
	(2001)			interplanted with *Paraserianthes falcantaria*. Extensively cultivated landscape		aseasonal			Linear		year
I	Davis and Philips (2005)	Ghana	Low	Average of four sites in unlogged, Eastern Upper Guinean rainforest	1000–2100	Predominantly aseasonal	6	2	10 m Linear	24	6
TP	Davis and Philips (2005)	Ghana	Low	Average of three oil palm and one cacao plantation sites	1000–2100	Predominantly aseasonal	6	2	10 m Linear	24	6
SL	Davis and Philips (2005)	Ghana	Low	Average of four selectively logged forest sites, extraction intensity unknown	1000–2100	Predominantly aseasonal	6	2	10 m Linear	24	6

Study information				Description given in publication			Trapping information				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
I	Escobar and Chacón de Ulloa (2000)	Colombia	Mid	Moist premontain rainforest, canopy ca. 30 m	4900	Dry 6–8	24	1	50 m Linear	48	12–1
PAS	Escobar and Chacón de Ulloa (2000)	Colombia	Mid	Grass, with isolated large trees	4900	Dry 6–8	24	1	50 m Linear	48	12–1
LS	Escobar and Chacón de Ulloa (2000)	Colombia	Mid	Canopy <15 m, dominated by *Cyathea* sp., with *Psychotria* sp., *Tibuchina* sp., *Clusia* sp.	4900	Dry 6–8	24	1	50 m Linear	48	12–1
I	Escobar (2004)	Colombia	Mid	Average of four moist premontain rainforest sites, canopy ca. 30 m	4900	Dry 6–8	32	6	50 m Linear	48	1–6
AC	Escobar (2004)	Colombia	Mid	Average of four sites of sugar cane, coffee	4900	Dry 6–8	32	6	50 m Linear	48	1–6

Study information				**Description given in publication**			**Trapping information**				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
				bushes and fruit trees							
PAS	Escobar (2004)	Colombia	Mid	Average of four pastures sites, with isolated large trees	4900	Dry 6–8	8	6	50 m Linear	48	1–6
LS	Escobar (2004)	Colombia	Mid	Canopy <15 m, dominated by *Cyathea* sp., with *Psychotria* sp., *Tibuchina* sp., *Clusia* sp.	4900	Dry 6–8	8	6	50 m Linear	48	1–6
I	Estrada and Coates-Estrada (2002)	Mexico	Low	'Pristine lowland rainforest'	4900	Dry 3–5 wet 6–2	800	288	10–15 m Linear	24	2–3. 5–6, 9–10
AF	Estrada and Coates-Estrada (2002)	Mexico	Low	Shaded coffee and cocoa, citrus and banana groves, ca. 20–25 yrs old	4900	Dry 3–5 wet 6–2	800	288	10–15 m Linear	24	2–3. 5–6, 9–10

Study information				Description given in publication			Trapping information				
Habi-tat	Reference	Country	Elev.	Site description	Mean mm rain yr^{-1}	Season	Total traps/ habitat	Trap events	Trap spacing	Sampling period (h)	Sampling season
I	Halffter et al. (1992)	Mexico	Low	Moist tropical forest	2800	Dry 2–3	24	1	Not given	12	5
CC	Halffter et al. (1992)	Mexico	Low	Clear-cut patch embedded in intact forest	2800	Dry 2–3	8	1	Not given	12	5
I	Howden and Nealis (1975)	Colombia	Low	*Terra firme* rainforest	2300	Dry 6–9 wet 1–3	10	1	Not given	120	2
CC	Howden and Nealis (1975)	Colombia	Low	Forest clearing	2300	Dry 6–9 wet 1–3	4	1	Not given	120	2
I	Klein (1989)	Brazil	Low	Average of three primary rainforest sites, canopy ca. 35 m	2200	Dry 7–9	24	1	17 m Linear	48	5–6
CC	Klein (1989)	Brazil	Low	Average of three sites, grass with areas of re-growth up to 2.5 m	2200 Dry 7–9		24	1	17 m Linear	48	5–6

Study information				**Description given in publication**			**Trapping information**				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
I	Larsen (unpublished)	Peru	Low	Primary tropical rainforest	NA	NA	10	6	50 m Linear	24	9
PAS	Larsen (unpublished)	Peru	Low	Cattle pasture	NA	NA	2	2	50 m Linear	24	9
I	Larsen and Lopera (unpublished)	Peru	Low	Primary tropical rainforest	2800	Wet 10–4	10	6	50 m Linear	24	5
CC	Larsen and Lopera (unpublished)	Peru	Low	Camp clearing	2800	Wet 10–4	5	4	50 m Linear	24	5
ES	Larsen and Lopera (unpublished)	Peru	Low	Young secondary growth mixed with bamboo	2800	Wet 10–4	5	4	50 m Linear	24	5
I	Lopera and Larsen	Costa Rica	Low	Primary tropical rainforest	4000	Dry 12–4 wet 5–11	10	4	50 m Linear	24	3, 12

Study information				Description given in publication			Trapping information				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
	(unpublished)										
ES	Lopera and Larsen (unpublished)	Costa Rica	Low	Young re-growth, dominated by *Byrsonima* sp., embedded within primary forest	4000	Dry 12–4 wet 5–11	10	4	50 m Linear	24	3, 12
LS	Lopera and Larsen (unpublished)	Costa Rica	Low	ca. 15 yr old re-growth, dominated by *Vochysia* sp., embedded within primary forest	4000	Dry 12–4 wet 5–11	10	4	50 m Linear	24	3, 12
TP	Lopera and Larsen (unpublished)	Costa Rica	Low	Average of two plantation sites, dominated by teak and *Gmelina arborea*	4000	Dry 12–4 wet 5–11	10	4	50 m Linear	24	3, 12
PAS	Lopera and Larsen	Costa Rica	Low	Cattle pasture	4000	Dry 12–4 wet 5–11	10	4	50 m Linear	24	3, 12

Study information				Description given in publication			Trapping information				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
	(unpublished)										
I	Medina and Kattan (1996)	Colombia	Low	Average of two, humid, late stage, closed canopy secondary forest	7500	Dry 1–3	10	1	25 m Linear	24	8–11
TP	Medina and Kattan (1996)	Colombia	Low	Average of two, *Bactris* sp. palm plantations	7500	Dry 1–3	10	1	25 m Linear	24	8–11
I	Medina et al. (2002)	Colombia	Mid	Natural forest, ca. 30–40 yrs	2631	Dry 7–8, 12–1 wet 4, 10	10	1	25 m Linear	24	3
I	Medina et al. (2002)	Colombia	High	Natural forest ca. 30–40 yrs	2631	Dry 7–8, 12–1 wet 4, 10	10	1	25 m Linear	24	3
TP	Medina et al. (2002)	Colombia	Mid	Exotic ash plantation, no understory	2631	Dry 7–8, 12–1 wet 4, 10	10	1	25 m Linear	24	3
AF	Medina et al.	Colombia	High	Native Andean alder	2631	Dry 7–8, 12–1	10	1	25 m	24	3

Study information				Description given in publication			Trapping information				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
	(2002)			plantation, understory 'similar to natural forest'		wet 4, 10			Linear		
PAS	Medina et al. (2002)	Colombia	High	Cattle pasture	2631	Dry 7–8, 12–1 wet 4, 10	10	1	25 m Linear	24	3
PAS	Medina et al. (2002)	Colombia	Mid	Cattle pasture	2631	Dry 7–8, 12–1 wet 4, 10	10	1	25 m Linear	24	3
I	Nummelin and Hanski (1989)	Uganda	Mid	Average of two moist evergreen rainforest sites	1500	Wet 8–12, 3–5	73 and 22	1	Not given	24	3–5, 9–11
TP	Nummelin and Hanski (1989)	Uganda	Mid	Average of two exotic *Pinus* sp. and *Cupressus* sp. timber plantations	1500	Wet 8–12, 3–5	16 and 6	1	Not given	24	3–5, 9–11
SL	Nummelin and	Uganda	Mid	Average of two	1500	Wet 8–12, 3–5	27 and	1	Not	24	3–5, 9–11

Study information				**Description given in publication**			**Trapping information**				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
	Hanski (1989)			selectively logged sites (21 m^3 ha^{-1} and 14 m^3 ha^{-1} extraction rates)			44		given		
I	Quintero and Roslin (2005)	Brazil	Low	Dimona site, primary rainforest, canopy ca. 35 m	2200	Dry 7–9	6	1	17 m Linear	48	6–7
ES	Quintero and Roslin (2005)	Brazil	Low	Dimona site, 10 yr old re-growth, 20 m canopy, *Cecropia* sp. dominated	2200	Dry 7–9	6	3	17 m Linear	48	6–7
I	Quintero and Roslin (2005)	Brazil	Low	Colosso site, primary rainforest, canopy ca. 35 m	2200	Dry 7–9	6	3	17 m Linear	48	6–7
ES	Quintero and Roslin (2005)	Brazil	Low	Colosso site, ca. 5 yr old, 5–6 m canopy,	2200	Dry 7–9	6	3	17 m Linear	48	6–7

Study information				Description given in publication			Trapping information				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
				Vismia sp. dominated							
I	Quintero and Roslin (2005)	Brazil	Low	Ciudade Powell site, primary rainforest, canopy ca. 35 m	2200	Dry 7–9	6	3	17 m Linear	48	6–7
LS	Quintero and Roslin (2005)	Brazil	Low	Ciudade Powell site, ca. 14 yr old re-growth, 25 m closed-canopy	2200	Dry 7–9	6	3	17 m Linear	48	6–7
I	Scheffler (2005)	Brazil	Low	Average of two seasonally deciduous tropical forest sites	1855	Wet 10–4	10	1	30 m Linear	48	10
PAS	Scheffler (2005)	Brazil	Low	Average of two pastures, no tree cover, fire maintained, burned 6 months before sampling	1855	Wet 10–4	10	1	30 m Linear	48	10

Study information				**Description given in publication**			**Trapping information**				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
CC	Scheffler (2005)	Brazil	Low	Average of two, 0.5 ha patches, burned, re-cleared annually	1855	Wet 10–4	10	1	30 m Linear	48	10
SL	Scheffler (2005)	Brazil	Low	Average of two sites logged in 1992, extraction of 1–4 stems ha^{-1}	1855	Wet 10–4	10	1	30 m Linear	48	10
I	Shahabuddin et al. (2005)	Indonesia	Mid	Average of four, lower montane forest sites; canopy 25–30 m, some recent selective logging	2500	Rainy 7–9 wet 10–1	40	6	10 m Linear	72	4 and 6
AC	Shahabuddin et al. (2005)	Indonesia	Mid	Average of four, 1 ha maize (*Zea mays*) fields	2500	Rainy 7–9 wet 10–1	40	6	10 m Linear	72	4 and 6
ES	Shahabuddin et al. (2005)	Indonesia	Mid	Average of four, 1–1.5 ha patches of 5–6-yr re-growth, canopy	2500 Rainy 7–9		10	6	10 m Linear	72	4 and 6

Study information				Description given in publication			Trapping information				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
				7–8 m	wet 10–1						
AF	Shahabuddin et al. (2005)	Indonesia	Mid	Average of four, 1–2 ha patches of ca. 5-yr old cacao trees with *Gliricidia sepium* shade cover	2500 Rainy 7–9 wet 10–1		10	6	10 m Linear	72	4 and 6
I	Spector (unpublished)	Bolivia	Mid	Upland evergreen tropical forest	1450	Dry 5–11	35	3 50 m Linear 24 1 and 2			
PAS	Spector (unpublished)	Bolivia	Mid	Grass, no tree cover	1450	Dry 5–11	32	3 50 m Linear 24 1 and 2			
ES	Spector	Bolivia	Low	Young secondary	1450	Dry 5–11	19	3 50 m			

Study information				Description given in publication			Trapping information				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
	(unpublished)			growth				Linear 24 1 and 2			
I	Vulinec (2002)	Brazil	Low	Caculandia site, 250 ha, upland *terra firme* forest, logged once, date unknown	2290	Dry 4–10	9	16	20 m Linear		10–3
LS	Vulinec (2002)	Brazil	Low	Caculandia site, average of three sites, re-growth from one cacao/banana plantation and two babçu palm dominated clear-cuts	2290	Dry 4–10	9	16	20 m Linear		10–3
I	Vulinec (2002)	Brazil	Low	Ducke site, average of two upland primary forest sites, and one	2100	Dry 6–11	9	15	20 m Linear		12–9

Study information				**Description given in publication**			**Trapping information**				
Habi-tat	**Reference**	**Country**	**Elev.**	**Site description**	**Mean mm rain yr^{-1}**	**Season**	**Total traps/ habitat**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
				primary forest site 200 m from river							
CC	Vulinec (2002)	Brazil	Low	Ducke site, average of 3 ha soccer field and 3 ha cleared field	2100	Dry 6–11	6	15	20 m Linear		12–9
LS	Vulinec (2002)	Brazil	Low	Ducke site, re-grown timber plantation >20 yrs	2100	Dry 6–11	9	15	20 m Linear		12–9
I	Vulinec (2002)	Brazil	Low	Caxiuana site, 33,00 ha primary forest	3000	Dry 6–11	9	15	20 m Linear		10–11

All 26 studies were incorporated into the meta-analysis. Elevation is classified as low ⩽1000 m, mid = 1000–2000 m and high >2000 m. Seasonality and sample season expressed as Julian calendar months.

Appendix B.

Summary of 12 reviewed studies of dung beetle response to tropical forest fragmentation

Reference	**Study number**	**Coun= try**	**Elev.**	**Intact forest type**	**System description**	**Mean mm rain yr^{-1}**	**Seasonality**	**Number frag.**	**Size range (ha)**	**Age range (yrs)**	**Total traps/fragment**	**Trap events**	**Trap spacing**	**Sampling period (h)**	**Sampling season**
Amezquita et al. (1999)	9	Colombia	Low	NA	Forest patches. Matrix: pasture, live fences	3667	Dry 12–3 wet 4–6, 10–11	3	4–70	na	20	1	30 m	168	1
Andresen (2003)	1	Brazil	Low	Primary rainforest, 35 m canopy	Rectilinear fragments. Matrix: 2–4 m regrowth and pasture	2200	Dry 7–9	4	1, 10	13–16	6	3 in 1 ha, 5 in 10 ha and intact	30 m	16	8–11
Chapman et al. (2003a)	2	Uganda	Mid	Moist, evergreen forest	Fragments with NTFP extraction. Matrix: mixed	1749	Dry 11–2, 6–9	22	1.09–49.6	ca. 50	20	1	5 m	24	5–5

Reference	Study number	Coun= try	Elev.	Intact forest type	System description	Mean mm rain yr^{-1}	Seasonality	Number frag.	Size range (ha)	Age range (yrs)	Total traps/fragment	Trap events	Trap spacing	Sampling period (h)	Sampling season
					crops										
Escobar (unpublished)	10	Mexico	Low	–	Forest patches	4900	Dry 3–5, wet 6–2	10	2.5–66	1–20	10	1	25–30 m	48	7–8
Estrada et al. (1999)	11	Mexico	Low	‘Pristine lowland rainforest’	Forest patches. Matrix: pasture and agroforestry	4900	Dry 3–5, wet 6–2	38	1–112	1–20	35 in <50 ha, 70 in >50 ha		10–15 m	24	4–9
Hingrat and Feer (2002)	3	French Guiana	Low	Average of three primary forest sites	Islands in reservoir	3000	Wet 1–7	7	1.1–38.3	5	5	1	25 m	120	4–5
Feer and Hingrat (2005)	4	French Guiana	Low	Average of three primary	Islands in reservoir	3000	Wet 1–7	7	1.1–38.3	5	5	1	25 m	120	4–5

Reference	Study number	Coun=try	Elev.	Intact forest type	System description	Mean mm rain yr^{-1}	Season-ality	Num ber frag.	Size range (ha)	Age range (yrs)	Total traps/fragment	Trap events	Trap spacing	Sampling period (h)	Sampling season
				forest sites											
Klein (1989)	5	Brazil	Low	Average of three primary rainforest sites, canopy ca. 35 m.	Rectilinear fragments. Matrix of pasture and 2–4 m regrowth	2200	Dry 7–9	6	1, 10	2–6	18	1	17 m	48	5–6
Larsen et al. (2005)	6	Venezuela	Low	Semi-deciduous tropical forest	Islands in reservoir	1100	Wet 5–10	30	0.16–181	16	Varied	50 m	5–6	24	5–7
Quintero and Roslin (2005)	7	Brazil	Low	Primary rainforest	Rectilinear fragments. Matrix: 5–6 m woody regrowth	2200	Dry 7–9	2	1, 10	21–25	6	3	17 m	96	6–7
Quintero and	7	Brazil	Low	Primary	Rectilinear	2200	Dry	2	1, 10	21–25	6	3	17 m	96	6–7

Reference	Study number	Coun= try	Elev.	Intact forest type	System description	Mean mm rain yr^{-1}	Seasonality	Number frag.	Size range (ha)	Age range (yrs)	Total traps/fragment	Trap events	Trap spacing	Sampling period (h)	Sampling season
Roslin (2005)				rainforest	fragments. Matrix: 25 m woody regrowth		7–9								
Quintero and Roslin (2005)	7	Brazil	Low	Primary rainforest	Rectilinear fragments. Matrix: 20 m woody regrowth	2200	Dry 7–9	2	1, 10	21–25	6	3	17 m	96	6–7
Vulinec (in review)	8	Brazil	Low	NA	Forest patches. Matrix: >150 yr savanna	2000	Dry 6–11	6	8.5–360.5	>50	10	1	50 m	48	6
Pineda et al. (2005)	12	Mexico	Mid	NA	<20 yr forest patches. Matrix:	1750	Wet 5–10	3	18–72	>50	16–18	1	25 m	48	4–10

Reference	**Study number**	**Coun= try**	**Elev.**	**Intact forest type**	**System descrip- tion**	**Mean mm rain yr^{-1}**	**Sea- son- ality**	**Num ber frag.**	**Size range (ha)**	**Age range (yrs)**	**Total traps/fr agment**	**Trap e- vents**	**Trap spa- cing**	**Sam- pling period (h)**	**Sampling season**
					crops, pasture, settlements										

Seven studies (in bold) were incorporated into the meta-analysis. Elevation is classified as low ≤1000 m, mid = 1000–2000 m and high >2000 m. Seasonality and sample season expressed as Julian calendar months.

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