



Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging

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Summary

1. Over 20% of the world's tropical forests have been selectively logged, and large expanses are allocated for future timber extraction. Reduced-impact logging (RIL) is being promoted as best practice forestry that increases sustainability and lowers CO₂ emissions from logging, by reducing collateral damage associated with timber extraction. RIL is also expected to minimize the impacts of selective logging on biodiversity, although this is yet to be thoroughly tested.

2. We undertake the most comprehensive study to date to investigate the biodiversity impacts of RIL across multiple taxonomic groups. We quantified birds, bats and large mammal assemblage structures, using a before-after control-impact (BACI) design across 20 sample sites over a 5-year period. Faunal surveys utilized point counts, mist nets and line transects and yielded >250 species. We examined assemblage responses to logging, as well as partitions of feeding guild and strata (understorey vs. canopy), and then tested for relationships with logging intensity to assess the primary determinants of community composition.

3. Community analysis revealed little effect of RIL on overall assemblages, as structure and composition were similar before and after logging, and between logging and control sites. Variation in bird assemblages was explained by natural rates of change over time, and not logging intensity. However, when partitioned by feeding guild and strata, the frugivorous and canopy bird ensembles changed as a result of RIL, although the latter was also associated with change over time. Bats exhibited variable changes post-logging that were not related to logging, whereas large mammals showed no change at all.

4. Indicator species analysis and correlations with logging intensities revealed that some species exhibited idiosyncratic responses to RIL, whilst abundance change of most others was associated with time.

5. *Synthesis and applications.* Our study demonstrates the relatively benign effect of reduced-impact logging (RIL) on birds, bats and large mammals in a neotropical forest context, and therefore, we propose that forest managers should improve timber extraction techniques more widely. If RIL is extensively adopted, forestry concessions could represent sizeable and important additions to the global conservation estate – over 4 million km².

Key-words: BACI, bat, before-after control-impact, bird, feeding guild, forest disturbance, forestry, Guyana, RIL, sustainable forest management

Introduction

Over 20% of the world's tropical forests have been subjected to selective logging, and at least a further 25% of

remaining primary forests are designated for timber extraction, over four million square kilometres (FAO 2010; Blaser *et al.* 2011). Given that nearly half the world's tropical forests have been or will be selectively logged, it is highly pertinent to consider the consequences of selective logging. Timber production forests are extensive, functionally diverse, and are important for the

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provision of many ecosystem services (Edwards *et al.* 2014a). Consequently, efforts to expand the role of logging estates in conservation strategies are being increasingly considered, and among the priorities to achieve this is the improvement of logging practices (Edwards *et al.* 2014a).

Selective logging is less detrimental to biodiversity than other large-scale disturbances faced by tropical forests, such as clear-felling, fire and fragmentation (Barlow *et al.* 2006; Gibson *et al.* 2011). Nevertheless, timber harvesting can result in negative outcomes, resulting in localized extinctions and changes to community composition (Fimbel, Grajal & Robinson 2001; Meijaard *et al.* 2005; Edwards *et al.* 2014b). Although our understanding of logging effects relative to other disturbance types is extensive, knowledge regarding the impacts of different selective logging techniques on biodiversity remain limited, in particular those that employ best practices. Forestry concessions that adopt best practices are expected to result in only negligible changes in biodiversity, and therefore, these areas could be important components of the global conservation estate if managed with long-term sustainability in mind (Wilson *et al.* 2010; Putz *et al.* 2012; Edwards *et al.* 2014a). Sustainably managed forests are reliant on ecosystem services provided by fauna, in particular the seed dispersal and pollination services of birds, bats and other mammals (Moran, Catterall & Kanowski 2009; Beaudrot, Rejmánek & Marshall 2013; Maas, Clough & Tschardtke 2013). However, to date, there have been few studies regarding the biodiversity impacts of best practice forestry, despite the importance of vertebrates for forest regeneration (Wunderle 1997; Cramer, Mesquita & Williamson 2007).

Reduced-impact logging (RIL) is a modern system of timber harvesting that endeavours to reduce the damage to forest structure associated with selective logging (Pinard & Putz 1996). Whilst the specific silvicultural treatments implemented under the umbrella of RIL are somewhat variable, RIL has been shown to reduce collateral damage caused by forestry operations, and benefit sustainability and forest recovery periods compared with conventional selective logging (CL) (Putz *et al.* 2012; West, Vidal & Putz 2014). RIL can improve ecosystem service provision relative to CL (Miller *et al.* 2011), and it is estimated that adoption across production forests globally would cut carbon emissions by 160 million tonnes each year, equivalent to *c.* 10% of carbon emissions from deforestation (Putz *et al.* 2008), if properly implemented (Griscom, Ellis & Putz 2014). Despite these advantages, uptake of RIL has remained slow, and conventional practices continue to dominate the industry (Blaser *et al.* 2011).

Given the evidence demonstrating the benefits of RIL associated with reducing logging damage, it may also be expected to reduce impacts on biodiversity, but this is yet to be thoroughly scrutinized (Peres *et al.* 2010; Edwards *et al.* 2012). As a result, there is no strong evidence base

to inform forestry policy and practice. Additionally, there is a lack of consensus in relation to the overall consequences of logging for biodiversity (Laufer, Michalski & Peres 2013; Struebig *et al.* 2013), as responses across studies and taxonomic groups are inconsistent. The equivocal findings may be due to sampling bias caused by pseudoreplication (Ramage *et al.* 2013), spatial scale (Hill & Hamer 2004), time frame and differing sampling methods (Laufer, Michalski & Peres 2013). Whilst analytical approaches can help to control for some of these problems (Struebig *et al.* 2013), the most effective way to overcome the first of these issues is to quantify responses temporally rather than relying on spatial inference. This can be achieved by adopting a before-after control-impact (BACI) experimental design (Lindenmayer 1999). Further uncertainty should be reduced by simultaneously sampling multiple taxonomic groups in response to one disaggregated disturbance type across meaningful spatial and temporal scales. Nonetheless, few logging studies meet these recommendations (Laufer, Michalski & Peres 2013; Ramage *et al.* 2013).

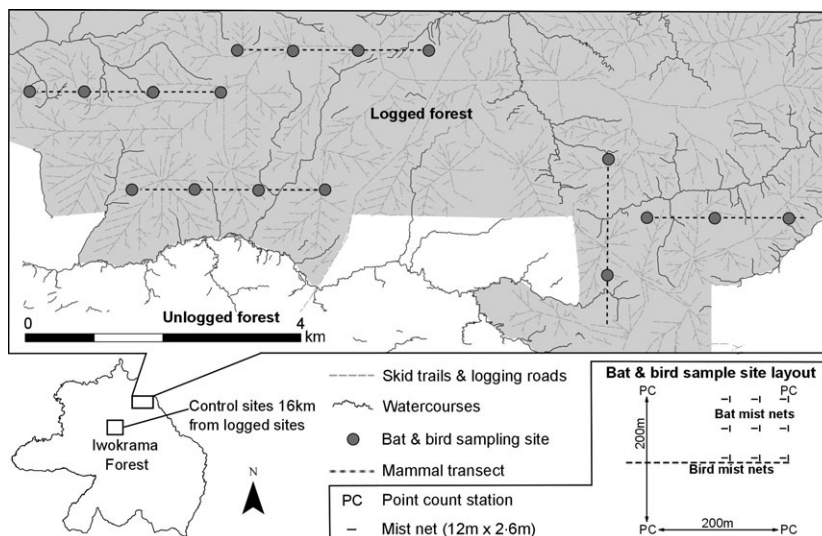
In this paper, we present a comprehensive multitaxa (birds, bats and large mammals) experiment to investigate vertebrate responses to RIL, using a BACI sampling regime. We quantify assemblage composition before and after logging and examine whether this is driven by logging intensity. Moreover, we assess effects partitioned by feeding guilds and forest-use strata and determine which species are the primary drivers and indicators of assemblage change.

Materials and methods

STUDY AREA AND DESIGN

The study was situated within Iwokrama Forest, central Guyana, which is a 3710 km² area lying between 4–5°N and 58–59°W, characterized by *terra firme* tropical rain forest (Fig. 1). There is no hunting in the study area, and timber operations are certified under the Forest Stewardship Council scheme. RIL in the Iwokrama Forest minimizes logging extraction routes via a pre-harvest inventory, which is used to plan the most efficient logging road and skid trail (tertiary extraction routes that typically do not open the canopy) network. A number of silvicultural techniques are implemented to reduce collateral damage and prevent large canopy openings, including timber being winched to skid trails, the use of minimum diameters and distances between felled trees, and directional felling by trained chainsaw operators. Additionally, linking vines are cut prior to felling to avoid connected trees being dragged down unintentionally along with the target tree. Mean logging intensity (number of trees removed) in the sample sites was 3.2 trees ha⁻¹ (range: 0.4–5.9), equivalent to a volume of 6.89 m³ ha⁻¹ (range: 1.1–14.1). This represents *c.* 6.3% of trees above 40 cm in diameter (for further details see Bicknell & Peres 2010). Average skid trail length was 152 m ha⁻¹ (range: 0–335) (see Table S1 in Supporting information), covering about 608 m² ha⁻¹ (6.08%) of the forest floor (based on the assumption that skid trails are, in general, 4 m wide). This is a slight underestimate of the total disturbance area as it does not

Fig. 1. Sample sites in Iwokrama Forest, Guyana, for birds and bats, and large mammal transects, logging roads and watercourses after reduced-impact logging. Lower left: location of logging sites in relation to control sites. Lower right: bat and bird mist net and point-count spatial survey design at each sample site.



account for logging gaps created by felled trees. Extraction intensities were measured within a 200-m radius from the centre of each sample site.

We used a BACI design to study vertebrate responses to RIL, with surveys conducted in the same locations 'pre'- and 'post'-logging. Birds and bats were sampled at 20 independent sites across the logging landscape. Three of these sites were primary forest controls situated 16 km from the logging area. All sites were spaced a minimum of 1 km from each other and were at least 500 m from unlogged areas post-logging. Across the same landscape, large mammals were surveyed along six transects, one of which was a control.

Surveys were conducted from 2008 to 2013, between November and April each year. Each site was surveyed over 3 days pre-logging and 3 days post-logging, and these were always conducted in the same month at each site to minimize possible effects of seasonal variation. Pre-logging surveys were conducted 6 months before logging began in the area, and post-logging surveys 12–16 months after logging. Control sites were sampled over the same time frame as logging sites. Before logging, all sites had no evident human disturbance.

FAUNAL SURVEYS

To comprehensively sample the bird community, we used both mist nets and point counts to include all forest strata and cryptic species. Four point-count stations were nested within each sample site at the corners of a 200-m grid. Stations were surveyed for 10 min on each of three mornings pre- and post-logging, between 06:00 and 08:00. This resulted in a total of 4630 point-count minutes, which were all conducted by a single experienced observer. The maximum detection radius was truncated to 100 m to minimize the potential for double counting. At the same sites, and on the same 3 days, eighteen mist nets (12 × 2.6 m, mesh size 36 mm) were set in a straight line to catch understorey birds from 06:00 to 18:00, pre- and post-logging, equating to 23 845 mist net hours in total.

To sample bats, we set 18 mist nets for four nights from 18:00 to 00:00 at each site, pre- and post-logging, resulting in 15 081 mist net hours in total. Nets were positioned in nine pairs throughout a 100 × 100 m grid, spaced every 50 m.

The large mammals, sampled along three-kilometre straight-line transects, comprised one large terrestrial rodent, red-rumped agouti *Dasyprocta leporina* and three primate species: Guiana spider monkey *Ateles paniscus*, Guianan red howler monkey *Alouatta macconnelli* and wedge-capped capuchin *Cebus olivaceus*. The transects were walked slowly early in the morning (06:30–10:00), pausing at regular intervals to scan the forest. Upon detection of target species, we counted the number of individuals. Each transect was repeatedly surveyed over a 16-day period pre- and post-logging, resulting in 345 km in total.

DATA ANALYSIS

We first combined data from bird point counts and mist nets in order to maximize our understanding of the entire bird community (Appendix S1, Supporting information). Rarefaction curves and accompanying confidence intervals were generated, after excluding recaptures, for each assemblage and feeding guild partition pre- and post-logging. We \log_{10} -transformed the standardized bird and bat abundance data per sample site pre- and post-logging. Assemblage changes pre- and post-logging were then visualized using non-metric multi-dimensional scaling (NMDS) from Bray-Curtis dissimilarity coefficients, implemented in PC-ORD v.6.07 (McCune & Mefford 2011). To best visualize the change in community structure, and magnitude of change pre- and post-logging, we plotted the NMDS with all pre-logging sites rescaled to a common centroid with successional vectors following McCune & Grace (2002).

Partial Mantel tests, conducted in PC-ORD, were used to detect statistical differences in assemblage change pre- and post-logging, whilst controlling for other factors that could influence change in community composition. Tests were first undertaken to control for geographic distance between sites, since controls were further from the logging sites than logging sites were to one another (Ramage *et al.* 2013). We then ran a second test to control for time between surveys (days between pre- and post-logging surveys), thus accounting for potential natural rates of change (hereafter 'turnover') so that any shifts in assemblage could be attributed to RIL with confidence. To test for statistical differences in the pre- and post-logging assemblage change between logging and control sites, we employed paired permutational

multivariate analysis of variance (ADONIS) tests from 999 permutations in R (R Core Team 2013). This analysis was paired by calculating the difference in abundance pre- and post-logging for every species at each site. These analyses were undertaken twice, firstly with the entire assemblage included and then with species comprising a single occurrence removed. Both approaches yielded consistent results, and therefore, the findings across all species are reported.

ADONIS tests were also used to determine covariates of assemblage change pre- and post-logging. We used direct measures of logging, rather than proxies (e.g. temperature, canopy cover) because they are used when planning logging operations and so better inform forestry management. The candidate variables were logging intensity, (trees per ha⁻¹ and volume of timber removed), skid trail density and time elapsed between logging activities and the post-logging surveys. We also included the time between pre- and post-logging surveys as a covariate to separate turnover from the impacts of RIL. We excluded volume of timber removed from the analyses as it was highly correlated with logging intensity (Pearson's: $r = 0.78$, $P < 0.001$), and the number of trees removed is a better measure of disturbance.

Ecological traits are fundamental to species' responses to habitat modification (Newbold *et al.* 2013), so to better understand the drivers of bird and bat assemblage response to RIL, we repeated all the analyses outlined above for partitions of the assemblages based on simple feeding guild (insectivorous or frugivorous) and forest-use strata (understorey or upper levels). We did not divide bats by strata as we only used understorey mist nets to sample this taxonomic group. The majority of birds (91% of detections) and bats (88%) were either frugivorous or insectivorous, and so other guilds (e.g. carnivores, omnivores, nectarivores) did not warrant separate analyses as they were only represented by a small number of species.

In order to categorize the individual species contributing most to the overall bird and bat assemblage change, we undertook indicator species analysis using INDVAL (Dufrene & Legendre 1997). Indicator values for each species were assigned from 999 permutations, conducted in PC-ORD. To understand responses of the indicator species, we correlated the matrices of these species with the NMDS ordination scores, using Kendall's tau rank correlation coefficient (McCune & Grace 2002) in PC-ORD. Subsequently, we correlated the result with the modelled variables mentioned above and plotted the coefficient against the change in abundance pre- and post-logging.

We did not undertake ordinations for large mammals as only four species were surveyed. Thus, to detect any differences pre- and post-logging, we used a Z-test (Buckland *et al.* 2001; Bicknell & Peres 2010) of encounter rates along each line transect.

Results

The combined bird data set consisted of 6849 individuals (4248 and 2601 pre- and post-logging, respectively) from 202 species (178 pre-logging, 148 post-logging). Point counts yielded 5561 individuals from 143 species, and 1288 birds from 59 species were captured in mist nets. The bat data set comprised 1144 (692 pre-logging, 452 post-logging) bat captures from 50 species (40 pre-logging, 39 post-logging), and 442 (271 pre-logging, 171 post-logging) detections of target species were recorded for large mammals.

Bird and bat rarefaction curves began to level off for the assemblages and their partitions, indicating that the communities were comprehensively sampled (Fig. S1, Supporting information). Confidence intervals of the curves overlapped for all partitions with the exception of insectivorous birds, where post-logging diversity was lower.

Bird and bat ordinations represented 73% and 81% of the assemblage dissimilarity, respectively. The first axis of the bird assemblage was most correlated with time between surveys ($r_{\text{tau}} = -0.450$) and the second axis with logging intensity ($r_{\text{tau}} = 0.338$). The bat ordination axes were poorly correlated with the variables, the greatest correlations being for Axis 1 with time between surveys ($r_{\text{tau}} = 0.183$) and Axis 2 with time since logging ($r_{\text{tau}} = 0.181$).

BIRD ASSEMBLAGE RESPONSE TO RIL

Change in the bird assemblage pre- and post-logging was congruent between the logged and control sites, and the majority of sites were negatively associated with NMDS Axis 1 and positively associated with Axis 2 (Fig. 2). Assemblage change did not differ significantly pre- and post-logging (significant partial Mantel; Table 1), indicating no effect of RIL at the assemblage level. However, two of the bird partitions exhibited a signal in response to logging; frugivorous and upper-level birds changed pre- and post-logging, and logged sites for these partitions were also different from control (Table 1). These partitions were also more often associated with Axis 2 than Axis 1 (Fig. 2b,d). Despite this, the variability in the bird assemblage and its partitions was not explained by the logging intensity variables, but time between surveys was a predictor for all partitions apart from the frugivores (Table 2).

BAT ASSEMBLAGE RESPONSE TO RIL

Change in the bat assemblage pre- and post-logging varied across the sites (Fig. 3). In general, the bat assemblage and partitions differed pre- and post-logging, although they did not differ from control (Table 1). Therefore, the changes cannot be attributed reliably to logging. The variability could not be explained by logging, but time between surveys was a predictor for frugivorous bats (Table 2).

SPECIES-SPECIFIC RESPONSES TO RIL

None of the primates or the agouti showed statistically significant differences pre- and post-logging (Z-test: $P > 0.05$ in all cases; Fig. S2c, Supporting information).

The species primarily driving the assemblage changes were those classified as indicators. These included twenty-seven bird species, 21 of which were more abundant pre-logging and six more abundant post-logging (Fig. 4a; Table S2; Fig. S2a, Supporting information). Seventeen of

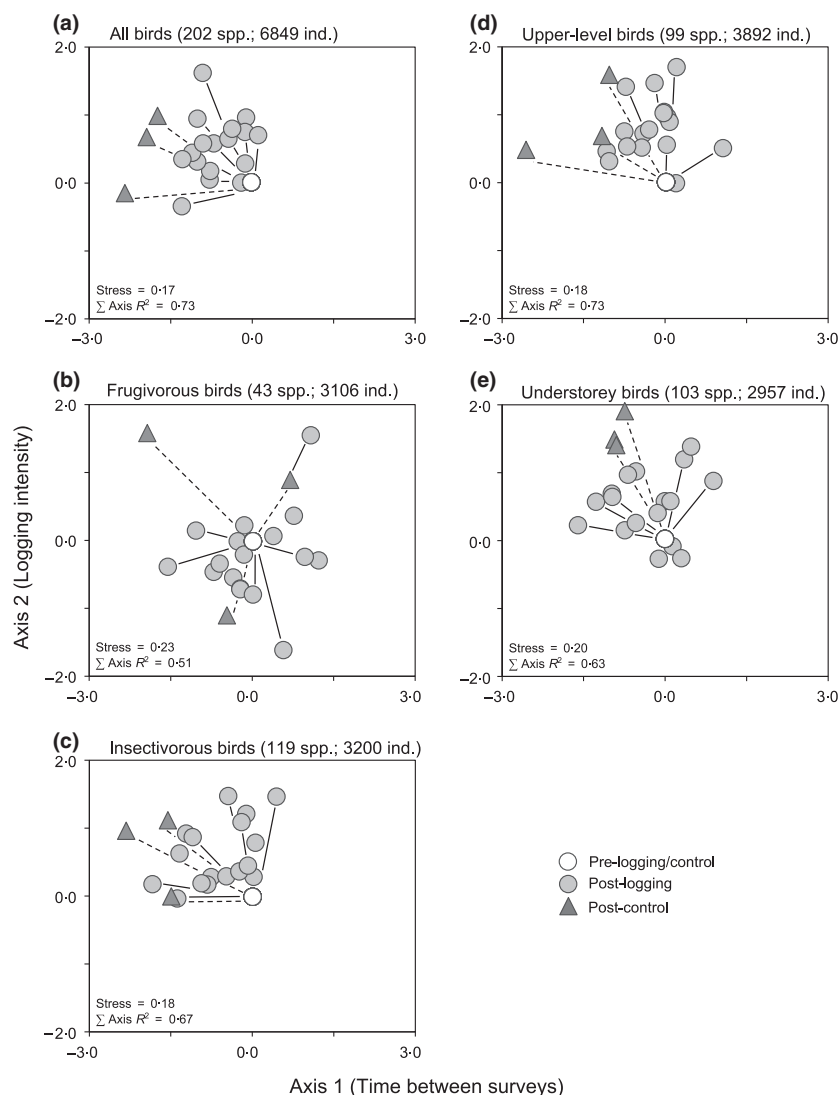


Fig. 2. Bird NMDS ordinations for all species (a), by feeding guild (b, c) and forest-use strata (d, e) at each site before and after reduced-impact logging. Each pre-logging and pre-control site is rescaled to zero and represented by the centroid (unfilled circle). The direction of the point from the centre indicates the change in assemblage composition at that site, and the magnitude of change is represented by the distance from the centroid.

Table 1. Partial Mantel tests of bird and bat assemblages pre- and post-reduced-impact logging, controlling for geographic distance between sites and time between surveys, and paired ADONIS tests of logging vs. control sites. The assemblages were analysed in their entirety, as well as partitioned by feeding guild and forest-use strata (birds only)

Assemblage-Partition	Partial Mantel controlling for geographic distance		Partial Mantel controlling for time between surveys		Paired ADONIS logging vs. control	
	R^2	P	R^2	P	F_{18}	P
All birds	0.28	0.015	0.35	0.002	1.66	0.015
Frugivorous birds	0.15	0.113	0.20	0.068	2.26	0.006
Insectivorous birds	0.15	0.073	0.18	0.048	1.34	0.138
Upper-level birds	0.05	0.343	0.13	0.145	1.87	0.005
Understorey birds	0.18	0.032	0.21	0.016	1.40	0.086
All bats	0.13	0.211	0.14	0.189	0.74	0.664
Frugivorous bats	0.21	0.134	0.21	0.124	0.48	0.770
Insectivorous bats	0.10	0.183	0.05	0.271	0.35	0.903

Bold signifies statistical significance at $P < 0.05$. Significant partial Mantel tests indicate that the pre- and post-logging assemblages are the same, and significant paired ADONIS tests show that the change in the logged sites was different from that in the control sites. Therefore, an effect of RIL only exists where the partial Mantel tests are non-significant, combined with a significant paired ADONIS test.

Table 2. ADONIS tests of entire bird and bat assemblages, as well as partitioned by feeding guild and forest-use strata (birds only), to examine associations with reduced-impact logging intensity, skid trail density, time elapsed since logging and time between the pre- and post-logging surveys at each sample site

Assemblage-Partition	Time between surveys		Logging intensity		Skid trail density		Time after logging	
	F_{35}	P	F_{35}	P	F_{35}	P	F_{35}	P
All birds	3.29	0.002	2.39	0.163	1.26	0.722	3.29	0.340
Frugivorous birds	3.01	0.082	1.68	0.213	1.27	0.376	1.42	0.329
Insectivorous birds	3.19	0.020	3.13	0.167	1.32	0.242	1.61	0.445
Upper-level birds	3.46	0.050	2.19	0.370	1.16	0.362	1.42	0.462
Understorey birds	2.92	0.003	2.63	0.127	1.37	0.219	1.52	0.453
All bats	2.21	0.309	1.73	0.391	0.88	0.710	0.67	0.918
Frugivorous bats	3.20	0.047	1.39	0.366	1.34	0.458	0.43	0.922
Insectivorous bats	2.10	0.887	1.26	0.260	0.39	0.812	0.43	0.768

Bold indicates statistical significance at $P < 0.05$.

the indicators were insectivorous antbirds, flycatchers and woodpeckers, five were omnivores, and five were frugivores. Those species with the most marked responses had the greatest difference between correlation coefficients with the two ordination axes. A strong positive correlation with the first ordination axis, but negative with the second, demonstrates an association with turnover and not RIL. Indicator species with the largest differences of this kind (>0.6) were the insectivorous *Herpsilochmus sticturus*, *Myrmotherula axillaris*, *Tyrannulus elatus*, *Tolmomyias assimilis* and *Willisornis poecilonotus*, and all of these species were more abundant pre- than post-logging. In contrast, species with a strong positive correlation with the second ordination axis, and negative with the first, were associated with the logging metrics, principally logging intensity. This was the case only for the insectivorous *Hypocnemis cantator*, which was more abundant post-logging. The majority of bird species were more correlated with Axis 1 than Axis 2 (Fig. 4a), supporting the assertion that turnover was the key predictor of assemblage change. The species identified as indicators by INDVAL exhibited the greatest disparity between their correlation with Axis 1 and Axis 2, independently meriting their selection as indicators.

From the bat assemblage, only three species were categorized as indicators, two more abundant pre-logging and one post-logging (Fig. 4b; Table S2; Fig. S2b, Supporting information). *Pteronotus parnellii* and *Chrotopterus auritus* were associated principally with Axis 1, but not with Axis 2, and thus time between surveys, although Axis 1 of the bat ordination was only weakly correlated with this variable. *Artibeus lituratus* was more correlated with Axis 2 than Axis 1, showing a greater (but still weak) association with time after logging. The majority of bat species were more correlated with Axis 1 than Axis 2 (Fig. 4b) and, like the birds, the indicator species exhibited the greatest disparity between their correlation with Axis 1 and Axis 2.

Discussion

As selective logging is the most widespread disturbance in tropical forests, the need for low-impact methods has never been more paramount. By means of a BACI study of multiple taxonomic groups, we provide evidence that RIL has limited effects on tropical forest biodiversity. Our data set is the most comprehensive of its kind, including numerous species from a variety of taxonomic and trophic groups, and therefore provides the most complete picture offered to date.

Our study highlights the importance of adopting BACI designs for use in impact studies. By conducting field studies before and after logging, we overcame issues associated with spatial pseudoreplication, which was considered a major cause of bias in a recent review of logging studies (Ramage *et al.* 2013). However, the review did not consider the effects of turnover through time, which, as demonstrated by our study, could lead to type I errors if not accounted for. Therefore, whilst supporting the recommendations of Ramage *et al.* (2013) that logging studies should test for autocorrelation between compositional and geographic distance, we show the importance of statistically testing for spatial and/or temporal turnover regardless of sampling design.

ASSEMBLAGE RESPONSES TO RIL

In this study, assemblage changes as a consequence of RIL were no greater than those attributable to background rates of turnover inherent within tropical communities (Phillips *et al.* 2004). Our study landscape was subject to logging intensities typical of RIL operations in the neotropics. Although it could be argued that our time frame post-logging was relatively short, research on CL in the neotropics has detected effects in bird and bat assemblages at comparable temporal scales under similar logging intensities (Mason 1996; Peters, Malcolm &

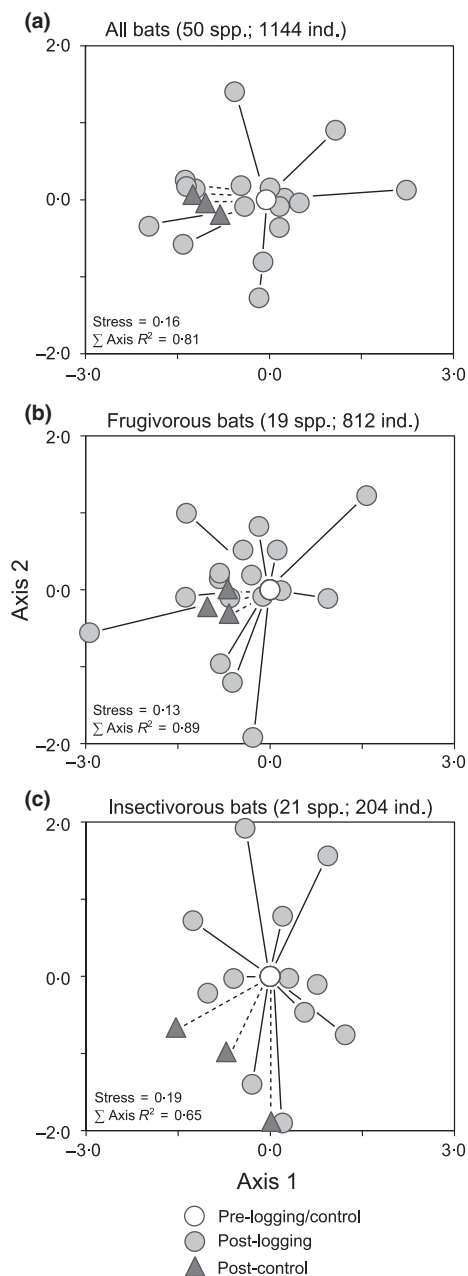


Fig. 3. Bat NMDS ordinations for all species (a), by feeding guild (b, c) at each site before and after reduced-impact logging. Each pre-logging and pre-control site is rescaled to zero and represented by the centroid (unfilled circle). The direction of the point from the centre indicates the change in assemblage composition at that site, and the magnitude of change is represented by the distance from the centroid.

Zimmerman 2006), whereas the previous RIL literature revealed only idiosyncratic responses at equivalent time-scales and harvest intensities (Azevedo-Ramos, de Carvalho & do Amaral 2006; Wunderle, Henriques & Willig 2006; Presley *et al.* 2008; Bicknell & Peres 2010). Our findings thus corroborate earlier assertions that RIL is a relatively benign forestry practice in terms of biodiversity.

The frugivorous and canopy bird assemblages were altered by logging. Whilst in general frugivores decline

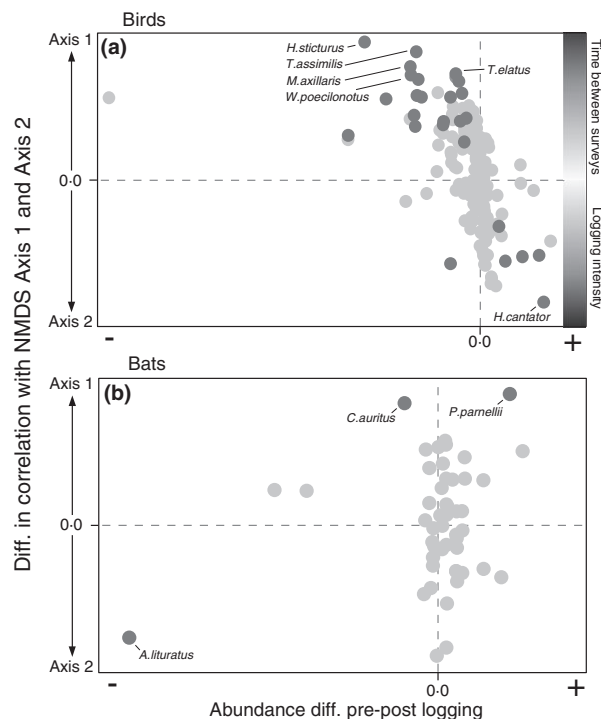


Fig. 4. Relationship between the change in abundance pre- and post-logging, and the difference in correlation coefficient (r_{1au}) with Axis 1 and Axis 2 of the assemblage ordinations, for every species of bird (a) and bat (b). Darker points show the indicator species as identified by INDVAL (see Table S2, Supporting information), and labelled species are those mentioned in the text. Only the indicator species exhibited significant differences pre- and post-logging. Species furthest from the zero centre (in the corners) show the greatest differences pre- and post-logging, which for birds are explained by either turnover (above zero line) or logging intensity (below zero line). The bat ordination axes were not strongly correlated with any of the logging variables measured.

following light and moderate disturbance (Gray *et al.* 2007), studies in the neotropics have shown short-term increases in their abundance following RIL (Wunderle, Henriques & Willig 2006). It is proposed that this is a result of fruit resource booms due to the rise in edge habitat (Wunderle, Henriques & Willig 2006) which, in turn, underpins changes in canopy dwelling frugivorous birds, such as the parrots, toucans and cotingas. Whilst frugivorous bats exploit fruits from pioneer and early successional plants, bird and bat dietary overlap is low in the neotropics (Mello *et al.* 2011), which may partially explain the differences observed between these two taxa in our study. Indeed, frugivorous bats have been shown to persist or even profit in logged neotropical forests (Clarke, Rostant & Racey 2005; Castro-Arellano *et al.* 2007; Presley *et al.* 2008). Likewise, insect abundances fluctuate considerably from year to year in tropical forests, responding to even small changes in weather or climatic conditions (Wolda 1992), having the potential to instigate changes in their predators (e.g. antbirds and flycatchers).

Of the 202 bird species in this study, 27 were considered indicators, and only one of these exhibited a clear

logging response. The increase in abundance of *H. cantator* is not surprising given that it is known to be a forest gap specialist (Stouffer & Borges 2001), and has been found to respond positively to disturbance in previous research (Haugaasen, Barlow & Peres 2003). The majority of changes among the bird indicator species were consistent with turnover rather than RIL and driven by canopy dwelling insectivores such as *H. sticturus* and *T. elatus*. Therefore, although the frugivore assemblage responded to RIL, the most marked changes in abundance pre- and post-logging were in fact among individual insectivores.

Three of the 50 bat species in this study were indicators, but none as a result of logging. Frugivorous bats, such as *A. lituratus*, changed with time in much the same way that many of the birds did, with shifts associated with turnover stronger than that caused by RIL. Species-specific logging responses among the phyllostomid bats lacked consistency. This is reflected in previous studies, some of which have shown *A. lituratus* to be both more abundant (Castro-Arellano *et al.* 2007) and others less abundant (Presley *et al.* 2008) in RIL forest, suggesting that this species may not be a consistent indicator of logging. In general however, frugivorous neotropical bats respond positively and insectivores negatively to logging (Clarke, Rostant & Racey 2005; Presley *et al.* 2008), and whilst there was some indication of this pattern in our study, the observed differences were mostly not statistically significant. The large mammal species surveyed had near identical abundances pre- and post-logging. This is consistent with previous work that has shown large mammals to persist in lightly disturbed forest, more so than other taxa (Gardner 2010), particularly in the absence of hunting (Meijaard *et al.* 2005).

Our study is one of a number based on research conducted in Iwokrama Forest, all focussed on ascertaining the impacts of RIL on biodiversity. These studies comprise a broad range of taxa (representing >400 species) and research methods, and because they are conducted under the same context, they provide a unique opportunity to disaggregate the effects of study design, circumstantial differences and site-specific sensitivity. In Iwokrama Forest, birds, bats, carnivores, ungulates, rodents and primates have all exhibited only limited responses to RIL (this study; Bicknell & Peres 2010; A. Roopsind, T. Caughlin, H. Sambhu, J. Fragoso & F. Putz, unpublished data). In contrast, dung beetles and amphibians are sensitive to RIL (Bicknell *et al.* 2014; M. Hölting *et al.* unpublished data). Although longer-term changes, and those over multiple cutting cycles, cannot yet be considered within Iwokrama, improved forest recovery times under RIL compared with CL (West, Vidal & Putz 2014) suggest that lag effects are likely to be less pronounced. In the only RIL case study with a time series, bird assemblages did not change markedly between 20 and 42 months post-logging (Wunderle, Henriques & Willig 2006). Likewise, possible spillover effects associated

with RIL have also received little attention, even though post-logging immigration is likely where logged areas are adjacent to primary forest, such as in Iwokrama. Nonetheless, best practice forestry always includes areas of concessions left unperturbed, and landscape topography often results in unlogged patches even under CL.

IMPLICATIONS FOR BIODIVERSITY CONSERVATION

Due to the importance of vertebrates as seed dispersal mediators, their retention in communities following RIL may explain, in part, why these forestry concessions recover to pre-disturbance ecological dynamics more rapidly than those logged using conventional methods (West, Vidal & Putz 2014). Faster recoveries lead to increased timber yields, and therefore, forest managers should be motivated to ensure that forestry is aligned with biodiversity conservation, although further investigations are needed to affirm the role of vertebrates in timber recovery times.

Without a comprehensive evidence base demonstrating the benefits of RIL, decision-makers have little incentive to drive improvements in forestry practice. In this regard, our findings clearly advocate the use of RIL in production forests, which represent nearly half of the remaining tropical forest biome. With a growing body of evidence highlighting the benign nature of RIL over conventional logging, explicitly incorporating RIL into national codes of practice should be a priority. It is also possible that the evidence presented in our study will help to promote the benefits of timber certification, under which sustainable forest management is a key component. Our study indicates that if production forests world-wide were to utilize RIL, this would represent a sizeable and important addition to the future global conservation estate. However, research in Iwokrama Forest has shown that some particularly sensitive taxonomic groups are still affected by RIL, although this is expected to be less pronounced than under CL. Additionally, management of forestry concessions is equally important to logging techniques. With the increased access created by logging concessions in previously undisturbed forest, a cascading combination of much more high-impact disturbance often follows (Gaveau *et al.* 2013), eventually resulting in the conversion of otherwise high-value forests (Laurance & Edwards 2014). Therefore, certification standards that include both RIL and sustainable management are likely to be fundamental to the long-term sustainability of tropical production forests, and governments and their forestry authorities must see timber as a long-term crop that is safeguarded between cutting cycles.

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.36vq2> (Bicknell, Struebig & Davies 2015).

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Supporting Information

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

Appendix S1. Method for combining the bird point count and mist net data.

Fig. S1. Rarefaction curves for birds and bats.

Fig. S2. Change in pre- and post-logging abundance of every species.

Table S1. Logging variables at each sample site.

Table S2. Bird and bat indicator species.