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Notes

Dung beetles as indicators for rapid impact assessments: Evaluating best practice forestry in the neotropics

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ABSTRACT

Dung beetles (Scarabaeidae: Scarabaeinae) are sensitive to habitat perturbations and are easily studied, making them an ideal taxonomic group with which to evaluate the effects of low-intensity anthropogenic disturbances such as Reduced-Impact Logging. Here we examine the effect of a certified Reduced-Impact Logging operation on dung beetles, and demonstrate their suitability for use in rapid ecological impact studies. We sampled dung beetle assemblages, environmental variables and timber extraction rates across four treatment groups in closed canopy and canopy gaps in logged and unlogged forest in Guyana. Community analysis revealed that logged forest supported a more uniform dung beetle assemblage compared to unlogged forest. Differences in assemblage structure were driven by dissimilarity between closed canopy treatments, as plots in artificial and natural canopy gaps supported comparable assemblages. Indicator analyses were conducted across treatments, using a new approach (CLAM) and two well-established methods (INDVAL, SIMPER). Two species respectively were classified as indicators of logged (*Hansreia affinis* and *Eurysternus caribaeus*) and unlogged forest (*Canthidium aff. centrale* and *Deltochilum (Calhyboma) carinatum*). BIO-ENV analysis demonstrated that tree extraction intensity, bare ground cover, and ground cover by leaf material were key factors influencing dung beetle assemblages. Despite the relatively low-impact of Reduced-Impact Logging reported by previous studies, we find that dung beetles are sensitive to even small changes in environmental conditions as a result of this form of anthropogenic disturbance. As dung beetles are a highly responsive taxonomic group, we illustrate that they represent a valuable taxon that can be used to critically evaluate best practice forestry operations and other disturbance activities, particularly in time constrained studies (e.g., rapid monitoring and environmental impact assessments). However, we recommend the use of multiple indicator analyses to monitor potential changes in assemblage composition, due to a lack of congruence between methods.

1. Introduction

In the neotropics, the area of degraded forest far exceeds that converted to alternative land-uses (Asner et al., 2005). The primary sources of degradation are selective logging, fragmentation and fire (Barlow et al., 2006; Peres et al., 2010), with 1.2 million ha of the Brazilian Amazon selectively logged each year (Asner et al., 2005). Timber harvesting in tropical forests has negative consequences for forest biodiversity (Barlow et al., 2006; Fimbel et al., 2001; Mason, 1996; Meijaard et al., 2005; Thiollay, 1997), albeit less severe than those arising from either fragmentation or fire (Barlow et al., 2006; Gibson et al., 2011). Given that a further 50 million hectares of the Brazilian Amazon are proposed as timber concessions (Veríssimo et al., 2002), understanding the impacts of selective logging is important for informing forestry policy regarding both biodiversity conservation, and forest regeneration dynamics, as biological communities underpin many essential ecosystem functions (Hooper et al., 2005).

Reduced-Impact Logging (RIL) is a modern system of timber harvesting that endeavours to reduce the collateral damage to forests associated with selective logging (Pinard and Putz, 1996), and attempts to better mimic natural tree-fall dynamics (Felton

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et al., 2006). It typically involves a pre-harvest tree inventory, which is subsequently used to plan the most efficient and least destructive extraction (skid) trail network in a Geographic Information System (GIS). Directional felling and vine cutting are also employed to prevent damage to adjacent trees, and felled timber is winched to skid trails to minimise extraction disturbance and infrastructure (for further details on RIL see: Pinard and Putz, 1996; Vidal et al., 1997; Mason and Putz, 2001). Compared with conventional selective logging, RIL has been shown to reduce tree mortality and total canopy gap fracture by up to 27 percent and 43 percent respectively (Johns et al., 1996; Pinard and Putz, 1996). RIL is expected to improve timber crop sustainability, carbon storage, and the provision of ecosystem services (Miller et al., 2011). Furthermore, it is estimated that implementation of the technique across production forests globally would cut carbon emissions by 160 million tons each year, equivalent to ~10 percent of carbon emissions from deforestation (Putz et al., 2008). Despite this, RIL is not a mandatory component of timber certification schemes and uptake has remained slow, with conventional practices continuing to dominate the industry (Mazzei et al., 2010).

Compared with conventional logging, RIL is also expected to provide benefits for biodiversity, although this is yet to be thoroughly demonstrated (Edwards et al., 2012; Peres et al., 2010). As a result, there is no strong evidence-base to inform conservation management and forestry policy. Of the studies that do exist, most have focused on vertebrates (Azevedo-Ramos et al., 2006; Bicknell and Peres, 2010; Felton et al., 2008; Khanaposhtani et al., 2013; Presley et al., 2008; Wunderle et al., 2006), finding that change in community composition is broadly governed by extraction rate and technique (Fimbel et al., 2001). Little is known about the effects of RIL upon invertebrates, despite the critical role they play in tropical forest ecosystem dynamics (Nichols et al., 2008). It is expected that invertebrates are affected by more fine-scale secondary changes that result from logging, and will therefore provide a complementary perspective on the consequences of best practice forestry operations.

Identifying appropriate indicators of ecosystem health has become increasingly important in conservation biology, with many taxonomic groups used to assess tropical forest disturbance, including both vertebrates (e.g. Banks-Leite et al., 2013) and invertebrates (e.g. Lachat et al., 2006). Dung beetles (Scarabaeidae: Scarabaeinae) are regarded as excellent bioindicators. They are particularly suitable for examining subtle effects of low-intensity habitat modifications such as RIL, because they are stenotopic and thus intrinsically sensitive to alterations in environmental conditions (Davis et al., 2001; Feer and Hingrat, 2005; Nichols and Gardner, 2011; Scheffler, 2005). Furthermore, they are diverse and taxonomically well characterised, sampling methods are inexpensive, community turnover occurs rapidly (Nichols and Gardner, 2011), they provide key ecosystem services important to forest dynamics (such as decomposition, secondary seed dispersal, nutrient cycling and parasite control; Davis et al., 2001; Feer and Hingrat, 2005; Nichols et al., 2008; Ponce-Santizo et al., 2006; Scheffler, 2005; Shahabuddin et al., 2005; Shepherd and Chapman, 1998; Vulinec, 2002), and they have been shown to be reliable indicators of tropical forest disturbance (Aguilar-Amuchastegui and Henebry, 2007; Barlow et al., 2010; Gardner et al., 2008a, 2008b; Lachat et al., 2006; Nichols and Gardner, 2011). They are also often considered a proxy for the wildlife communities (primarily large mammals) that provide the faeces upon which they feed (Hanski and Cambefort, 1991; Nichols et al., 2009), making their value as indicators disproportionally high (Nichols and Gardner, 2011).

In this study we aimed to: (i) assess the effects of RIL on a neotropical dung beetle assemblage in order to inform production forest management policies and (ii) demonstrate the use of dung beetles as forest impact indicators, and as a highly effective tool for evaluating levels of forest disturbance in rapid and easily replicated monitoring programmes. As part of our study, we use a consensus approach of three analytical techniques to identify indicator species, in order to ensure that we identified all indicators from our rapid assessment dataset. The research was undertaken at an experimental timber operation in the Iwokrama Forest, Guyana, enabling us to sample in logged (RIL) and unlogged areas and to test for differences in natural (tree-fall) and artificial (logged) canopy gaps. We use community analyses to quantify variation in dung beetle assemblage composition in each of the treatments, and examine whether this is associated with changes in local environmental conditions and/or RIL extraction rates.

2. Methods

2.1. Study area

The Iwokrama Forest in central Guyana is a 3,710 km^2 area of tropical forest managed by the Iwokrama International Centre for Rainforest Conservation and Development (IIC) (Fig. 1). Lying between 4° and 5° N, and 58° and 59° W, the study system is characterised by *terra firme* tropical rainforest, dominated by timber species that include *Chlorocardium rodiei* (Schomb), *Eperua falcate* (Aubl.), *Dicorynia guianensis* (Amsh), *Mora excelsa* (Benth) and *Swartzia leiocalycina* (Benth). Rainfall averages 3000 mm/yr, with a rainy season from April to July. Temperatures range from a mean minimum of 22 °C at night during July, to a maximum of 36 °C during October.

Timber operations in the Iwokrama Forest are certified by the Forestry Stewardship Council, and every stage of the extraction process is conducted with environmental sustainability in mind. Harvesting methods go beyond RIL guidelines, with extraction road densities ~25 percent lower than current recommendations (GFC, 2002). Research into growth rates also permit accurate Annual Allowable Cuts (the annual harvest rate and interval period at which sustainability can be maintained) for primary timber species to be calculated, coupled with a 60 year polycyclic felling rotation. RIL within the logged sites used in this study was completed 12 months prior to field surveys. Logging intensity ranged between 1.2 and 5.1 trees/ha (mean = 3.7; S.D. = 1.3), while the volume equivalent varied from 4.8 to 24.0 m^3/ha (mean = 14.7; S.D. = 5.4).

2.2. Experimental design

To quantify the effects of RIL on dung beetle assemblages, 20 plots were sampled, five in each of four treatment groups: (1) canopy gaps in RIL forest; (2) closed canopy in RIL forest; (3) canopy gaps in unlogged (control) forest, and; (4) closed canopy in unlogged (control) forest. In RIL forest, the canopy gaps were artificially created by logging operations, where a timber tree had been felled and extracted. In unlogged forest, canopy gaps were natural tree-fall openings. All sample plots were positioned more than 500 m apart and greater than 200 m from forestry block boundaries to minimise potential edge effects and assemblage spill-over.

To best mimic the conditions of a rapid biological monitoring assessment, but also to account for bias caused by seasonal effects independent from RIL, the sampling of treatments was conducted on a rotational basis (Andresen, 2008b) over a single season in April and May 2009. Elsewhere in north-eastern Amazonia (French Guiana and northern Brazil), studies have demonstrated that dung beetle abundance and assemblage composition does not vary between seasons (Barlow et al., 2010; Feer and Pincebourde, 2005; Gardner et al., 2008b), and so our sampling procedure should generate findings that are representative of other times of the year.

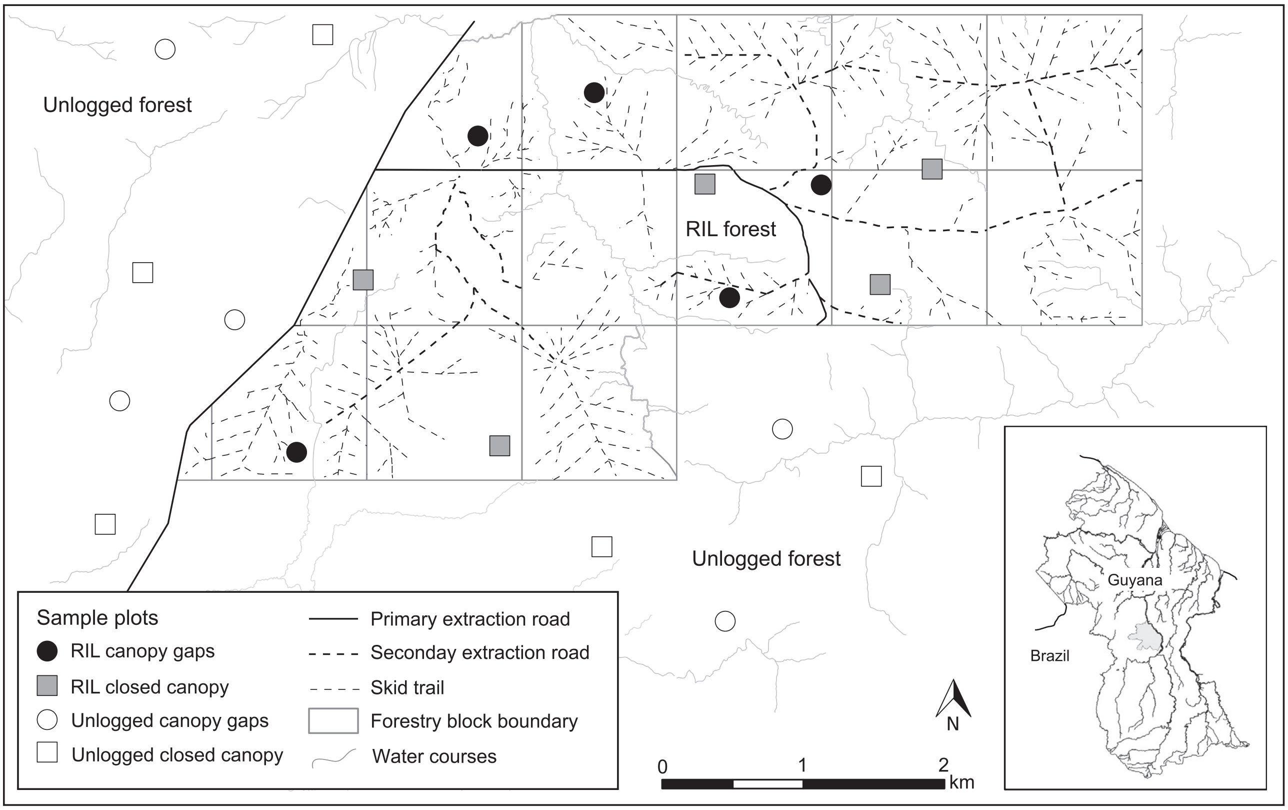

Fig. 1. Sample plots across the four treatments within and outside RIL operations in the Iwokrama Forest. Inset indicates the location of the Iwokrama Forest (grey area) in central Guyana, South America.

2.3. Dung beetle sampling

Dung beetles were sampled using pitfall and flight interception traps (FIT). Eight pitfall traps and one FIT were set per plot for three nights, totalling 540 trap nights (480 and 60 pitfall and FIT nights respectively). The pitfall traps consisted of a plastic container (12 cm diameter and 15 cm deep) baited with approximately 30 g of human faeces, which is considered to be the most effective attractant used in neotropical dung beetle studies (Barlow et al., 2010; Gardner et al., 2008b). Each FIT consisted of a vertical wall of black netting measuring 2 × 1 m, which captured dung beetles in flight. Each morning, traps were checked, emptied and re-baited. Beetles were preserved and subsequently identified to species level where possible or, where there was uncertainty, to morphospecies.

2.4. Environmental variables

Data pertaining to microclimate and habitat variables that are known to be affected by forestry operations (Felton et al., 2006), in addition to being important to dung beetles (Halffter and Arellano, 2002), were gathered from within each plot: tree-fall gap size (m^2; where applicable), canopy cover (percentage value using a spherical densitometer), minimum and maximum temperature (°C), leaf litter depth (cm; mean depth across 10 random points), and ground cover (mean percentage value estimated across five randomly placed 5 × 5 m quadrats) of leaf material, large woody debris (≥15 cm diameter), small woody debris (<15 cm diameter) and bare soil. Data on RIL extraction rates were provided by the IIC and calculated per 1 km^2 logging block.

2.5. Assemblage analysis

As sites closer together may naturally contain more similar assemblages than those further apart (Soininen et al., 2007), we checked for the occurrence of spatial autocorrelation in our dataset, and quantified its extent, using Mantel tests of geographic distance against the Bray-Curtis coefficients of the dung beetle communities in each of the logged and unlogged plots (as recommended by Ramage et al., 2013). Mantel tests were conducted in the program Genalex (Peakall and Smouse, 2006) from 999 permutations.

Differences in the environmental variables between the RIL and control plots were tested using an independent samples *t*-test. BIO-ENV analysis (Clarke and Ainsworth, 1993), conducted in PRIMER v.5 (Clarke and Gorley, 2001), was employed to determine the correlation between the environmental variables and the dung beetle assemblage, based on a community distance matrix derived from the Bray-Curtis dissimilarities.

To examine the completeness of our dung beetle sample and compare species diversity between RIL and unlogged plots, we generated individual-based observed species richness rarefaction curves, with associated confidence intervals in EstimateS 8.2.0 (Colwell, 2006). We also calculated the mean of five commonly used species richness estimators (ICE, CHAO2, JACK1, JACK2, and BOOTSTRAP), from 999 randomisations of observed species richness, to examine whether there were differences between the samples.

For all further analyses, standardised abundance data ($\log_{10}$ transformed) were used per plot, rather than per trap, to ensure that sample representation was sufficient to allow meaningful comparisons of the dung beetle assemblages to be made between treatments. Community statistics were applied at two levels, comparing: (i) all plots in RIL forest with all those in unlogged forest (hereafter referred to as '*RIL*' treatment), and; (ii) RIL canopy gaps with unlogged canopy gaps, and RIL closed canopy with unlogged closed canopy (hereafter, '*Canopy Gap*' and '*Closed Canopy*' treatments respectively). No further combinations were tested as there was no a priori ecological justification to do so. These separate analyses were conducted to determine the overall impact of RIL on dung beetle communities, as well as to ascertain whether canopy gaps or closed canopy areas were driving any differences found between RIL and unlogged forest.

Assemblage-wide variation in dung beetle responses to RIL were determined via free ordination provided by non-metric multidimensional scaling (NMDS), coupled with analysis of similarity (ANOSIM) between treatments (*RIL*, *Canopy Gap* and *Closed Canopy*). The NMDS, based on Bray-Curtis dissimilarity coefficients, was implemented in PC-ORD v.6.07 (McCune and Mefford, 2011). Five hundred iterations and 250 runs of both real and randomised data were used to produce a final ordination of minimum stress consisting of two axes. ANOSIM was computed from 999 permutations in R (R Core Team, 2013). Analyses were conducted with all species included, and then with 'rare' species omitted. Species were considered 'rare' if they were either captured fewer than three times across all plots, or if they were present in fewer than three plots. All approaches yielded consistent results and, therefore, the findings across all species are reported.

2.6. Indicator species analysis

In order to best identify species contributing most to the overall assemblage response to RIL, we undertook a series of indicator species analyses. Two well-established approaches were used, similarity percentages (SIMPER; Clarke, 1993) and indicator value analysis (INDVAL; Dufrêne and Legendre, 1997). We then compared results to those from a recently developed classification method (CLAM; Chazdon et al., 2011). All indicator methods were applied across the *RIL*, *Canopy Gap* and *Closed Canopy* treatments.

SIMPER was conducted in PRIMER to determine the species that contributed most to dissimilarity in community structure. The SIMPER approach uses a species abundance matrix to compute the mean contribution of individual species to the Bray-Curtis dissimilarities between all pairs of sampling plots within each treatment.

In comparison, INDVAL uses a species abundance matrix to assess the degree to which a species exhibits specificity (uniqueness to a particular treatment) and fidelity (frequency of occurrence in a particular treatment). Indicator values for each species are assigned as a result of a random reallocation procedure from 999 permutations of plots among treatments, which we conducted in PC-ORD.

CLAM is a new multinomial model which uses pooled species abundance data from two groups to classify species into four categories: (1) 'group A specialist'; (2) 'group B specialist'; (3) 'generalist', and; (4) 'too rare to classify' (Chazdon et al., 2011). The analysis was conducted in the program CLAM (Chao and Lin, 2011) using two super-majority specialization thresholds ($K = 0.667$, $p = 0.001$; $K = 0.667$, $p = 0.005$). Both yielded identical indicators, so only the former is reported hereafter as it the most conservative and considered to be appropriate for assemblage-wide classifications (Chazdon et al., 2011).

3. Results

Mantel tests of geographic distances between sites with corresponding ecological distances confirmed that the effects of spatial autocorrelation in our assemblage dataset were weak and non-significant (logged $R^2 = 0.08$; unlogged $= R^2 < 0.01$; $p > 0.05$). Therefore, patterns of assemblage signals within our dataset can be reliably attributed to treatment rather than natural processes of distance-decay.

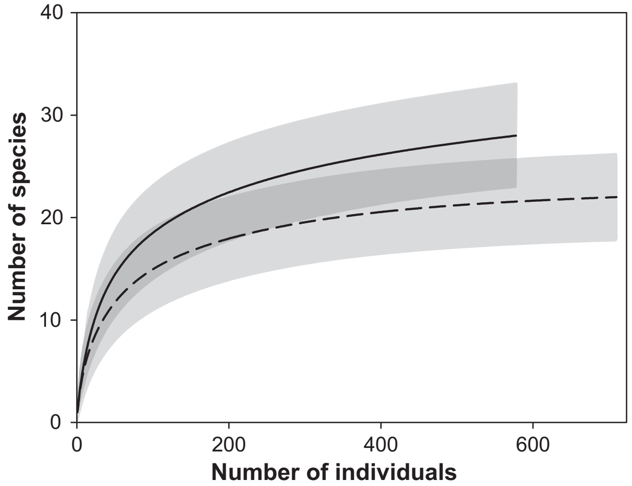

Fig. 2. Dung beetle individual-based rarefaction curves for unlogged (solid line) and RIL (dashed line) forest. Shaded areas indicate 95% confidence intervals.

3.1. Species diversity

Across our 20 sampling sites, we recorded 34 species of dung beetle from 1290 individuals (RIL: 711; unlogged: 579). Two species, *Canthon (Canthon) triangularis* and *Hansreia affinis*, accounted for 45 percent of total captures, with a further 11 species comprising 48 percent, and the remaining 21 species representing just 7 percent of the overall sample (Table S1). Although observed richness was lower in RIL forest than unlogged forest (26 and 31 species respectively), rarefaction curves and richness estimators showed no statistical difference in species diversity because confidence intervals overlapped (Fig. 2; mean of richness estimators: RIL = 32.4; unlogged = 35.8).

3.2. Association of dung beetle assemblage with environmental variables

No differences in the environmental variables were apparent between RIL and unlogged forest (all $p > 0.05$), with the exception of small woody debris which was greater in the control plots ($t_{18} = 0.59$, $p = 0.034$) (Table S2). The BIO-ENV model with highest correlation identified RIL extraction rate, bare ground cover and leaf cover as the key factors influencing dung beetle assemblages, explaining 46.2 percent of the variation in community composition.

3.3. Assemblage response to RIL

The NMDS ordination represented 77 percent of the assemblage dissimilarity, and showed differences between RIL and unlogged forest (Fig. 3). Analysis of the *RIL* treatment showed that dung beetle assemblages were more uniform in logged plots than their unlogged counterparts (ANOSIM: $R = 0.21$, $p = 0.001$). Examination of the *Canopy Gap* and *Closed Canopy* treatments, demonstrated that the primary source of this dissimilarity was between closed canopy plots in the logged and unlogged forest (ANOSIM: $R = 0.2$, $p = 0.049$), with no differences apparent between natural and artificial canopy gaps (ANOSIM: $R = 0.1$, $p = 0.22$).

3.4. Indicator species

Seven species accounted for 50 percent of the SIMPER dissimilarity between *RIL* treatments (Table S1). *Hansreia affinis* was the greatest contributor to dissimilarity, and was consistently identified by CLAM and INDVAL as an indicator of all logged treatments at

Table 1
Classification of dung beetle indicator species by CLAM (Chazdon et al., 2011) and IndVal (Dufrêne and Legendre, 1997), across the different levels of analysis: RIL, Canopy Gaps, Closed Canopy (see methods for definitions). Only species selected as indicators by one or more of the analytical techniques are listed.

Species	RIL			
	CLAM classification[a]	IndVal classification[b]	IndVal stat	IndVal *p*
Hansreia affinis	RIL	RIL	0.76	0.002*
Eurysternus caribaeus	Not indicator	RIL	0.71	0.002*
Canthidium aff. centrale	Unlogged	Not indicator	0.47	0.088
Deltochilum (Calhyboma) carinatum	Unlogged	Not indicator	0.45	0.1
	Canopy gaps			
	CLAM classification[a]	IndVal classification[b]	IndVal stat	IndVal *p*
Hansreia affinis	RIL	RIL	0.73	0.045*
Canthidium aff. centrale	Unlogged	Not indicator	0.50	0.165
	Closed canopy			
	CLAM classification[a]	IndVal classification[b]	IndVal stat	IndVal *p*
Hansreia affinis	RIL	RIL	0.80	0.026*
Eurysternus caribaeus	Too rare	RIL	0.72	0.033*
Deltochilum (Calhyboma) carinatum	Unlogged	Not indicator	0.51	0.402

[a] Based on the supermajority specialization threshold ($K = 0.667$, $p = 0.001$).
[b] IndVal does not provide a too rare classification.
* IndVal significant at the $p < 0.05$ level.

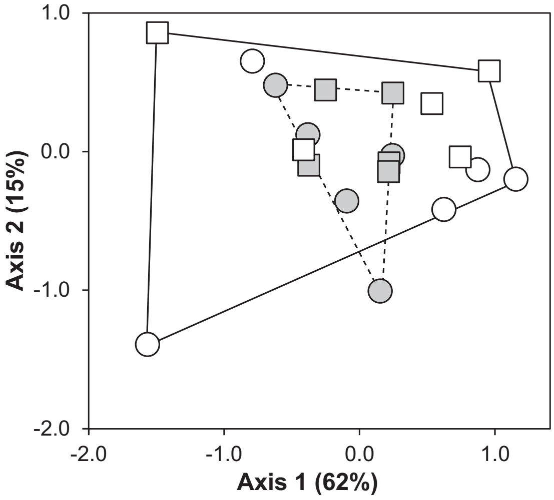

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of dung beetle assemblage structure across the four treatments within and outside Reduced-Impact Logging operations: filled circles, RIL canopy gaps; filled squares, RIL closed canopy; unfilled circles, unlogged (control) canopy gaps; unfilled squares, unlogged (control) closed canopy. Solid line surrounds all unlogged plots; dashed line surrounds all RIL plots. The first NMDS axis explains 62% of dung beetle assemblage, and the second axis 15%. Stress = 0.11.

the *RIL*, *Canopy Gap*, and *Closed Canopy* levels (Table 1; Fig. 4). The four remaining species ranked in top five by SIMPER (*Canthon (Canthon) triangularis*, *Dichotomius* sp. 2, *Dichotomius aff. boreus, and Trichocanthon sordidus*) were not considered indicators by CLAM or IndVal, and CLAM and IndVal did not provide a consensus on the selection of other indicator species. *Eurysternus caribaeus* was identified as an indicator of *RIL* by IndVal, but not via CLAM (Fig. 4a). When examined at the *Canopy Gap* and *Closed Canopy* treatment level, IndVal selected the species as a specific indicator of RIL closed canopy, although CLAM considered it too rare to classify (Fig. 4b,c). *Canthidium aff. centrale* was identified by CLAM as an indicator of unlogged forest (Fig. 4a), particularly unlogged canopy gaps (Fig. 4b). However, this species was not selected by IndVal as an indicator of any treatment at either level. *Deltochilum (Calhyboma) carinatum* was classed as an indicator of unlogged forest by CLAM (Fig. 4a), but not by IndVal. When scrutinized at the level of *Canopy Gap* and *Closed Canopy*, CLAM considered this species an indicator of unlogged canopy (Fig. 4c).

4. Discussion

The outcome of this research clearly demonstrates the suitability and use of dung beetles as a focal taxonomic group for investigating the effects of disturbance within a restricted study period. Biodiversity survey design is typically a balance between sampling sufficient individuals to detect a statistical signal, and keeping within financial and/or time constraints (Gardner et al., 2008a). Dung beetle studies frequently utilise a sampling effort much greater than that needed to determine alterations in community composition at any given site (e.g. Barlow et al., 2010). Here, we show that using a rapid sampling regime, even subtle changes in dung beetle assemblages can be detected using community- and species-level analytical techniques (providing catch rates are comparable or greater). Despite the high number of dung beetles that were too rare to be classified by CLAM, we were still able to identify indicator species within a restricted time-frame, highlighting their value for rapid biological monitoring and environmental impact assessments. Additionally, species identification has previously been a substantial limitation to studies of this kind, but now that dung beetle taxonomy is well documented, online species catalogues and identification keys are becoming increasingly available and free to access.

4.1. Assemblage response to RIL

In this study, RIL management activities were reflected by changes in dung beetle assemblage composition, demonstrating that the taxonomic group is sensitive to even low-intensity habitat modification. Our results build on the findings of a meta-analysis examining dung beetle responses to disturbance (Nichols et al., 2007), and provide further evidence of their indicator value. It is relatively well documented that shifts in dung beetle communities are primarily driven by two factors: local environmental variables (e.g. vegetation structure, soil structure, microclimate) (Halffter and Arellano, 2002) and dung availability (Nichols et al., 2009). RIL has been shown to have only minimal impacts on vegetation structure at the harvesting intensities employed in the Iwokrama

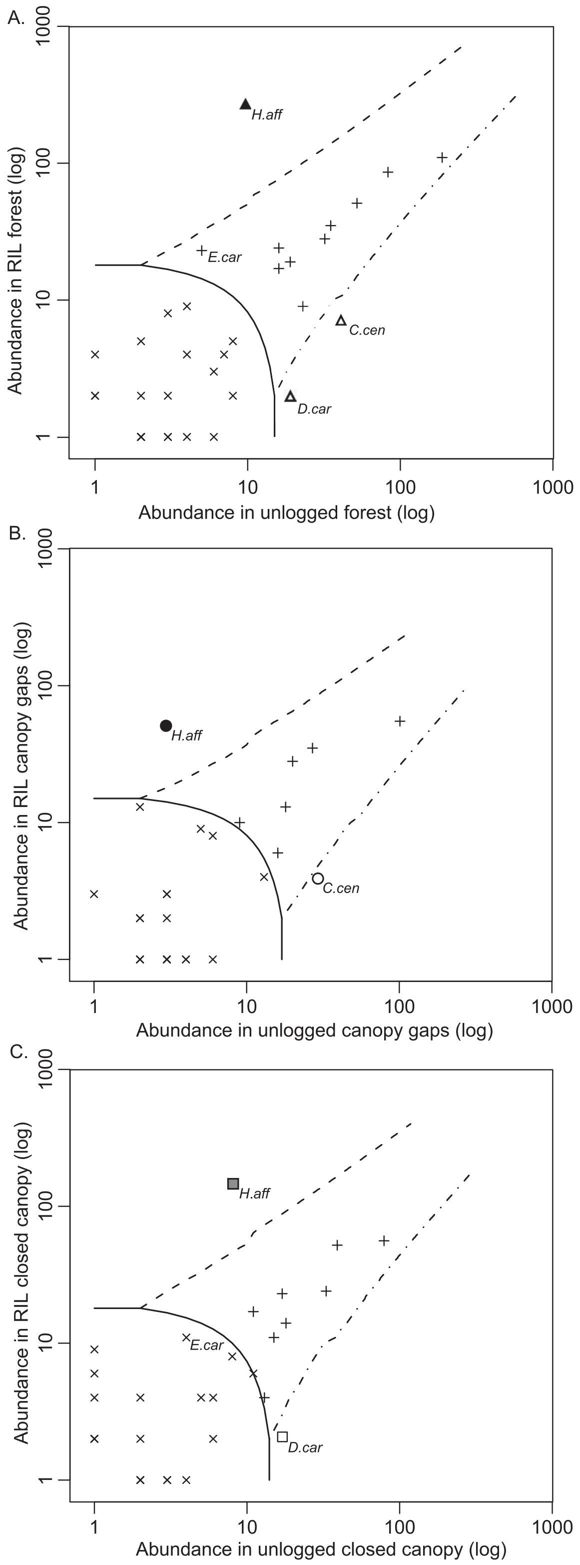

Fig. 4. Classification of dung beetle indicator species by CLAM: (A) *RIL* treatment; (B) *Canopy Gap* treatment, and; (C) *Closed Canopy* treatment (see methods for definitions). Only species listed in Table 1 are labelled. Black triangles: RIL specialists; unfilled triangles: unlogged specialists; black circles: RIL canopy gap specialists; unfilled circle: unlogged canopy gap specialists; grey-filled squares: RIL closed canopy specialists; unfilled squares: unlogged closed canopy specialists; + generalists; × too rare to classify. Dashed lines represent CLAM thresholds for specialist and generalist classes, and solid lines indicate the threshold at which species are too rare to classify.

Forest (Felton et al., 2006; Pinard and Putz, 1996; van de Hout and Zagt, 2003), with the exception of extraction trails. In French Guiana, *H. affinis* and *E. caribaeus* are positively associated with forest edges (Feer, 2008) and other disturbed areas (Price and Feer, 2012). Given that our analyses classified these species as indicators of RIL, it is probable that extraction trails contribute significantly to the dung beetle community changes. However, many primary forest species are likely to be intolerant of the elevated temperatures that are associated with such infrastructure (Andresen, 2005, 2008a; Gardner et al., 2008b; Larsen, 2007), and our analyses suggest that two species (*D. carinatum* and *C. aff. centrale*) are not well adapted to changes arising from an increase in edge habitat. Importantly, from a best-practice forestry perspective, our study shows that artificial and natural canopy gaps did not differ in terms of dung beetle assemblage or the environmental variables measured, suggesting that RIL gaps successfully mimic natural tree-fall gaps. Despite this, our results point towards a need for greater research attention to be directed towards investigating the impacts of RIL at a microhabitat scale, as we found that bare ground and leaf material coverage are important variables underpinning dung beetle assemblage composition.

Observed changes in the dung beetle community may also be explained by a shift in the relative availability of large mammal faeces, in particular that from primates (Feer and Pincebourde, 2005; Ponce-Santizo et al., 2006; Vulinec et al., 2006) which comprise high biomass in neotropical forests (Parry et al., 2007). Primate densities are known to be correlated with logging intensity (Chapman et al., 2000), and in the Iwokrama Forest are affected by RIL (Bicknell and Peres, 2010). However, until it is known whether dung beetles have affinities to faeces from particular species (Holter and Scholtz, 2007; Nichols et al., 2009; but see also: Feer and Pincebourde, 2005; Gardner et al., 2008b; Whipple and Hoback, 2012), it is difficult to verify how the relative availability of dung resources may influence the beetle assemblage.

4.2. Indicator analyses

Employing multiple approaches to classify indicator species maximised our ability to detect indicators of logging in our rapid assessment dataset, and highlighted the importance of using several techniques to classify species. Previous dung beetle studies have demonstrated the reliability of IndVal for separating species indicative of habitat modification (e.g. Barlow et al., 2010; Gardner et al., 2008b; Verdú et al., 2011; Viegas et al., 2014), but none utilise more than one indicator classification algorithm as we have here. While IndVal and SIMPER account for variation between sample plots, CLAM is multinomial and less sensitive to spatial and temporal disparity independent from the treatment being studied (Chazdon et al., 2011). This has its benefits, but can also be considered to be a shortcoming given the spatiotemporal heterogeneity inherent within most ecosystems.

CLAM is designed for use in bivariate comparative studies (e.g. treatment versus control, before versus after) and, consequently, is limited to comparisons between just two groups. However, one advantage of CLAM is that the procedure explicitly considers a threshold of rarity, meaning that species that are 'too rare' cannot be classified. Conversely, IndVal does not discriminate between species that are too rare to classify and those that are non-indicators (Cleary et al., 2006), and the SIMPER procedure does not use thresholds, only rank contributions to the different groups (Clarke, 1993). Furthermore, CLAM is useful in that it also distinguishes species that are generalists, from those that demonstrate specificity to one habitat/treatment (i.e. are indicators).

According to Chazdon et al. (2011), CLAM is more sensitive than IndVal in regard to classifying indicator species. Using the conservative super-majority specialization thresholds, CLAM categorised all indicators identified by IndVal with the exception of *E. caribaeus*, but also classified other species as indicators that were not detected by IndVal. This indeed suggests greater sensitivity of CLAM, and highlights the lack of congruence between methods, particularly given that *E. caribaeus* is considered an indicator of disturbance by other studies (Avendaño-Mendoza et al., 2005; Carpio et al., 2009). Nonetheless, in rapid assessments, where more analytical power is gained by pooling data into treatments, CLAM can detect indicator species that may not be classified by other techniques.

The SIMPER technique appeared to be sensitive to the overall number of captures per species. For example, *D. aff. boreus* (the fifth most abundant species) was ranked highly by SIMPER (fourth) despite the fact that the species was equally abundant between treatments, and the level and nature of within-treatment dissimilarity were identical. This pattern was similar for the other species ranked highly by SIMPER, which were also generally abundant species, the only exception was that of *H. affinis*, which was unanimously classified as an indicator by the other analytical techniques, as well as being highest ranked by SIMPER. This appears to be an artefact of the calculations SIMPER employs to compare between groups and, therefore, we conclude that care should be taken when interpreting the outputs from this similarity percentages method for the identification of reliable indicator species.

5. Conclusions

Whilst it is likely that the measures taken in RIL operations minimise the impacts of commercial forestry on biodiversity, we show that dung beetles are highly sensitive indicators of even low-intensity anthropogenic habitat disturbance. Our findings demonstrate that short-term studies using Scarabaeinae as a focal taxonomic group can be a highly effective method of monitoring the consequences of even environmentally-sensitive extractive industries in production forests and, as a consequence, should be adopted as tool for supporting ecological impact monitoring activities. Also, in light of our findings, we recommend the use of multiple indicator analyses to monitor potential changes in assemblage composition, due to a lack of congruence between methods.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2014.02.030.

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