Environmental Conservation



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Research Paper

Cite this article: França FM et al. (2024) Selective logging intensity and time since logging drive tropical bird and dung beetle diversity: a case study from Amazonia. *Environmental Conservation* **51**: 112–121. doi: 10.1017/S0376892923000334

Received: 21 June 2023 Revised: 24 November 2023 Accepted: 24 November 2023 First published online: 2 January 2024

Keywords:

Amazon rainforest; birds; dung beetles; forest management; functional diversity; habitat degradation; tropical forests

Corresponding author: Filipe M França; Email: filipe.machadofranca@bristol.ac.uk

*These authors contributed equally

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Selective logging intensity and time since logging drive tropical bird and dung beetle diversity: a case study from Amazonia

Filipe M França^{1,2,*} ⁽⁰⁾, Wallace Beiroz^{3,*} ⁽⁰⁾, Christian B Andretti⁴, Thiago VV Costa⁵ ⁽⁰⁾, Fernando Z Vaz-De-Mello⁶ ⁽⁰⁾, Juliana M Silveira⁷ ⁽⁰⁾ and Julio Louzada⁸ ⁽⁰⁾

¹School of Biological Sciences, University of Bristol, Bristol, UK; ²Programa de Pós-Graduação em Ecologia, Universidade Federal do Pará, Belém, PA, Brazil; ³Programa de Pós-Graduação em Ecologia e Monitoramento Ambiental (PPGEMA), Centro de Ciências Aplicadas e Educação (CCAE) da Universidade Federal da Paraíba (UFPB), Rio Tinto, PB, Brazil; ⁴Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil; ⁵Instituto de Recursos Naturais, Universidade Federal de Itajubá, Itajubá, MG, Brazil; ⁶Universidade Federal de Mato Grosso, Cuiabá, MT, Brazil; ⁷Lancaster Environment Centre, Lancaster University, Lancaster, UK and ⁸Departamento de Biologia, Universidade Federal de Lavras, Lavras, MG, Brazil

Summary

Understanding how selective logging affects biodiversity is crucial to planning cost-effective conservation strategies in tropical forests, yet there is limited understanding of its impacts on fauna functional diversity in the tropical Americas. We assessed how selective logging intensification and time since logging influence multiple metrics of fauna functional integrity in the Brazilian Amazon by collecting bird and dung beetle data within 48 logging management units that had experienced varying exploitation intensities between 1.5–2.0 and 5.0–6.0 years before the faunal surveys. We investigated assemblage responses and used functional attributes to assess changes in functional diversity, specialization, originality and species rarity. Using point counts and pitfall traps, we collected 5081 records of 182 bird species and 7892 dung beetles from 45 species. Logging intensification led to significant declines in most dung beetle responses and bird body mass, whereas time since logging was a key driver of dung beetle and bird functional and taxonomic diversity. Our study presents novel empirical evidence of how logging intensification effects vary across taxa, ecological metrics and time since logging, which is key to informing forest conservation and further investigating environmental degradation impacts on tropical biodiversity.

Introduction

Tropical forests house exceptional biodiversity and play a disproportionate role in global ecosystem services, including climate and precipitation regulation (Staal et al. 2018). However, these ecosystems face significant threats due to climatic and local anthropogenic disturbances (Moura et al. 2021, López-Bedoya et al. 2022, Lapola et al. 2023). With the strong global demand for timber and the widespread nature of timber-harvesting operations, logging is one of the main drivers of tropical forest degradation (Putz et al. 2012).

The impacts of selective logging on tropical biodiversity are commonly assessed using taxonomic diversity metrics (e.g., species richness and composition) and ecological processes (Slade et al. 2011, Burivalova et al. 2014). However, selective logging can also affect functional diversity by favouring species with some specific traits (Edwards et al. 2014b, Ding et al. 2019) – for example, specialists in canopy gaps and vine tangles (Schnitzer et al. 2020). Studies have also shown that integrating functional traits can complement taxonomic diversity metrics (Cerullo et al. 2023), providing valuable insights into the resilience of species and ecosystems to environmental degradation (Mouillot et al. 2013). Moreover, functional diversity tends to better predict biodiversity–ecosystem functioning relationships than taxonomic diversity metrics (Tilman 2001, Gagic et al. 2015).

Despite the increasing use of functional diversity metrics to investigate the impacts of landuse change on tropical biodiversity, there remains limited understanding of how selective logging affects faunal functional diversity. For example, only three out of 35 such publications have assessed the influence of logging on fauna functional diversity within Tropical America forests (see Table S1 in Appendix S1 for details). Moreover, most empirical studies in tropical logged forests are focused on single taxa (e.g., Hamer et al. 2015, Cerullo et al. 2019; but see Edwards et al. 2012, Bicknell et al. 2015) and/or have compared functional diversity metrics between selectively logged and undisturbed forests without accounting for differences in harvesting intensities (e.g., Baraloto et al. 2012a, Ewers et al. 2015). However, selective logging is





not a uniform disturbance, and mean effect sizes and the mechanisms driving biodiversity responses to logging may vary among taxonomic groups (Burivalova et al. 2014) and with time since logging (Ernst et al. 2006, Kpan et al. 2021). Consequently, we need empirical evidence on how logging intensification and time since logging influence multiple metrics of faunal functional integrity to better understand post-logging biodiversity recovery and inform effective management and conservation strategies for tropical forests.

Here, we assess the influence of selective logging intensification and time since harvesting operations on the taxonomic and functional diversity of birds and dung beetles (Coleoptera: Scarabaeinae) in the Brazilian Amazon. We focus on birds and dung beetles as our focal taxa due to their cost-effectiveness as bioindicators (Gardner et al. 2008) and contributions to key ecological processes such as seed dispersal and nutrient cycling (Nichols et al. 2008, Godínez-Alvarez et al. 2020). Our dataset includes 7892 dung beetles and 5081 bird records from 45 and 182 species, respectively, surveyed within 48 logging management units distributed along a logging intensification gradient. We draw on this unique dataset to investigate the ecological impacts of selective logging on tropical forest fauna, asking three questions. First, how do bird and dung beetle functional and taxonomic diversity respond to logging intensification and time since disturbance? Here, we predict that logging intensification will result in lower bird and dung beetle functional and taxonomic diversity (Burivalova et al. 2014), which will be lower in recently logged forests (Fig. 1a; Kpan et al. 2021). Second, are beetle and bird responses to logging and time since disturbance driven by the loss of individuals across all species or by a non-random replacement of individuals among species? We expect logging to act as an environmental filter selecting for more functionally similar species (Edwards et al. 2014a), which will drive higher compositional dissimilarity through losses in abundances of forestspecialist species (i.e., abundance gradients) without significant abundance replacement (i.e., balanced variation in abundance; Fig. 1b). Thirdly, how do changes in disturbance-sensitive species influence biodiversity responses to logging and time since logging? We expect that taxonomic and functional diversity changes will be driven by the loss of rare and more disturbance-sensitive species (Fig. 1c; Leitão et al. 2016).

Methods

Study region

Our study focuses on the 1.7 Mha Jari Florestal forest concession in the north-eastern Brazilian Amazonia (00°27′-01°30′S, 51°40′-53°20'W; Fig. 2). The region experiences a tropical monsoon climate (Amw, Köppen) and has an average altitude of 203 m, annual temperature of 26.6°C and annual rainfall of 2357 mm. The logging concession covers c. 544 000 ha of native forest and follows reduced-impact logging (RIL) practices on a 30-year rotation. The native forests are often dominated by Dinizia excelsa Ducke (Fabaceae, Mimosoideae), which represents c. 50% of timber species harvested in some Amazonian regions (Barbosa 1990). Logging operations are conducted within 10-ha logging management units $(250 \times 400 \text{ m})$ and involve mapping, measuring and identifying commercially viable trees with a diameter at breast height of \geq 45 cm. Logging intensities (i.e., the number of removed trees; França et al. 2016) vary across logging management unities, and RIL practices include directional felling to minimize damage to other trees and cutting lianas on large trees during the inventory stage (Putz et al. 2012).

Experimental design

We followed the operational plan provided by the logging concession to select 48 management units (hereafter 'sampling sites') distributed across two regions of the concession: Bituba (selectively logged in 2006) and Gueti (selectively logged in 2009), which are ≥ 10 km apart, while distances among sampled sites ranged from 0.25 to 19.00 km (average 9.70 ± 7.00; mean ± SD) within each region. To assess logging impacts on a continuum, we chose sampling sites along a gradient of increased logging intensity, ranging from 0 (two unlogged control sites per region; Fig. 2) to 76 removed trees during harvesting operations (31.9 ± 20.5 across both regions) – which is within the average harvesting intensities in both study regions (Bituba: 32.60 ± 16.55 and Gueti: 23.20 ± 14.30 removed trees).

Fauna surveys

Fieldwork took place between January and March 2010 for dung beetles and between July and September 2011 for birds, *c*. 1.5–2.0 and 5.0–6.0 years after logging operations in the Gueti and Bituba regions, respectively. We conducted bird and beetle surveys in the 48 sampling sites, including 44 logged and 4 unlogged sites. We included three additional control areas for dung beetles in the same study concession, which demonstrated that beetle assemblages in our control units accurately represent undisturbed primary forests in the study region as a whole (see Appendix S2, Table S2).

At each sample site, we established three fixed-width (75-m) point counts (PCs) spaced at least 170 m apart (the maximum distance between PCs within a site was 200 m) and located c. 50 m from the sampling site's border. Each PC had four 10-min visits on 2 consecutive days and at different times of the day (from 30 min before sunrise to 10h30 and from 15h30 to 30 min before sunset). All bird surveys were conducted by one experienced observer (CBA), who recorded all observed and heard birds during each survey. The highest number of individuals recorded for a species during any of the four visits was considered the final count for that species at each PC. Vocalizations were recorded using digital audio recorders (Sound Device 701 or Sony PCM D50) and a shotgun microphone (Sennheiser ME 66), and these were further examined by two ornithologists (CBA and TVVC) to determine bird identification. All recordings are archived at the Arquivos Sonoros da Amazônia Library of the National Institute of Amazonian Research (Brazil).

Dung beetles were collected using six pitfall traps baited with *c*. 35 g of fresh dung (4:1 pig-to-human ratio; Marsh et al. 2013). Traps were spaced 100 m apart in a 2×3 rectangular grid and located at least 75 m away from the sampling site edges to ensure even coverage and spatial independence (Mora-Aguilar et al. 2023). Pitfall traps were plastic containers (19 cm diameter and 11 cm deep) buried flush with the ground, part-filled with a saline-killing solution (c. 200 mL) and protected from the rain with a plastic lid. We restricted our sample window to 24 h to minimize the probability of attracting dung beetles from outside the sample sites and logging units with different intensities (Da Silva & Hernández 2015). All trapped dung beetles were processed and identified to species level (or morphospecies level when the former level was not possible) using a key to the New World's Scarabaeinae genera and subgenera (Boucomont 1928, Génier 1996, Canhedo 2006, Vaz-de-Mello et al. 2011, Cupello



Figure 1. Expected influence of logging intensification and time since logging on Amazonian fauna (a) taxonomic and functional diversity metrics, (b) abundance-based dissimilarity components and (c) community-weighted rarity index. Taxonomic metrics include species richness (i.e., total number of species per sampling site), abundance (i.e., total number of individuals per sampling site) and community-weighted biomass (i.e., average biomass of each species weighted by their abundance in each sampling site), whereas functional metrics include diversity (FDq; i.e., functional dissimilarity between species in a community), specialization (FSp; i.e., level of specialism in a community based on generalist/specialist species distribution across the functional space) and originality (FOr; i.e., level of functional redundancy between species in a community); see the 'Methods' section for further details. Abundance (i.e., individuals' turnover between species losing and gaining individuals between sites). The community-weighted rarity index is based on species' abundance, geographical range (distribution in a given space) and habitat breadth (occurrence across different habitats); further details are provided in the 'Methods' section.



Figure 2. The location of our 10-ha sample sites (circles) within the Jari landholding. Bituba and Gueti regions were selectively logged in 2006 and 2009, c. 1.5–2.0 and 5.0–6.0 years before faunal surveys, respectively.

2018, Cupello & Vaz-de-Mello 2018, González-Alvarado & Vazde-Mello 2021). Voucher specimens are deposited at the Federal University of Lavras (UFLA/CREN: Coleção de Referência de Escarabeíneos Neotropicais) and the Entomological Section of the Zoological Collection in the Federal University of Mato Grosso (Brazil).

Amazonian fauna taxonomic and functional responses to selective logging

To investigate how bird and dung beetle functional and taxonomic diversity respond to logging intensification and time since disturbance (first question), taxonomic diversity metrics were the total abundance, species richness and biomass for each sampling site (see details in Fig. 1). To estimate the biomass of each taxonomic group, we used the species community-weighted mean body mass (CWMbm), which was calculated by averaging the body mass of each species weighted by its relative abundance and summing these values for all species present at each sampling site (for more details, see Lavorel et al. 2008).

For functional diversity, we used the following bird attributes: activity period, foraging stratum, feeding guild and body mass. Species-level body mass and activity period data were obtained from *EltonTraits* 1.0 (Wilman et al. 2014). Foraging strata, feeding guilds and other missing information were extracted from Terborgh et al. (1990) and Johnson et al. (2011). For dung beetles, we obtained activity period, dietary preference, body mass and functional traits from previous experiments conducted in our study region (Beiroz et al. 2017, 2018). Dung beetle species-level body mass was measured as the mean dry mass of sampled individuals. Nesting behaviour (e.g., rollers, tunnellers or dwellers) was assigned at the genus level. We adopted these bird and dung beetle functional attributes to calculate three functional metrics: (1) diversity (FDq) using Rao's quadratic entropy index, which incorporated all mentioned traits for each taxonomic group in the 'picante' R package (Kembel et al. 2010); (2) specialization (FSp),



which determines the average distance of a species from the others in the functional space (Mouillot et al. 2013); and (3) originality (FOr), which measures redundancy or singularity (Mouillot et al. 2013) and was calculated by dividing the minimum functional distance of each species (>0) by the maximum overall distance in the principal coordinate analysis generated by Gower's distance between species in each sampling site.

Partitioning Bray-Curtis dissimilarity into abundance gradients and balanced variation

To assess whether beetle and bird responses to logging and time since disturbance are driven by the loss of individuals across all species or by a non-random replacement of individuals among species (second question), average Bray-Curtis dissimilarities were calculated and compared between logged and control sites to assess the impact of logging intensification, as well as among control sites to represent natural variation in unlogged forests (i.e., control dissimilarity), which demonstrated that Bituba and Gueti had faunal assemblages with similar species compositions (see Table S3). We used the 'betapart' package (Baselga & Orme 2012) to calculate the Bray-Curtis dissimilarity partitioned into two components (Baselga 2017): (1) balanced (i.e., individuals' substitution among different species) and (2) gradient (i.e., subsets resulting from individuals' loss from one site to another across all species; see details in Appendix S2 & Fig. S1). Abundance data were log-transformed before calculating Bray-Curtis dissimilarity components.

Determining species rarity as a proxy of disturbance-sensitive species

To examine whether changes in disturbance-sensitive species influence biodiversity responses to logging and time since logging (third question), we used data from a long-term monitoring project conducted in the same concession and following standardized methodological protocols (from 2009 to 2013; see Gardner et al. 2008). Using only 2011 data for both taxa, we obtained species' distributions and abundances beyond the logged regions and encompassing primary forests and *Eucalyptus* spp. plantations (Beiroz et al. 2017). Our rarity index therefore is based on species' local abundances, geographical range and habitat breadth (following Leitão et al. 2016; see details in Appendix S3).

For each species, we calculated local abundances as the mean number of individuals excluding sites where species were not observed. The geographical range was determined using the coordinates of all sampling points where species were recorded, calculating the relative area of occurrence. If a species was sampled in up to two sampling points, we calculated the area of a 1-km buffer around the sampling points. Habitat breadth was determined using the Outlying Mean Index, which measures the species' realized niche based on environmental conditions axes in a principal component analysis (Palomares et al. 2016). Environmental conditions considered were annual mean temperature, temperature annual range, annual precipitation and the precipitation of the driest month from the WorldClim database with 30-s resolution (Fick & Hijmans 2017), in addition to the forest classification provided by the logging concession (lowland forests, submontane forests and Eucalyptus plantations). Rarity also incorporated two field-surveyed environmental metrics: (1) canopy openness, assessed using semi-hemispheric photography at 1.5 m above ground level and Gap Light Analyser software to analyse photos (Frazer et al. 1999); and (2) soil sand content (g/kg), collected at up to 10–cm depths beside each trap and combined into a composite sample for each sample unit (for methodological details, see França et al. 2018).

We calculated the rarity index as the mean values of the species traits weighted by their Pearson's correlation (following Leitão et al. 2016). Before calculating the integrative rarity index, we standardized the species traits to have a mean of 0 and a standard deviation of 1 (Schielzeth 2010). This ensured that the rarity index ranged from 0 to 1, mirroring the metrics' range. We slightly modified the index used in previous studies by subtracting our values from 1, indicating that a rarity index of 0 represents the most common species, whereas values of 1 indicate the rarest species.

Data analysis

To examine the influence of logging intensification and time since disturbance on bird and dung beetle responses (first question), we built generalized linear models (GLMs) using logging intensity, concession region (i.e., Bituba \times Gueti; as a proxy of time since logging) and their interaction as our explanatory variables. For both taxa, we used the following distributions: (1) quasi-Poisson for species richness; (2) negative binomial for abundances; and (3) Gaussian for biomass, FDq, FSp and FOr (see details in Table S4). To assess whether beetle and bird responses to logging intensification and time since disturbance were driven by abundance losses or replacements (second question), we applied GLMs having total Bray-Curtis dissimilarity and their balanced and gradient components as response variables. A Gaussian model was fitted for the beetle Bray-Curtis gradient component, while a Gamma distribution was used for all of the other models with beetle and bird Bray-Curtis dissimilarities. Finally, to investigate the influence of logging intensification and time since disturbance on disturbance-sensitive bird and beetle species (third question), we used the community-weighted rarity index per sampling unit as the response variable and a linear model (LM) with a Gaussian error distribution. All analyses were run in R software (R Core Team 2023). See Table S4 (Appendix S2) for a summary of models and variables for each research question.

Results

We recorded 5081 bird records and collected 7892 dung beetles from 182 and 45 species, respectively. We found 44.7 \pm 2.8 and 41.4 \pm 8.2 (mean \pm SD) bird species in control and logged sites, respectively. For dung beetles, we registered 193.7 \pm 56.7 and 161.0 \pm 99.4 individuals and 20.7 \pm 1.7 and 19.0 \pm 3.8 species in control and logged sites, respectively.

Logging intensification

We found a significant negative effect of logging intensification on dung beetle abundance ($\chi^2 = 11.13$, p = 0.0008; Fig. 3a), species richness ($F_{1,46} = 11.13$, p = 0.01; Fig. 3b), functional specialization ($F_{1,46} = 9.68$, p = 0.0032; Fig. 3c) and functional originality ($F_{1,46} = 4.42$, p = 0.04; Fig. 3d). We also observed that logging intensification enhanced taxonomic dissimilarity ($\chi^2 = 0.67$, p = 0.0016; Fig. 3e) and the Bray–Curtis gradient component ($\chi^2 = 4.62$, p = 0.016; Fig. 3f). Except for a negative effect on bird body mass ($F_{1,46} = 3.91$, p = 0.05; Fig. 3g), we did not find any significant effects of logging intensification on bird responses.



Figure 3. (a) Dung beetle abundance, (b) species richness, (c) functional specialization, (d) functional originality, (e) Bray–Curtis dissimilarity, (f) Bray–Curtis gradient component and (g) bird body mass responses to selective logging intensification (i.e., number of removed trees per hectare) in the Brazilian Amazon. Grey dots show 10-ha sampled units with different logging intensities and the grey shadow in regression lines represents their 95% confidence intervals. See Fig. S1 for details on Bray–Curtis dissimilarity components.

Time since logging

We observed higher dung beetle biomass ($\chi^2 = 21.5$, p ≤ 0.0001 ; Fig. 4a) and functional diversity ($\chi^2 = 13.14$, p = 0.0007; Fig. 4b), as well as bird abundance ($\chi^2 = 4.8$, p = 0.0008; Fig. 4c), species richness ($\chi^2 = 11.07$, p = 0.001; Fig. 4d), functional specialization ($\chi^2 = 11.51$, p = 0.001; Fig. 4e), functional originality ($\chi^2 = 5.25$, p = 0.026; Fig. 4f) and species rarity ($\chi^2 = 40.93$, p ≤ 0.0001 ; Fig. 4g) within forests with greater recovery times since selective logging. By contrast, recently logged forests had higher dung beetle abundance ($\chi^2 = 11.87$, p = 0.0006; Fig. 4h), species richness ($\chi^2 = 6.19$, p = 0.016; Fig. 4i) and functional specialization ($\chi^2 = 5.53$, p = 0.02; Fig. 4j), as well as higher bird biomass ($\chi^2 = 13.93$, p = 0.0005; Fig. 4k) and functional dissimilarity ($\chi^2 = 0.54$, p = 0.0001; Fig. 41).

Discussion

We provide novel empirical evidence of the impacts of selective logging on tropical fauna biodiversity. Logging intensification drove declines in bird body mass and dung beetle taxonomic and functional responses whilst increasing dissimilarity in dung beetle species composition. We also demonstrate that recently logged forests displayed lower dung beetle body mass and functional diversity, as well as lower bird richness, functional specialization, originality and rare species. Combined, these findings support previous research demonstrating that logging intensification impacts can vary among biodiversity groups (Burivalova et al. 2014) whilst highlighting the importance of post-logging time for biodiversity recovery in tropical American forests.

Logging intensification's impacts on tropical fauna vary across taxa and biodiversity metrics

We provide empirical evidence that dung beetles may be more sensitive to selective logging compared to birds; most dung beetle taxonomic and functional metrics varied across our logging intensification gradient, but only bird body mass showed a significant decline with increasing logging intensity (Fig. 3). The steeper beetle responses could be attributed to their heightened sensitivity to environmental changes, including warmer and drier





Figure 4. Dung beetle and bird responses to time since selective logging in the Brazilian Amazon. Bituba (light grey) and Gueti (dark grey) forests were selectively logged in 2006 and 2009, c. 5.0–6.0 and 1.5–2.0 years before data collection, respectively. (a) Dung beetle body weight, (b) dung beetle Raos' quadratic entropy, (c) number of bird individuals, (d) number of bird species, (e) bird functional specialization, (f) bird functional originality, (g) bird rarity, (h) number of dung beetle individuals, (i) number of dung beetle species, (j) dung beetle functional specialization, (k) bird body weight and (l) bird functional dissimilarity.

microclimates in logged forests (Asner et al. 2006, Yamada et al. 2014). Dung beetles may also face increased competition for limited food resources (Horgan & Fuentes 2005), potentially impacted by logging's negative effects on mammals (Felton et al. 2010, Poulsen et al. 2011). Additionally, changes in sunlight exposure and drying winds, particularly in forest gaps that are more common in highly and recently logged forests (Asner et al. 2004, Zhang et al. 2023), could affect the quality of food resources for dung beetles. Consequently, selective logging may lead to the loss of forest interior-specialist dung beetle species (as supported

by observed changes in beetle functional specialization; Fig. 3c), resulting in decreased overall dung beetle diversity as logging intensity and its impacts on microclimate increase (Hosaka et al. 2014, Edwards et al. 2017). The observed increases in Bray–Curtis dissimilarity and the abundance gradient component further support logging-induced effects on beetle assemblage dissimilarities being primarily driven by the loss of individuals rather than their substitution across sampled sites (Baselga 2017).

There are three potential reasons for the impacts of logging intensification on bird species richness, composition and

functional diversity metrics being masked. Firstly, our study region consists mainly of primary forests with minimal disturbance levels (Hethcoat et al. 2019), providing resources for birds' foraging and breeding (Kupfer et al. 2006) whilst facilitating the dispersal of individuals from undisturbed to logged forests (Gilroy & Edwards 2017). Secondly, the relatively low logging intensities in our forest concession compared to other tropical regions could contribute to maintaining avian biodiversity (Wunderle et al. 2006). Lowintensity logging and RIL have been associated with increased flowering and fruiting, supporting generalist species' ability to forage in logged forests (Peh et al. 2005, Burivalova et al. 2014). Lastly, our findings could also be influenced by methodological biases related to the lack of pre-logging baseline data (Christie et al. 2020) and the easier bird detection in logged tropical forests (Woltman 2003). Nonetheless, our findings align with previous studies on temporal changes in bird assemblages (Wunderle et al. 2006) and demonstrate their high functional redundancy in Amazonian forests (Hidasi-Neto et al. 2012).

Post-logging recovery of tropical biodiversity fauna

Forests that were sampled some 5-6 years after selective logging exhibited higher bird species richness, abundance, functional specialization and functional originality, as well as higher dung beetle body mass and functional diversity (Fig. 4). While underscoring the positive relationship between post-disturbance recovery time and biodiversity in logged tropical forests, these findings may be explained by the availability of food resources for faunal communities - for example, forest structure can recover with time since logging (Broadbent et al. 2006), which may result in higher rates of energy flow (Malhi et al. 2022), flowering and fruiting (Ewers et al. 2015) within older logged forests. Moreover, the higher functional specialization, originality and rarity of birds in older logged forests suggest that functionally unique and rare species may also increase with post-logging forest recovery. These results also indicate a reduced functional space in recently logged forests, probably due to logging-induced environmental filters to sensitive species (Baraloto et al. 2012, Ding et al. 2019). Rare species are often the first to be lost following disturbances, attributable to their sensitivity to environmental changes (Montejo-Kovacevich et al. 2018) and smaller habitat ranges and population sizes (Williams et al. 2009, Harnik et al. 2012). Their unique combination of functional traits (Umaña et al. 2017) and position at the edge of community functional spaces (Leitão et al. 2016) further contribute to the observed decrease in functional specialization and originality in recently logged forests.

Implications for biodiversity research, conservation and sustainable forest management

Understanding the trade-offs between the conservation value and timber production in Amazonian logged forests is globally significant. The region holds the largest remaining stock of tropical timber and over 10% of known species worldwide (Guayasamin et al. 2021). As African and Asian timber stocks decline, the demand for tropical hardwood is expected to increase, putting pressure on expanding timber concessions and intensifying harvesting in Amazonia's forests.

Our study provides valuable insights for future research, sustainable management and biodiversity conservation in tropical logged forests. The heightened sensitivity of dung beetles compared to birds demonstrates the relevance of research investigating multi-taxa responses to forest disturbances (Pardini et al. 2009, Silveira et al. 2016), emphasizing that conservation and management practices should consider the varying responses of different taxa to enhance biodiversity outcomes in tropical logged forests. Yet, current environmental regulations in the Brazilian Amazon focus solely on tree populations (CONAMA, Resolution 1/2015), overlooking the cascading effects of harvest operations on faunal assemblages, soil biodiversity and ecological processes. Given that timber concessions in Brazil's public forests cover 1.6 million ha, with an estimated potential for 35 million ha (Sist et al. 2021), there is a pressing need to improve forest conservation legislation and its enforcement by addressing the consequences of logging on various biodiversity groups and their associated ecological processes (França et al. 2017).

Our findings indicate that older logged forests are likely to recover rare and disturbance-sensitive species when compared to recently logged forests. This result, combined with the large amount of old-growth forests within our study region (Hethcoat et al. 2019), elucidates the relevance of maintaining logged forests free of additional disturbances and designing concessions that incorporate undisturbed patches and logged forests at varying post-harvesting ages to enhance concession-level forest biodiversity and recovery (Chazdon 2003). Future research should explore how concession design and selective logging practices can further improve the recovery of logging-sensitive species across a longer post-logging timeframe, ideally through a before-after controlimpact approach (Christie et al. 2020). This knowledge would advance understanding of the conservation value of production forests, providing guidance for cost-effective post-harvest interventions aimed at conserving biodiversity and restoring the environmental resilience of selectively logged tropical forests (Cerullo & Edwards 2019).

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0376892923000334.

Acknowledgements. We are very grateful to Jari Florestal for logistical support and soil texture analyses. We owe special thanks to Edivar Correa, Jucelino dos Santos and Maria Orlandina for their invaluable assistance during fieldwork; Amanda P Arcanjo for supporting dung beetle identifications; and Vanesca Korasaki, Jos Barlow and Toby Gardner for support with funding and experimental design. We are also grateful to Alexander Lees, two reviewers and Nicholas Polunin for their valuable contributions that improved our manuscript.

Author contribution. Conceptualization: FMF and WB. Investigation: FMF, WB, CBA and TVVC. Data curation: FMF, WB, CBA, TVVC and FZVM. Formal analysis: FMF and WB. Funding acquisition: FZVM, JMS and JL. Resources: FZVM and JL. Project administration: FMF, WB, CBA and JMS. Writing – original draft: FMF and WB. Writing – review & editing: FMF, WB, TVVC and JMS. All authors gave final approval for publication.

Financial support. This research was funded by grants from the Brazilian Research Council (CNPq): MCTI/CNPq/FAPs (No. 34/2012) and CNPq-PELD site 23 (PELD-JARI; 403811/2012-0). FMF acknowledges funding provided by the National Council for Scientific and Technological Development (CNPq; Synergize: MCTIC/Sinbiose 442354/2019-3) and the University of Bristol via PolicyBristol (SynPAm; ID: 1989427), Climate and Net Zero Impact Awards (Scaling-up TAOCA; ID: 170839), Cabot Seedcorn 2023 (Voices of Amazonia; ID: 2258319) and Elizabeth Blackwell Institute Rapid Research Funding (CO-SPACE; ID: 2208557) during data analysis and manuscript writing; and funding that was awarded by CAPES (BEX5528/13-5) and CNPq (383744/2015-6) during the fieldwork. FMF, WB, FZVM and JL also acknowledge CNPq for funding support through the INCT-SinBiAm (INCT 406767/2022-0) and



PPBio-AmOr networks (441257/2023-2). FZVM thanks CNPq for the 1A productivity fellowship (313397/2021-0).

Competing interests. No potential competing interests were reported by the authors.

Ethical standard. The authors assert that all procedures contributing to this work comply with applicable national and institutional ethical guidelines. Insect surveys occurred with appropriate state and federal permits (Brazil: SISBIO #1620-3/10068). Datasets used in this manuscript are available at the TAOCA biodiversity platform (https://www.taoca.net/).

References

- Asner GP, Broadbent EN, Oliveira PJC, Keller M, Knapp DE, Silva JNM (2006) Condition and fate of logged forests in the Brazilian Amazon. Proceedings of the National Academy of Sciences of the United States of America 103: 12947– 12950.
- Asner GP, Keller M, Silva JNM (2004) Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. *Global Change Biology* 10: 765–783.
- Baraloto C, Hardy OJ, Paine CET, Dexter KG, Cruaud C, Dunning LT, et al. (2012) Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *Journal of Ecology* 100: 690–701.
- Barbosa RI (1990) Análise do Setor Madeireiro do Estado de Roraima. Acta Amazonica 20: 193–209.
- Baselga A (2017) Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution* 8: 799–808.
- Baselga A, Orme CDL (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* 3: 808–812.
- Beiroz W, Sayer E, Slade EM, Audino L, Braga RF, Louzada J, et al. (2018) Spatial and temporal shifts in functional and taxonomic diversity of dung beetles in a human-modified tropical forest landscape. *Ecological Indicators* 95: 518–526.
- Beiroz W, Slade EM, Barlow J, Silveira JM, Louzada J, Sayer E (2017) Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change. *Insect Conservation and Diversity* 10: 94–106.
- Bicknell JE, Struebig MJ, Davies ZG (2015) Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging. *Journal of Applied Ecology* 52: 379–388.
- Boucomont A (1928) Coprophages d'Amérique du Sud nouveaux ou peu connus. Bulletin de la Société entomologique de France 33: 186–194.
- Broadbent EN, Zarin D, Asner GP, Peña-Claros M, Cooper A, Littel R (2006) Recovery of forest structure and spectral properties after selective logging in lowland Bolivia. *Ecological Applications* 16: 1148–1163.
- Burivalova Z, Şekercioğlu ÇH, Koh LP (2014) Thresholds of logging intensity to maintain tropical forest biodiversity. *Current Biology* 24: 1893–1898.
- Canhedo VL (2006) Revisão taxonômica do gênero Anomiopus Westwood, 1842 (Coleoptera, Scarabaeidae, Scarabaeinae). Arquivos de Zoologia 37: 349.
- Cerullo GR, Edwards DP (2019) Actively restoring resilience in selectively logged tropical forests. *Journal of Applied Ecology* 56: 107–118.
- Cerullo GR, Edwards FA, Mills SC, Edwards DP (2019) Tropical forest subjected to intensive post-logging silviculture maintains functionally diverse dung beetle communities. *Forest Ecology and Management* 444: 318–326.
- Cerullo GR, França F, Finch T, Erm P, Griffiths H, Louzada J, et al. (2023) Sparing old-growth maximises conservation outcomes within selectively logged Amazonian rainforest. *Biological Conservation* 282: 110065.
- Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 51–71.
- Christie AP, Abecasis D, Adjeroud M, Alonso JC, Amano T, Anton A, et al. (2020) Quantifying and addressing the prevalence and bias of study designs in the environmental and social sciences. *Nature Communications* 11: 6377.
- Cupello M (2018) On the types species of the New World dung beetle genus Canthidium Erichson, 1847 (Coleoptera: Scarabaeidae: Scarabaeinae), with an annotated checklist of species. *Zootaxa* 4388: 451.

- Cupello M, Vaz-de-Mello FZ (2018) A monographic revision of the Neotropical dung beetle genus Sylvicanthon Halffter & Martínez, 1977 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini), including a reappraisal of the taxonomic history of 'Canthon sensu lato'. *European Journal of Taxonomy* 467: 1–205.
- Da Silva PG, Hernández MIM (2015) Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. *PLoS ONE* 10: e0126112.
- Ding Y, Zang R, Lu X, Huang J (2019) Functional features of tropical montane rain forests along a logging intensity gradient. *Ecological Indicators* 97: 311–318.
- Edwards DP, Tobias JA, Sheil D, Meijaard E, Laurance WF (2014a) Maintaining ecosystem function and services in logged tropical forests. *Trends in Ecology* & *Evolution* 29: 511–520.
- Edwards DP, Woodcock P, Edwards FA, Larsen TH, Hsu WW, Benedick S, et al. (2012) Reduced-impact logging and biodiversity conservation: a case study from Borneo. *Ecological Applications* 22: 561–571.
- Edwards FA, Edwards DP, Larsen TH, Hsu WW, Benedick S, Chung A, et al. (2014b) Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Animal Conservation* 17: 163–173.
- Edwards FA, Finan J, Graham LK, Larsen TH, Wilcove DS, Hsu WW, et al. (2017) The impact of logging roads on dung beetle assemblages in a tropical rainforest reserve. *Biological Conservation* 205: 85–92.
- Ernst R, Linsenmair KE, Rödel MO (2006) Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biological Conservation* 133: 143–155.
- Ewers RM, Boyle MJW, Gleave RA, Plowman NS, Benedick S, Bernard H, et al. (2015) Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications* 6: 6836.
- Felton AM, Felton A, Foley WJ, Lindenmayer DB (2010) The role of timber tree species in the nutritional ecology of spider monkeys in a certified logging concession, Bolivia. *Forest Ecology and Management* 259: 1642–1649.
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315.
- França FM, Frazão FS, Korasaki V, Louzada J, Barlow J (2017) Identifying thresholds of logging intensity on dung beetle communities to improve the sustainable management of Amazonian tropical forests. *Biological Conservation* 216: 115–122.
- França FM, Louzada J, Barlow J (2018) Selective logging effects on 'brown world' faecal-detritus pathway in tropical forests: a case study from Amazonia using dung beetles. Forest Ecology and Management 410: 136–143.
- França FM, Louzada J, Korasaki V, Griffiths H, Silveira J, Barlow J (2016) Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. *Dryad Digital Repository* 53: 1098–1105.
- Frazer G, Canham C, Lertzman K (1999) Gap Light Analyzer (GLA), Version 2.0: Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs, Users Manual and Program Documentation. Burnaby, BC, Canada: Simon Fraser University; Millbrook, NY, USA: Institute of Ecosystem Studies.
- Gagic V, Bartomeus I, Jonsson T, Taylor A, Winqvist C, Fischer C, et al. (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences* 282: 20142620.
- Gardner TA, Barlow J, Araujo IS, Ávila-Pires TC, Bonaldo AB, Costa JE, et al. (2008) The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters* 11: 139–150.
- Génier F (1996) A revision of the Neotropical genus Ontherus Erichson (Coleoptera: Scarabaeidae, Scarabaeinae). Memoirs of the Entomological Society of Canada 128: 1–170.
- Gilroy JJ, Edwards DP (2017) Source-sink dynamics: a neglected problem for landscape-scale biodiversity conservation in the Tropics. *Current Landscape Ecology Reports* 2: 51–60.
- Godínez-Alvarez H, Ríos-Casanova L, Peco B (2020) Are large frugivorous birds better seed dispersers than medium- and small-sized ones? Effect of body mass on seed dispersal effectiveness. *Ecology and Evolution* 10: 6136–6143.

- González-Alvarado A, Vaz-de-Mello FZ (2021) Towards a comprehensive taxonomic revision of the Neotropical dung beetle subgenus Deltochilum (Deltohyboma) Lane, 1946 (Coleoptera: Scarabaeidae: Scarabaeinae): division into species-groups. *PLoS ONE* 16: e0244657.
- Guayasamin J, Ribas C, Carnaval A, Carrillo J, Hoorn C, Lohmann L, et al. (2021) Evolution of Amazonian biodiversity. In: C Nobre, A Encalada, E Anderson, F Roca Alcazar, M Bustamante, C Mena et al. (eds), Amazon Assessment Report – Part 1 (pp. 2.3–2.42). New York, NY, USA: United Nations Sustainable Development Solutions Network.
- Hamer KC, Newton RJ, Edwards FA, Benedick S, Bottrell SH, Edwards DP (2015) Impacts of selective logging on insectivorous birds in Borneo: the importance of trophic position, body size and foraging height. *Biological Conservation* 188: 82–88.
- Harnik PG, Simpson C, Payne JL (2012) Long-term differences in extinction risk among the seven forms of rarity. *Proceedings of the Royal Society B: Biological Sciences* 279: 4969–4976.
- Hethcoat MGM, Edwards DPD, Carreiras JJMB, Bryant RRG, França FFM, Quegan S (2019) A machine learning approach to map tropical selective logging. *Remote Sensing of Environment* 221: 569–582.
- Hidasi-Neto J, Barlow J, Cianciaruso MV (2012) Bird functional diversity and wildfires in the Amazon: the role of forest structure. *Animal Conservation* 15: 407–415.
- Horgan FG, Fuentes RC (2005) Asymmetrical competition between Neotropical dung beetles and its consequences for assemblage structure. *Ecological Entomology* 30: 182–193.
- Hosaka T, Niino M, Kon M, Ochi T, Yamada T, Fletcher C, et al. (2014) Impacts of small-scale clearings due to selective logging on dung beetle communities. *Biotropica* 46: 720–731.
- Johnson EI, Stouffer PC, Vargas CF (2011) Diversity, biomass, and trophic structure of a central Amazonian rainforest bird community. *Revista Brasileira de Ornitologia* 19: 1–16.
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.
- Kpan TF, Ernst R, Rödel M-O (2021) Follow the forest: slow resilience of West African rainforest frog assemblages after selective logging. *Forest Ecology and Management* 497: 119489.
- Kupfer JA, Malanson GP, Franklin SB (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography* 15: 8–20.
- Lapola DM, Pinho P, Barlow J, Aragão LEOC, Berenguer E, Carmenta R, et al. (2023) The drivers and impacts of Amazon forest degradation. *Science* 379: eabp8622.
- Lavorel S, Grigulis K, McIntyre S, Williams NSG, Garden D, Dorrough J, et al. (2008) Assessing functional diversity in the field – methodology matters! *Functional Ecology* 22: 134–147.
- Leitão RP, Zuanon J, Villéger S, Williams SE, Baraloto C, Fortunel C, et al. (2016) Rare species contribute disproportionately to the functional structure of species assemblages. *Proceedings of the Royal Society B: Biological Sciences* 283: 20160084.
- López-Bedoya PA, Bohada-Murillo M, Ángel-Vallejo MC, Audino LD, Davis ALV, Gurr G, et al. (2022) Primary forest loss and degradation reduces biodiversity and ecosystem functioning: a global meta-analysis using dung beetles as an indicator taxon. *Journal of Applied Ecology* 59: 1572–1585.
- Malhi Y, Riutta T, Wearn OR, Deere NJ, Mitchell SL, Bernard H, et al. (2022) Logged tropical forests have amplified and diverse ecosystem energetics. *Nature* 612: 707–713.
- Marsh CJ, Louzada J, Beiroz W, Ewers RM (2013) Optimising bait for pitfall trapping of Amazonian dung beetles (Coleoptera: Scarabaeinae). *PLoS ONE* 8: e73147.
- Montejo-Kovacevich G, Hethcoat MG, Lim FKS, Marsh CJ, Bonfantti D, Peres CA, et al. (2018) Impacts of selective logging management on butterflies in the Amazon. *Biological Conservation* 225: 1–9.
- Mora-Aguilar EF, Arriaga-Jiménez A, Correa CMA, da Silva PG, Korasaki V, López-Bedoya PA, et al. (2023) Toward a standardized methodology for sampling dung beetles (Coleoptera: Scarabaeinae) in the Neotropics: a critical review. *Frontiers in Ecology and Evolution* 11: 1096208.

- Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution* 28: 167–177.
- Moura RS, Noriega JA, Cerboncini RA., Vaz-de-Mello FZ, Klemann-Jr L (2021) Dung beetles in a tight-spot, but not so much: quick recovery of dung beetles assemblages after low-impact selective logging in central Brazilian Amazon. *Forest Ecology and Management* 494: 119301.
- Nichols E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* 141: 1461–1474.
- Palomares F, Fernández N, Roques S, Chávez C, Silveira L, Keller C, et al. (2016) Fine-scale habitat segregation between two ecologically similar top predators. *PLoS ONE* 11: e0155626.
- Pardini R, Faria D, Accacio GM, Laps RR, Mariano-Neto E, Paciencia MLB, et al. (2009) The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. *Biological Conservation* 142: 1178–1190.
- Peh KS-H, Jong J de, Sodhi NS, Lim SL-H, Yap CA-M (2005) Lowland rainforest avifauna and human disturbance: persistence of primary forest birds in selectively logged forests and mixed-rural habitats of southern Peninsular Malaysia. *Biological Conservation* 123: 489–505.
- Poulsen JR, Clark CJ, Bolker BM (2011) Decoupling the effects of logging and hunting on an afrotropical animal community. *Ecological Applications* 21: 1819–1836.
- Putz FE, Zuidema PA, Synnott T, Peña-Claros M, Pinard MA, Sheil D, et al. (2012) Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters* 5: 296–303.
- R Core Team (2023) *R: The R Project for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1: 103–113.
- Schnitzer SA, Michel NL, Powers JS, Robinson WD (2020) Lianas maintain insectivorous bird abundance and diversity in a neotropical forest. *Ecology* 101: e03176.
- Silveira JM, Louzada J, Barlow J, Andrade R, Mestre L, Solar R, et al. (2016) A multi-taxa assessment of biodiversity change after single and recurrent wildfires in a Brazilian Amazon forest. *Biotropica* 48: 170–180.
- Sist P, Piponiot C, Kanashiro M, Pena-Claros M, Putz FE, Schulze M, et al. (2021) Sustainability of Brazilian forest concessions. *Forest Ecology and Management* 496: 119440.
- Slade EM, Mann DJ, Lewis OT (2011) Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. *Biological Conservation* 144: 166–174.
- Staal A, Tuinenburg OA, Bosmans JHC, Holmgren M, Van Nes EH, Scheffer M, et al. (2018) Forest-rainfall cascades buffer against drought across the Amazon. *Nature Climate Change* 8: 539–543.
- Terborgh J, Robinson SK, Parker TA, Munn CA, Pierpont N (1990) Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60: 213–238.
- Tilman D (2001) Functional diversity. In: *Encyclopedia of Biodiversity* (pp. 109–120). Amsterdam, The Netherlands: Elsevier.
- Umaña MN, Zhang C, Cao M, Lin L, Swenson NG (2017) A core-transient framework for trait-based community ecology: an example from a tropical tree seedling community. *Ecology Letters* 20: 619–628.
- Vaz-de-Mello FZ, Edmonds WD, Ocampo FC, Schoolmeesters P (2011) A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa* 2854: 1.
- Williams SE, Williams YM, VanDerWal J, Isaac JL, Shoo LP, Johnson CN (2009) Ecological specialization and population size in a biodiversity hotspot: how rare species avoid extinction. *Proceedings of the National Academy of Sciences of the United States of America* 106: 19737–19741.
- Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* 95: 2027–2027.
- Woltman S (2003) Bird community responses to disturbance in a forestry concession in lowland Bolivia. *Biodiversity and Conservation* 12: 1921–1936.



- Wunderle JM, Henriques LMP, Willig MR (2006) Short-term responses of birds to forest gaps and understory: an assessment of reduced-impact logging in a lowland Amazon forest. *Biotropica* 38: 235–255.
- Yamada T, Yoshioka A, Hashim M, Liang N, Okuda T (2014) Spatial and temporal variations in the light environment in a primary and selectively

logged forest long after logging in Peninsular Malaysia. *Trees – Structure and Function* 28: 1355–1365.

Zhang B, Fischer FJ, Coomes DA, Jucker T (2023) Logging leaves a fingerprint on the number, size, spatial configuration and geometry of tropical forest canopy gaps. *Biotropica* 55: 354–367.