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Sparing old-growth maximises conservation outcomes within selectively logged Amazonian rainforest

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ABSTRACT

Timber extraction threatens a vast area of tropical ecosystems, making it vital to design productive harvesting operations that limit biodiversity declines. Contrasting management options span a continuum from less-intensive, land-sharing logging applied over a larger area to land-sparing operations that combine intensive harvesting with the preservation of old-growth forest. Combining company-reported extraction rates with dung beetle surveys along an Amazonian logging gradient, we explore how individual species' abundances, geometric mean population sizes, functional diversity, and trait characteristics vary across simulated logging concessions and production targets. We substantially extend previous studies by evaluating 8000 mixed-harvesting scenarios and by assessing the profitability of contrasting practices. Simply maximising old-growth protection delivers the highest species' abundances and population sizes for species negatively affected by logging. Maximising old-growth also supports communities with a functional trait dissimilarity (FDis, RaoQ) and functional structure of nesting guilds, biomass, pronotum volume, front leg area, and front:back leg ratio traits that closely resembles old-growth forest. Functional evenness (FEve), richness (FRic), and divergence (FDiv) did not vary across logging strategies. Some 3 % of mixed approaches outperform extreme sparing (which maximises old-growth retention through intensive logging) but still involve substantial sparing, enabled by intensified logging elsewhere. However more-extensive business-as-usual harvesting is up to 90 % more profitable than extreme sparing, suggesting active policy mechanisms, standards, or regulations would be needed to make spatially-concentrated logging operations (which benefit biodiversity) more commercially attractive. Old-growth sparing appears key to limiting biodiversity declines within tropical timber concessions, but would require payments to compensate for reduced profits.

1. Introduction

A major cause of the extinction crisis is the appropriation of hyper-diverse tropical rainforest ecosystems for timber production (Barlow et al., 2018; Botanic Gardens Conservation International, 2021; Davis et al., 2020; Maxwell et al., 2016). Half of remaining tropical forest is estimated to lie within designated timber extraction zones (Blaser & International Tropical Timber Organization, 2011). With global timber demands forecast to grow 30 % by 2050 (Kok et al., 2018) and huge areas of rainforest subjected to pervasive illegal logging (Brancalion et al., 2018; Hethcoat et al., 2019), managing tropical logging impacts has become a key frontier for the protection of wild nature.

Logging can damage ecosystems and associated benefits. Timber overexploitation is a major driver of tree population extirpation (Botanic

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Gardens Conservation International, 2021) and generates sometimes-precipitous declines in small-ranged endemic and old-growth specialist biodiversity (Lavery et al., 2020; Miranda et al., 2020; Pinho et al., 2020). By dissecting rainforests with road systems that enhance fire risk and edge effects, logging compacts soils, increases non-target tree mortality, leads to persistent shifts in nutrient dynamics and soil carbon balance, and opens up rainforests to pressures from mining, hunting, illegal logging, and land prospecting (Edwards et al., 2014a; Poulsen et al., 2009; Riutta et al., 2021; Swinfield et al., 2020). Tropical logging also impacts local and indigenous people via land conflicts and harvesting of important trees (Bousfield et al., 2021), and exacerbates global climate change by emitting an estimated 1.1 Gt CO_2e year^{-1} (Pearson et al., 2017).

Yet despite these harms, well-managed logged forests retain significant conservation value (Edwards et al., 2014b; Malhi et al., 2022) and offer an important opportunity for cost-effectively protecting tropical nature (Fisher et al., 2011), including under emerging nature and climate agendas (Cerullo and Edwards, 2019; Griscom et al., 2020). Timber products contribute to local and national economies (Harrison et al., 2020), and arguably, well-managed concessions can help safeguard forests (and their substantial remaining biodiversity) beyond protected areas (Buřivalová et al., 2020; Buřivalová et al., 2022; Gaveau et al., 2013). Designing productive timber landscapes that involve only limited losses of forest-dwelling wildlife without stimulating leakage of timber harvesting elsewhere is therefore a key research challenge (Betts et al., 2021; Harris & Betts, 2023). Within permanent selectively logged concessions, the option space for meeting production targets whilst conserving biodiversity spans a continuum ranging from less-intensive, land-sharing logging applied over a larger area to land-sparing operations that combine intensive localised harvest with the preservation of unharvested old-growth forest elsewhere in the landscape (Betts et al., 2021; Edwards et al., 2014a).

The few empirical comparisons of land-sparing or -sharing logging to date have shown contrasting results, partly driven by methodological discrepancies. In Malaysian Borneo, Edwards et al. (2014a) found more bird, dung beetle, and ant species had higher abundances under land-sparing than -sharing but they did not construct detailed species-abundance vs timber-yield relationships, precluding assessment of localised logging impacts. Montejo-Kovacevich et al. (2018) found intermediate logging scenarios in the Brazilian Amazon maximised more butterfly species' abundances than land sparing, but tested only a single production target and a narrow set of production options. Lastly, Griscom et al. (2018) found that hypothetical land-sharing concessions under secure forest tenure and certification delivered better carbon and multi-taxa outcomes than sparing, whereas Runting et al. (2019) concluded that improved management outperformed simple sparing for delivering quality mammal habitat across East Kalimantan. However, the literature-derived estimates of species richness and expert-generated Delphi scores both these two studies used to assess biodiversity impacts can be misleading proxies for evaluating conservation outcomes (Buřivalova et al., 2014; Mukherjee et al., 2015). No study has assessed how the profitability of applying contrasting sparing or sharing harvesting regimes varies with concession-wide biodiversity conservation outcomes.

In this study we advance the land-sparing/sharing framework considerably by using species-level, field-derived abundance estimates collected for an entire community of dung beetles across a wide range of logging intensities (including unlogged forest), within a natural forest logging concession in the Brazilian Amazon. Tropical dung beetles are sensitive to differences in forest management (Beiroz et al., 2018; França et al., 2016) and are strong indicators of compositional changes for many taxa within our landscape (Barlow et al., 2007). We assess how a broad suite of sharing, sparing and intermediate harvesting regimes impact conservation outcomes (Betts et al., 2021), including functional and trait diversity– which vary along sparing-sharing gradients in farming systems (Cannon et al., 2019) and underpin ecosystem functioning within logged landscapes (Bässler et al., 2014; Gossner et al., 2013; Griffiths et al., 2015). To better reflect the reality of logging operations in tropical concessions, we investigate multiple harvesting regimes beyond the typical 'two-compartment' bounds of traditional sparing-sharing analyses (which permit one harvest intensity, plus sparing), instead considering numerous 'multi-compartment' wood production systems that enable a mixture of different harvesting intensities across the concession (Betts et al., 2021; Feniuk et al., 2019; Finch et al., 2019).

Specifically, we ask: 1) Which logging approach along a land-sparing to land-sharing continuum maximises concession-wide abundances of individual species? 2) Which out of extreme land-sharing (where logging occurs at the lowest intensity that still meets concession-wide production targets), extreme land-sparing (where old-growth is maximised by harvesting logged areas at legal harvest limits), and a suite of intermediate, two-compartment logging approaches maximises community-averaged geometric mean abundances, relative to old-growth baselines? 3) Do more sophisticated multi-compartment scenarios outperform any of these simpler approaches in maximising community-averaged geometric mean abundances? 4) How does functional diversity and representation of key functional traits vary along the sparing-sharing continuum? And 5) How profitable would it be for concession managers to depart from business-as-usual practices and apply extreme-sharing or extreme-sparing at concession scales? We investigate these questions across a range of timber production targets by constructing detailed abundance-yield curves for 53 dung beetle species previously sampled within an Amazonian logging concession (França et al., 2017, 2022), and estimating the financial outcomes of a subset of logging scenarios. Our results will help concession managers identify options for improving biodiversity conservation and ecosystem outcomes across 35 Mha of Brazilian Amazonia open for logging (Sist et al., 2021).

2. Methods

2.1. Field sampling and estimating species' responses to harvesting

2.1.1. Study site

The study site was within the 1.7 million ha Jari Florestal logging concession in Pará, north-eastern Brazilian Amazon (Fig. S1). Our sampling was situated within 544,000 ha of natural forest undergoing reduced-impact logging (RIL) under 30-year harvest cycles (Supplementary Methods, Study site).

2.1.2. Sampling design

We combined two *Jari Florestal* dung beetle datasets along with logging information provided by logging company harvesting records to determine how beetle abundances vary with harvesting intensity. The datasets were a BACI-design logging sampling study (França et al., 2016) and a space-for-time assessment (França et al., 2022), respectively. We combined only directly comparable data from the two datasets, consisting of beetle data collected between 10-months and 1-year post-logging. All dung beetle data compiled were sampled January–March 2010 and June–July 2012, although previous research within our study concession has demonstrated little variability in dung beetle species richness, abundance and rank abundance between seasons (Gardner et al., 2008). We summarised all beetle abundance and timber harvesting data at the scale of the 10-ha parcels, which is also the scale at which we considered sparing to operate in this analysis. Dung beetles in our concession respond to management practices at this scale (França et al., 2017), which represents the size of a typical logging planning unit. We used a combination of pre-logging harvesting plans and post-logging harvesting records to stratify dung beetle sampling across 87 parcels spanning a gradient of harvesting intensities, from old-growth, unlogged forest to intensively harvested parcels. Unlogged parcels were located at least 6.5 km from logged parcels, to minimize logging spill-over effects

(França et al., 2017). For dung beetle surveys, six pitfall traps were buried in each parcel for 24 h, with traps spaced 100 m apart and at least 75 m from the parcel edge (see Supplementary Methods, Sampling design).

2.1.3. Identifying taxa

All dung beetles were identified to species or morphospecies level by F.F. Since we undertook more extensive sampling of old-growth forests in the west rather than south of the concession, and because previous work both in the study concession and in other lowland Amazonian rainforest has revealed high beta diversity of dung beetle communities (Beiroz et al., 2018), we excluded from analyses 10 species found only in logged plots in the south (Fig. S1), as their absence from all plots sampled in the west could be a result of species turnover rather than any reflection of species' habitat preferences. This resulted in our removing 425 individuals from the dataset, leaving us with a dataset of 15,085 individuals of 53 (morpho-) species, 9 of which were uniquely found in primary forest. Removal of species did not lead to lower total abundance or reduced biomass estimates in southern relative to western parcels, and we provide sensitivity analyses of including these 10 species in the Supplementary Methods.

2.1.4. Dung beetle traits

For our sampled species, we extracted trait information from beetles collected across three primary forest sites in the Jari Florestal landholding (Griffiths et al., 2016b) to determine the following functional traits: i) body mass, ii) front leg length/body mass iii) pronotum width/body mass, iv) back leg length/front leg length (Griffiths et al., 2016b; Nunes et al., 2021; Supplementary Methods, Dung beetle traits). We assigned genus averages for the 11 species missing trait data (Edwards et al., 2021), along with nesting guild information from literature sources (Beiroz et al., 2018).

2.1.5. Estimating harvesting intensity

We used company logging records showing the total number of trees harvested in 5000 logging parcels (50,000 ha) of previously unlogged forest as our harvesting intensity data. These records showed the georeferenced locations of logged trees, along with parcel identities for each logged tree. For a subset of 921 parcels, we also had company-provided information on the volume of logs removed per parcel—an additional measure of harvesting intensity. However, since volume of logs removed per parcel and number of trees logged per parcel were strongly correlated in our concession (Pearson's $r = 0.92$, Fig. S2), we used trees removed as our measure of harvesting intensity (França et al., 2017; Montejo-Kovacevich et al., 2018).

2.1.6. Estimating species abundance

For each (morpho)species (hereafter, 'species'), we summed trap-level abundances for each parcel (across all 6 traps) to estimate abundance at a given harvesting intensity, including within zero-yielding, unlogged parcels. Parcels sampled in the BACI study generated two abundance estimates – one of zero-yielding old growth, and one of the same parcel after it had been harvested. In total, this resulted in 120 abundance-yield parcel measurements (consisting of 83 unique parcels distributed throughout the forest, 33 parcels of which were sampled again post-logging). Forty-six of our abundance-yield measurements were from old-growth parcels and the remaining 74 from harvested parcels, whilst ~40 % (29 out of 74) logged parcels sampled were also censused prior to logging. This ensured that we had high coverage in undisturbed forest to ensure proper sampling of baselines (Barlow et al., 2010) whilst the before/after sampling design also helped limit the risk that historical factors or environmental gradients (rather than logging intensity per se) drive our observed abundance-yield relationships (França et al., 2016).

2.1.7. Building abundance-yield curves

For each of 53 beetle species we derived an abundance-yield curve (sensu Green et al. 2005) between species abundance and harvesting intensity using our 120 abundance-yield parcel measurements (Fig. S3; see Fig. S4 for excluded species curves). We constructed curves using one of two alternative models, describing a wide range of potential curve fits (Phalan et al., 2011) and selecting as best-fitting the model with the lowest AIC value, which we selected as a test statistic as it penalises overfitting. We used bootstrapping to incorporate uncertainty about abundance-yield curve shapes into our assessment of conservation outcomes (see Supplementary Methods, Building abundance-yield curves).

2.2. Constructing logging concession scenarios

Next, to characterise the conservation outcomes of different logging approaches, we constructed a wide range of logging concession scenarios (see Fig. 1 for overview), beginning each scenario with a common starting baseline of 5000 10-hectare parcels (50,000 ha) of old-growth forest. We began by defining scenario parameters (production targets and maximum harvesting intensity), and created a suite of scenarios to reach these production targets, following either a two-compartment or a multi-compartment approach. Finally, to enable assessment of how our scenario concessions compared to observed logging practices, we created a business-as-usual scenario, where logging followed company-reported logging intensities.

2.2.1. Setting parameters

We set relative production targets (P) in each scenario according to the harvest intensity (HI, number of trees extracted) across one logging rotation, based on company logging records. The recorded harvest was 132,670 trees, at a mean logging intensity of 27 trees removed per ten-hectare parcel. We limited the maximum permissible harvesting intensity for any scenario to 65 trees per parcel, which is roughly equivalent to the maximum harvesting intensity allowed using logging machinery according to Brazilian forestry law (Castro et al., 2021). The maximum logging intensity observed in company logging records corresponded to 173 trees removed in a parcel (Fig. S5). This is because the harvesting regulations apply to 100 ha averages, allowing logging intensities to be higher within certain parcels and balanced by lower intensities in other parcels, such the 100-ha limit is not breached. Our maximum permissible harvest intensity is thus lower than realised within 7 % (372/5000) of parcels in our study area (Fig. S5). Given the scarcity of extremely high-intensity logging, we use a maximum of 65 trees per parcel (i.e. <8 trees/ha), which is supported by our biodiversity sampling and associated models (maximum intensity sampled = 71). This intensity falls below thresholds beyond which the carbon, timber recovery, and forest structure benefits of RIL over conventional logging diminish greatly (Roopsind et al., 2018; Sist and Nguyen-Thé, 2002). To explore the consequences of different production levels, P, our scenarios span a range of P between 0.5 and 2 times the observed current recorded harvest.

2.2.2. Two-compartment logging

We devised a series of 517 two-compartment logging scenarios, which involved all logged parcels being harvested at the same intensity, plus sparing of old-growth forest (except in the case of extreme sharing; see below). Thus, for given production target (P) and scenario, the area of old-growth forest spared (OG_S) was determined by the harvest intensity in logged areas (HI_L). Under extreme sharing, all parcels were logged at the minimum HI_L needed to meet P, with virtually no old-growth parcels spared. The HI_L under extreme sharing varied from 14 to 54 trees harvested per parcel as P increased from 0.5 to 2 times the observed current recorded harvest. By contrast, under extreme sparing, all logging occurred at the maximum permissible harvest ($HI_L = 65$), with the area of old-growth spared varying from 3980 to 918 parcels as P increased (see Table S3).

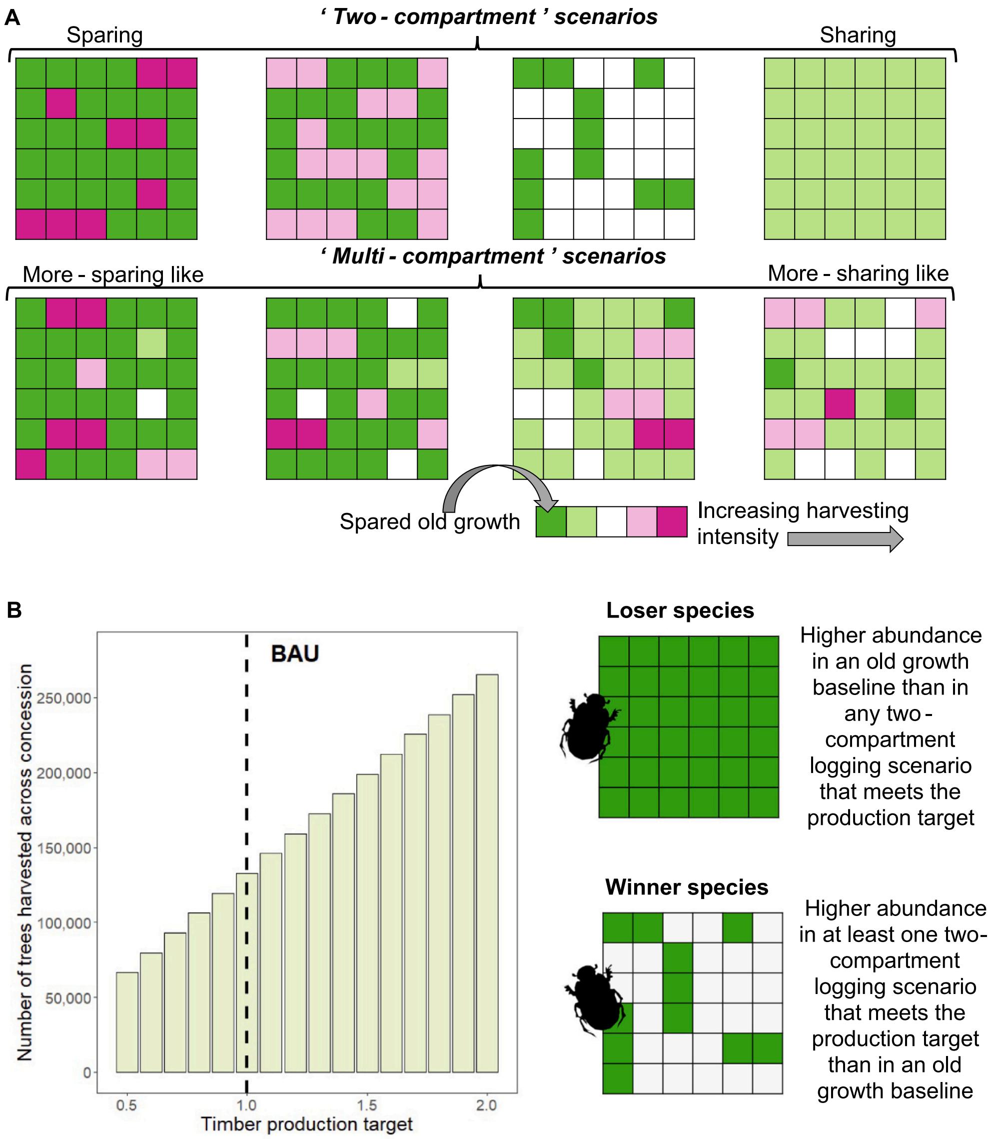

Fig. 1. Schematic overview of concepts discussed in this study. Our analyses compare the conservation outcomes and profitability of many different logging scenarios within a logging concession in the Brazilian Amazon. Scenarios include 517 'two-compartment' scenarios, which span the sparing-sharing continuum as originally conceived, along with 8000 more complex 'multi-compartment' scenarios, which enable up to five unique harvest intensities across the concession. (A: *top*) shows a simplified depiction of two-compartment scenarios, where for a given concession made up of logging parcels (grid squares), the area of old-growth forest spared (dark green) for a particular timber production target is determined by the harvest intensity within the logged compartment, which is always harvested at a single intensity. Thus, under sparing, high-intensity logging (dark pink) leads to the largest amount of old-growth forest spared, whereas under sharing all parcels are logged at the lowest harvest intensity that meets the overall production target (light green). Intermediate scenarios fall between sparing and sharing, with intermediate harvesting intensities (grey, light pink). Multi-compartment scenarios (*A: bottom*) involve up to 5-unique harvest intensities (including zero-yielding old-growth forest) being applied across the concession, with more-sparing like scenarios having a higher proportion of old-growth forest spared than more-sharing like ones. (B: *left*) We assessed scenarios spanning a range of production targets from 0.5 to 2 times the actual timber production (132,670 trees harvested) achieved over 50,000 ha of concession under business-as-usual management (dashed line; BAU), according to company logging records. We classified species as winners or loser species for a given production target depending on whether they showed higher abundance in a two-compartment logging scenario, or in an all-old-growth baseline concession. Note that the scenario representations are provided for visualisation purposes only; our scenario construction was non-spatial. Dung beetle icons are credited to Kristina Gagalova (CC BY-SA 3.0). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2.3. *Multi-compartment logging*

Our multi-compartment scenarios were more complex, and involved each of the 5000 parcels within a concession independently assuming one of up to five distinct HI_L values between 0 (i.e. old-growth) and the maximum permissible harvest intensity (HI_L = 65). We used a distribution-based approach to create multi-compartment scenarios, randomly drawing five harvest intensity values spanning the range of harvest intensities from two underlying data distributions (see Supplementary Methods, Multi-compartment logging), and ensuring we explored scenarios containing zero-yielding portions. In total, we created ~8000 scenarios (~500 for meeting each 0.1 increment of P between 0.5 and 2), allowing for a robust assessment of whether more-sophisticated harvest regimes outperform simple two-compartment sparing. We used this distribution-based approach to scenario construction rather than an optimisation algorithm as we are interested in visualising the biodiversity outcomes of suboptimal approaches to meeting production targets (Finch et al., 2020).

2.2.4. *Business-as-usual logging*

Under business-as-usual logging, each parcel within the 5000-parcel logging concession assumes the HI_L values observed in historical company logging records (so P = 1). Business-as-usual is therefore a single multi-compartment scenario, taking company-reported harvesting intensity values (Fig. S5).

2.3. *Estimating financial outcomes*

To explore the financial implications of shifting away from business-as-usual logging within our landscape, we used data on the natural distribution of >155,000 trees of 153 merchantable timber species, on the costs of their harvest, and on sale prices to estimate the profitability of two-compartment sharing, two-compartment sparing, and business-as-usual operations. These sparing and sharing scenarios represent the 'extremes' of two-compartment scenario-space and thus span the range of financial outcomes associated with our scenarios. We simulated scenarios in a spatially explicit manner over a 1490-hectare (149 parcel) area of old-growth forest elsewhere in the *Jari Florestal* concession for which we had access to complete pre-logging tree inventories. We estimated the net revenue of harvests using species-specific processed timber prices, yield information, and extraction costs, which included the costs of wages, forest censuses, the total costs of road network construction, and skidding and roundlog transport costs across the concession (Supplementary Materials, Economic Analyses). To account for different ways of deploying land-sparing spatially, we investigated extreme sparing under two configurations: block sparing (where one contiguous block of forest was logged at high intensity until the production target was met, with the remaining parcels off-limits to logging) and fragmented sparing (where logging preferentially targeted parcels in order of profitability until the production target was met). All scenarios followed legal restrictions regarding 100-hectare harvest intensity limits and minimum cutting diameters (>50 cm DBH), and produced an equal amount of timber (4023 trees, equivalent *to* $P = 1$). We visualised all economic outcomes per unit area (USD$/ha), volume of wood produced ($/m^3) and per tree harvested ($/tree).

2.4. Evaluating conservation outcomes

To evaluate species' responses to logging, we used our constructed abundance-yield curves to identify species as either winners or losers from logging (see below) for a particular production target. We then used the curves to determine the conservation outcomes of two-compartment, multi-compartment, and business-as-usual scenarios for each species and the sampled community as a whole, compared with an old-growth baseline. Lastly, we investigated how the functional diversity and functional trait structures of dung beetle communities varied as the approach to meeting P shifted from sharing to sparing logging approaches.

2.4.1. Classifying winners and losers

Species were classified as logging winners if, for a particular production target, their predicted abundance was higher under any logging scenario than under an old-growth baseline (Phalan et al., 2011). Species whose predicted abundance was smaller under all logging scenarios than under an old-growth baseline were classified as losers. Winners can therefore transition into losers if at higher production targets that necessitate more intensive logging in order to meet the target, no logging scenario performs better than old-growth). For each production target value of P, we further split species according to whether they had higher relative abundances under extreme sharing scenarios, extreme sparing scenarios, or some intermediate.

2.4.2. Weighted geometric mean relative abundance

To summarise community-wide outcomes for a given logging concession scenario across all species, we used weighted geometric means. Geometric mean abundance exhibits several desirable traits as a biodiversity indicator over arithmetic mean, including reflecting risk of taxon extinction, and capturing the importance of comparatively small abundance changes among less-common species (Buckland et al., 2011; Santini et al., 2017; van Strien et al., 2012). For geometric mean analyses, we followed Buckland et al. (2011) in converting species counts to measures of relative abundance, where for each species i, its abundance within a two-compartment scenario j, was expressed relative to its abundance in an old-growth baseline, $A_{0,i}$, as $A_{i,j}/A_{0,i}$. Since relative abundances were a multiplicative measure, we used a log scale when averaging across species (Buckland et al., 2011). We also applied weightings so that for a given species in a two-compartment scenario, where the log relative abundance $ln(A_{i,j}/A_{0,i})$ at a particular harvesting intensity HI was known with less certainty, a lower weighting $W_{HI,i}$ was given—and therefore the species had less of an influence on the overall mean. For each two-compartment scenario, we calculated the geometric mean relative abundance of all species GM_j as:

$$GM_j = exp\left[\sum_{i=1}^{53} W_{HI,i} ln\left(A_{i,j}/A_{0,i}\right) \Big/ \sum_{i=1}^{53} W_{HI,i}\right] \tag{1}$$

where the scenario-wide abundance for each species in the two-compartment scenario $A_{i,j}$, was given as the sum of its abundance in the spared proportion s of the concession, plus its abundance in the harvested compartment:

$$A_{i,j} = \left[A_{HI,i}(1-s)\right] + A_{0,i}s \tag{2}$$

For species i, we calculated the weighting $W_{HI,i}$ for a given harvesting intensity HI as the reciprocal of the square of the bootstrap-derived standard error SE of $ln\left(A_{i,j}/A_{0,i}\right)$:

$$W_{HI,i} = \frac{1}{SE_{HI,i}^2} \tag{3}$$

For the multi-compartment and business-as-usual logging scenarios, we calculated the weighted geometric means in similar fashion as for the two-compartment scenario in Eq. (1), except that we summed relative abundances across k compartments:

$$GM_j = exp\left[\sum_{i=1}^{53} \omega_{i,j} ln\left(\alpha_{i,j}/A_{0,i}\right) \Big/ \sum_{i=1}^{53} \omega_{i,j}\right] \tag{4}$$

where $\alpha_{i,j}$ was the scenario-wide abundance of species i in the particular multi-compartment scenario j:

$$\alpha_{i,j} = \sum_{k=1}^{5} A_{i,k} \tag{5}$$

and total weighting across compartments $\omega_{i,j}$ was the sum of the weights for species i, at each compartment and harvest intensity, thereby ensuring that the different weightings associated with each compartment's $\underline{HI}$ were accounted for:

$$\omega_{i,j} = \sum_{k=1}^{5} W_{i,k} \tag{6}$$

2.4.3. Assessing functional diversity and functional trait structure under different logging approaches

We used five indices to describe the functional diversity outcomes of logging (see Table S1). These indices describe two broad aspects of functional diversity: (1) how much of functional trait space is filled by existing species (Functional Richness; FRic) and (2) how this space is filled (Functional Dispersion, FDis; Functional Divergence, FDiv; Functional Evenness, FEve; and RaoQ, another measure of functional dispersion; Schleuter et al., 2010; Villéger et al., 2008). These functional diversity indices treat traits as coordinates in multidimensional functional space and we considered how each varied across the sparing-to-sharing continuum, compared with business-as-usual logging and an old-growth baseline (Villéger et al., 2008; Laliberté and Legendre, 2010; Edwards et al., 2021; see Supplementary Methods, Assessing functional diversity). We focused all trait analyses on the current timber production target (where $P = 1$).

We also investigated how the representation of key functional traits underpinning ecosystem processes in our study area (Griffiths et al., 2015, 2016b; Table S2) varied under different logging approaches. We first calculated the concession-wide abundance across all species for a continuum of scenarios spanning land-sharing to land-sparing logging (see two-compartment logging above), and then determined how this abundance was apportioned by nesting traits (i.e., by determining the percentage of abundance comprised of tunnellers, rollers and dwellers). We also divided each of the continuous dung beetle traits (body mass, front leg length/body mass, pronotum width/body mass, and back leg length/front leg length) into quintiles, and calculated for each scenario the percentage of total abundance falling within each of these quintiles.

3. Results

3.1. Winners and losers

At the current timber production target, there were a similar number of winners and losers from logging (winners = 49 % and losers = 51 % of 53 species), but an increasing percentage of species were losers at higher timber production targets (Fig. 2). Among losers, land sparing gave the maximum abundance for the largest number of species (Fig. 2). Only 13 % (3 species) of losers preferred sharing logging approaches at current production targets, and no loser species had their highest abundance under intermediate logging (Fig. 2). At current logging production targets, 73 % (19 species) of winners preferred land-sharing logging approaches, compared with 23 % (6 species) for intermediate approaches (Fig. 2). A sensitivity analysis that added the 10 species that we excluded because the western sampling block might lie outside their range revealed similar patterns as Fig. 2, although there were a larger percentage (57 % of 63 species) of winner species, 72 % (26 species) of which had their abundance maximised under sharing at the current production target (Fig. S6).

3.2. Weighted geometric mean relative abundance

3.2.1. Two-compartment scenarios

For all species, and for the subset of species classified as logging losers, weighted geometric mean relative abundance was maximised under two-compartment sparing across all production value ranges of P (Fig. 3A & B). For winner species, the best strategy changed depending on P but abundances were almost always highest under sharing approaches (Fig. 3C). Business-as-usual logging was better than extreme sharing and worse than extreme sparing for all species and loser species (dashed lines; Fig. 3A & B). This pattern was reversed for winner species, where sharing outperformed business-as-usual logging and sparing did worse (dashed line; Fig. 3C). All of these patterns were robust to the inclusion of the species never recorded in the western block (Fig. S7).

3.2.2. Multi-compartment scenarios

For all species combined, 3 % of multi-compartment scenarios (237 out of 8000 considered) delivered higher weighted geometric mean relative abundance than extreme two-compartment sparing (points above red line in Fig. 4A, hereafter referred to as 'better-performing scenarios'). This rose to ~9 % of scenarios (700 out of 8000) when including species never recorded in the western block of the concession (although this fell to <2 % of these where production targets >1; Fig. S8). Multi-compartment scenarios only outperformed extreme sparing where $P < 1.3$, and all better-performing scenarios with higher geometric mean abundance were characterized by a high proportion of old-growth forest, paired with parcels of medium- to high-yield logging. All better-performing multi-compartment scenarios had 20–80 % of their concession area covered with old-growth forest, together with a maximum harvesting intensity of between 37 and 100 % of the maximum permissible *HI*. All better-performing multi-compartment scenarios where $P > 0.8$ had at least 20 % of their concession maintained under a harvesting intensity of >80 % the maximum permissible *HI*. Hence, all high-performing multi-compartment solutions involved considerable sparing.

For loser species, extreme sparing (where old-growth retention was maximised by harvesting intensively in logged areas) performed better than every complex multi-compartment scenario we examined (Fig. 4B), a pattern that was robust to the inclusion of additional range-unverified

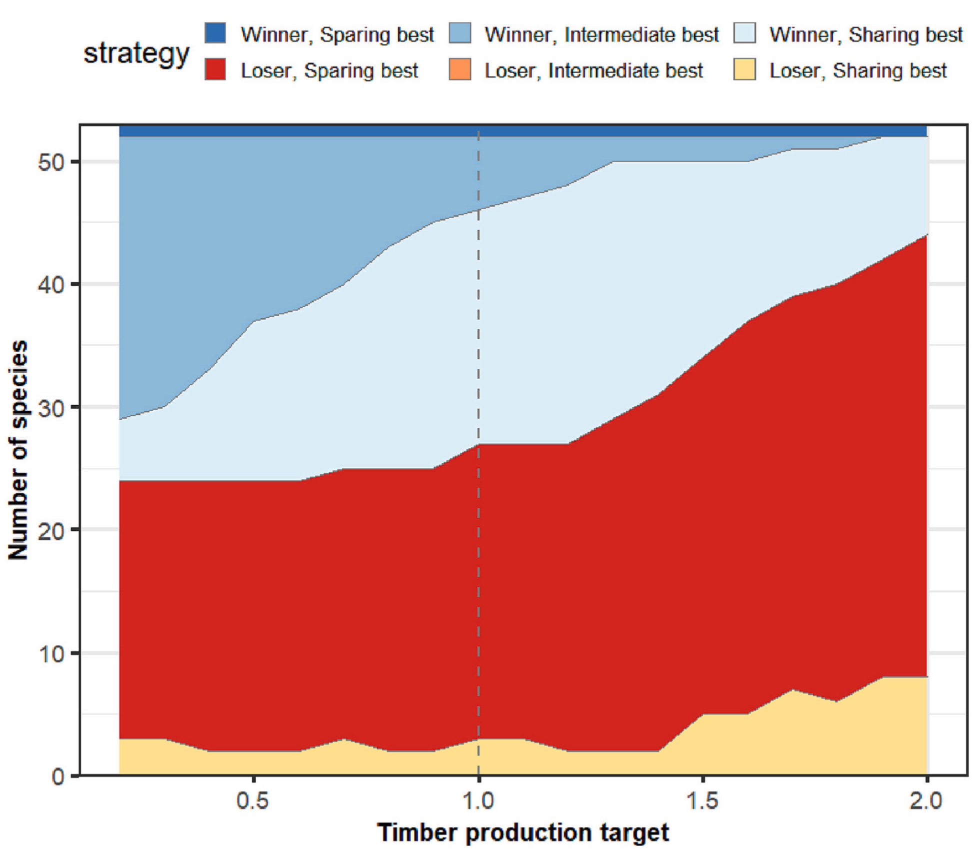

Fig. 2. Proportion of species achieving higher abundance under land sparing, land sharing, or an intermediate (two-compartment) strategy in a Brazilian logging concession. Dashed vertical line is the level of timber production (P) achieved through business-as-usual logging. Winner species (colours in upper line) are predicted to have higher abundance under a scenario involving logging than in an all old-growth baseline. Losers (colours in bottom line) are predicted to have smaller abundances under all logging production strategies compared with an old-growth baseline. Note that we found no Loser species that had their highest abundance under intermediate logging. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

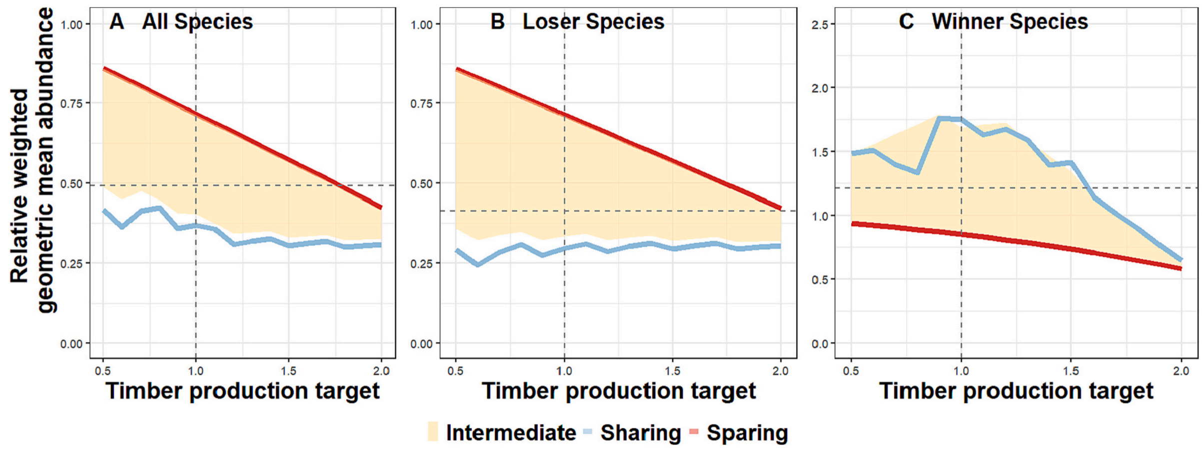

Fig. 3. Geometric mean abundance of 53 dung beetle species in two-compartment scenarios, relative to an old-growth baseline, as timber production targets (P) vary. Shading shows the range of outcomes associated with two-compartment strategies intermediate between extreme sharing and extreme sparing. Vertical dashed lines show current timber production ($P = 1$) from business-as-usual logging. The horizontal dashed line is the current predicted geometric abundance under business-as-usual logging. All species (A) are split into Loser species (B) and Winner species (C). Winner species are those that have larger abundance sizes under some logging scenarios compared with the old-growth baseline (vice versa for Losers). Red lines show the geometric mean abundance from extreme sparing, and blue lines from extreme sharing logging scenarios. The timber production target is shown relative to current production in 50,000 ha of the Jari Florestal logging concession. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

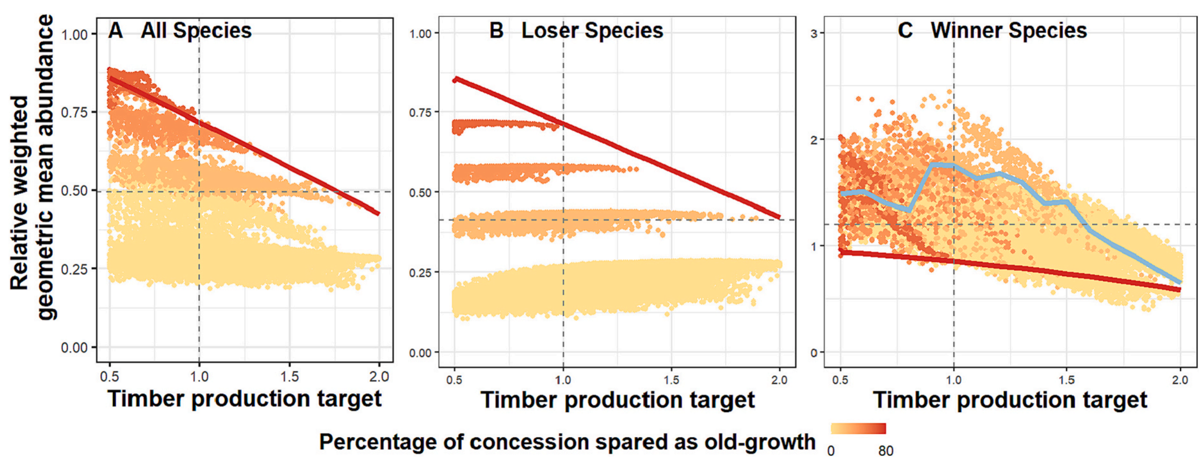

Fig. 4. Geometric mean abundance of 53 dung beetle species achieved in ~8000 5-compartment logging scenarios, relative to an old-growth baseline, as timber production targets (P) vary. Each point shows a unique feasible combination of 5-compartment logging that reaches a given production target, P, with the colour of points showing the percentage of the concession retained as old-growth per scenario. The red line shows the outcome under extreme two-compartment sparing; the blue line under two-compartment sharing. Vertical dashed lines show current timber production ($P = 1$) from business-as-usual logging. The horizontal dashed line is the current predicted geometric abundance under business-as-usual logging. All species (A) are split into winner (B) and loser species (C), based on the two-compartment analyses summarised in Fig. 1. Winner species are those that have larger abundance under some logging scenarios compared with old-growth baseline (vice versa for Losers). The timber production target is shown relative to current production in 50,000 ha of the Jari Florestal logging concession. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species (Fig. S8). Again, multi-compartment scenarios containing a larger proportion of old-growth forest had higher geometric mean relative abundance than scenarios containing less old-growth forest. For winner species, as expected, the vast majority of multi-compartment scenarios performed better than extreme sparing (Fig. 3C). However, across a range of values of P, several multi-compartment scenarios also outperformed extreme sharing (above the blue line; Fig. 4C; Fig. S8). Some of these better-performing scenarios still had up to 60 % of their concession covered with old-growth forest, together with a maximum harvest intensity of 40–100 % of the maximum permissible *HI*. Indeed, up until $P = 1.9$, it was possible to have 20 % of the concession maintained under old-growth, and for winners to still have a higher geometric abundance than under extreme sharing, so long as at least 20 % of compartments were operating at maximum *HI*.

3.3. Functional diversity and functional trait structure under different logging approaches

Land-sparing logging approaches maximised both functional dispersion (FDis) and RaoQ, outperforming sharing, business-as-usual, and any intermediate approaches (Fig. 5A, B). FDis and RaoQ values under land-sparing logging approached those in an old-growth baseline (Fig. 5A, B). By contrast, FEve and FRic were relatively unaffected by either logging or the logging approach (Fig. S9 A, B), retaining similar values to old-growth and business-as-usual logging under both sharing and sparing. FDiv was marginally lower under sparing than under sharing, but in both instances fell well below the values observed in an old-growth baseline (Fig. S9 C).

The representation of individual functional traits that underpin key dung beetle-mediated ecosystem processes in our study area (Griffiths

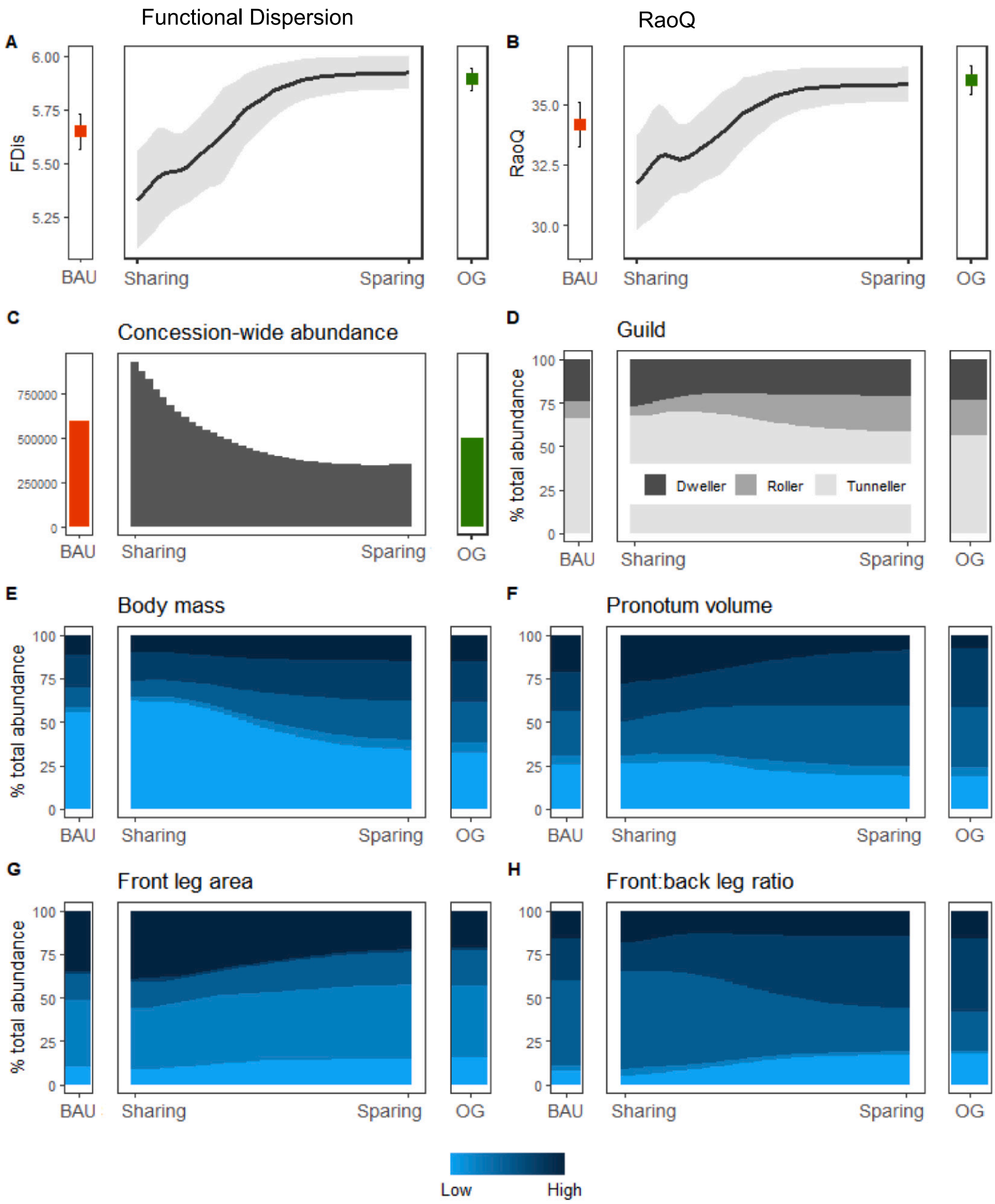

Fig. 5. Functional diversity and trait structure of dung beetle communities under different logging approaches along a two-compartment sparing/sharing continuum. (A) Functional Dispersion (FDis) and (B) RaoQ are two measures of the of functional trait dissimilarity among species in a given scenario (weighted by abundance). (C) Concession-wide abundance across scenarios. (D) Proportional abundance of communities made up of species with tunnelling, dwelling or roller nesting guilds. *E*-H show how the proportion of scenario-wide abundances varies between quintiles for each of the following traits: (E) Biomass; (F) Pronotum volume; (G) Front leg area; and (H) Front:back leg ratio. All scenarios along the sharing-sparing continuum meet a fixed timber production target, represented by the current timber production target within the study concession (i.e., $P = 1$). Plots either side of the main panels show the outcomes associated with business-as-usual logging (BAU, *left*) and an old-growth baseline (OG, *right*). For A and B, the line shows the mean observed across 1000 bootstraps, with error bars showing the standard deviation around the mean.

et al., 2015, 2016b) (Table S2) also varied under different logging approaches. Total dung beetle abundance, summed across all species, was highest under land-sharing logging (Fig. 5C). This was due to the hyperabundance of a winner species that benefitted from logging, *Onthophagus bidentatus*, which represented 24 % of total abundance under sharing (cf. 3 % under sparing, 2 % under an old-growth baseline, and 17 % under business-as-usual), and resulted in sharing having the highest biomass of any scenario (Fig. S10). Proportional representation of key functional traits, however, was more similar to old-growth baselines under land-sparing logging than under either sharing or business-as-usual approaches (Fig. 5D–H). For instance, the proportional abundance of tunneller, roller, and dweller species was more similar to old-growth baselines under sparing logging than sharing logging Fig. 5D), whereas the smallest 20 % of species comprised 62 % of abundance under land-sharing approaches (and 56 % under business-as-usual) but just 34 % under land-sparing (similar to the 33 % under an old-growth baseline; Fig. 5E).

3.3.1. *Profitability of sharing, sparing and business-as-usual*

All logging scenarios were profitable within our study concession, but business-as-usual logging ($USD 819 per ha) and extreme sharing ($USD 716 per ha) were more profitable than either sparing scenario (block = $USD 433 per ha; fragmented = $USD 559 per ha; Fig. 6). This was despite sharing requiring much greater investment in logging road infrastructure than sparing. Overall, road network costs under business-as-usual and sharing road network costs were 125 % and 110 % higher, respectively, than block sparing, with sharing logging costing $7.30/m^3 harvested, compared to $4.20/m^3 for sparing. The higher profitability of business-as-usual and more-extensive sharing was similar regardless of whether we considered profitability per m^3 of timber produced or per tree logged (Fig. S11), with this higher profitability driven by more-extensive logging approaches enabling the exploitation of larger of volumes of the highest-value tree species across the concession. Sharing logging did however lead to a much larger area being affected by road networks, with 100 % of the logging parcels made accessible through road networks under sharing compared with ~42 % under sparing.

4. Discussion

Mitigating logging impacts is a major frontier for the conservation of tropical nature, but how to design logged forest landscapes that meet desired production levels whilst minimizing biodiversity declines and associated loss of ecological functions remains a key unanswered question. Combining 120 estimates of the relative abundance of each of 53 (morpho)species of Amazonian dung beetle with parcel-level data on tree extraction, and species' trait information, we find that increasing the area of unlogged forest spared within timber concessions resulted in higher species' abundances (for loser species harmed by logging), higher geometric mean population sizes (for losers and for all species combined), and a functional diversity and functional trait structure more closely resembling that of old-growth forest. Our results suggest that to protect sensitive species, future logging policies within licensed concessions— including within the 35 Mha of potential state and national forest concession area in the Brazilian Amazon (Sist et al., 2021) — should consider maximising unlogged forest portions within concessions, rather than applying more extensive lower-yielding, intermediate or mixed harvesting practices across a larger concession area.

For loser species, simply maximising old-growth forest by harvesting logged parcels at maximum permissible harvest limits ('extreme sparing') resulted in the highest geometric mean population sizes across timber production targets (P), outperforming sharing and intermediate approaches, and more-complex mixed scenarios characterized by a mixture of harvest intensities across the concession. However, when evaluated across all species (i.e. across winners that have higher abundance under logging than in old-growth baselines, and across losers), 3 % (237/8000) of mixed approaches had modestly improved conservation outcomes relative to maximising the retention of old-growth forest via extreme sparing. This suggests that the incorporation of low- or intermediate-yielding concession parcels alongside sparing of undisturbed habitat can increase the abundance of more open-habitat adapted or edge-tolerant species – as previously demonstrated in forests and on farms (Montejo-Kovacevich et al., 2018; Feniuk et al., 2019; Finch et al., 2020). Nevertheless, the additional community-wide benefits of mixed logging approaches only held at relatively low production targets (only two mixed scenarios had better conservation outcomes than extreme sparing at production targets above current levels, i.e., where $P > 1$), and all high-performing mixed scenarios still involved substantial sparing of old-growth (20–80 % of the concession). Critically, all high-performing mixed scenarios still involved more sparing than under business-as-usual management, underscoring the relevance of larger amounts of old-growth protection for improving conservation outcomes under any future logging regime implemented in our study area.

Extreme sparing also resulted in a community with the highest functional trait dissimilarity, and a functional trait structure most closely resembling that of old-growth forest. This is the first direct evidence that sparing-logging policies may best maintain functional traits known to underpin ecosystem functions (Griffiths et al., 2016b), mirroring patterns previously found in agricultural and secondary forest systems in Colombia (Cannon et al., 2019; Edwards et al., 2021). Our finding that sparing resulted in a dung beetle community with the largest proportion of rollers and large bodied beetles has potentially important implications for nutrient recycling, dung removal, soil infiltration rates, and seed dispersal dynamics (Griffiths et al., 2016a; Keller et al., 2022). Land-sparing logging also resulted in a similar functional dispersion (FDis) and RaoQ (two measures of the dissimilarity of functional traits in trait space) as old-growth baselines, outperforming

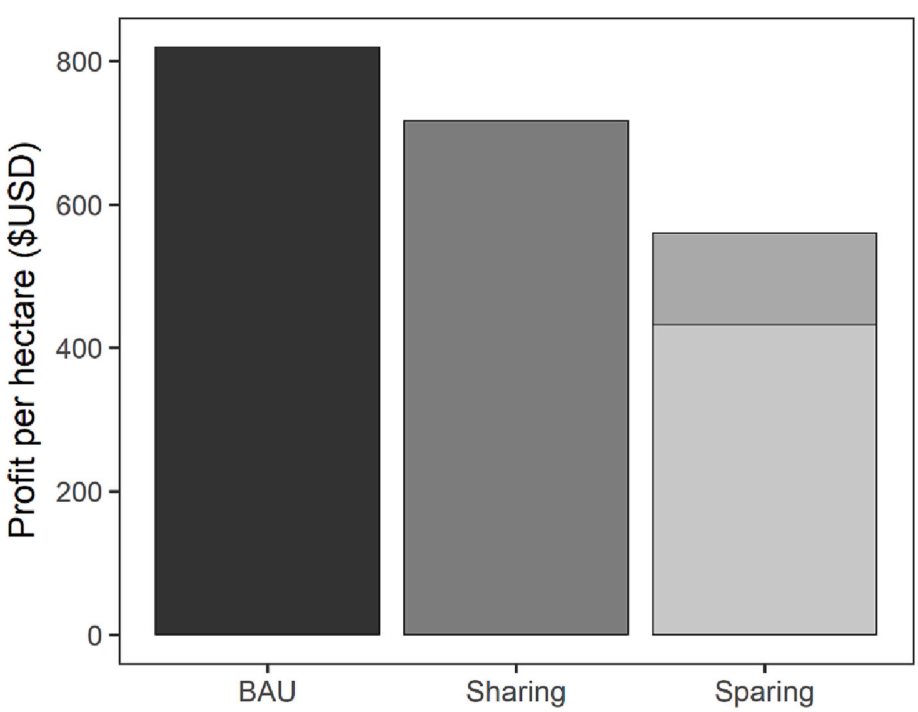

Fig. 6. Profits associated with different logging scenarios, based on the observed distributions of >155,000 trees including of 153 merchantable species, across 1490 ha of old-growth forest in the *Jari Florestal* concession. Profit estimates were generated using spatially-explicit harvest simulations, and consider net revenue based on species-specific timber prices, yield information, and extraction costs for 153 timber species. To account for different ways of deploying land-sparing spatially, we investigated two configurations: block sparing (where high-intensity harvest was restricted to one contiguous block until the production target was met, with the remaining parcels off-limits to logging; *lighter grey, sparing*) and fragmented sparing (where high-intensity logging preferentially targeted parcels in order of profitability; *darker grey, sparing*). All scenarios followed legal restrictions regarding 100-ha harvest intensity limits and minimum cutting diameters (>50 cm DBH), and produced an equal amount of timber (4023 trees, equivalent *to* $P = 1$).

sharing, business-as-usual, and any intermediate approaches. This broader spread of species traits post-logging implies that sparing-logging may better buffer against the loss of ecosystem functions under environmental perturbations such as climate change (Cooke et al., 2019), which increasingly reduce the ecological functions performed by dung beetles in Amazonia (França et al., 2020).

Functional evenness (FEve; how evenly species abundances are distributed in functional trait space) and functional richness (FRic; the total volume of functional space occupied by a given set of species) remained at similar values to old-growth and business-as-usual logging under both sharing and sparing. This corresponds with previous findings that FEve and FRic can be more resilient to degradation (Cerullo et al., 2019; Guerra Alonso et al., 2022), possibly because functional redundancy at larger spatial scales buffers some of the localised effects of disturbance (Edwards et al., 2021; Guerra Alonso et al., 2022; Nunes et al., 2021). However, functional divergence (FDiv; how the relative abundance of species is related to the most unique functional traits) fell well below old-growth baseline values under all logging scenarios, probably because they all resulted in notable abundance declines among rare forest-dependent species forest that contribute disproportionately to unique functional roles (França et al., 2020).

Our findings support sparing-related conservation benefits demonstrated for ants, dung beetles, and birds in Borneo, (Edwards et al., 2014a), for dung beetles and management-sensitive butterflies in the Brazilian Amazon (França et al., 2017; Montejo-Kovacevich et al., 2018), and broader evidence highlighting the irreplaceable conservation value of old-growth rainforest (Barlow et al., 2016;Gibson et al., 2011; Maxwell et al., 2019; Piponoit et al., 2019b). However, our results contrast with studies reporting that low to intermediate harvests benefit many Amazonian butterflies (Montejo-Kovacevich et al., 2018), and which find no clear species responses to varying logging intensities (Griscom et al., 2018; Wearn et al., 2017). We suggest these differences could be because we undertook more complete sampling (and so included relatively more old-growth specialists; (Buřivalova et al., 2014; Lavery et al., 2020) because fruit-feeding butterflies are easier to trap in disturbed forest understories, or because species richness (as used in Griscom et al., 2018) is a poor biodiversity indicator since it treats scarce specialists and common generalists as equivalent (Buřivalova et al., 2014) and fails to account for variation in species' abundance (Balmford, 2021; Betts et al., 2021).

The sparing-sharing paradigm provides a flexible tool for investigating the impacts of management regimes on biodiversity (Runting et al., 2019) but our approach has several limitations. First, we consider a single taxonomic group, which was only surveyed one-year post-logging. Whilst dung beetles are good indicators of compositional changes in many taxa within our landscape (Barlow et al., 2007), and, conservatively, appear less likely to favour sparing compared with other groups (Balmford, 2021), future work needs to better capture post-logging trajectories (Betts et al., 2021; Cerullo et al., 2019). For example, rapid species recovery post-harvest could shift benefits more towards sharing, though evidence suggests limited recovery of old-growth assemblages following primary habitat disturbance among neotropical dung beetles (Barlow et al., 2016; Edwards et al., 2021; Milheiras et al., 2020; Noriega et al., 2021; Nunes et al., 2021). Secondly, we only considered risks from formal logging: we did not address the concern that by retaining high-value stems sparing could potentially attract illegal loggers (Edwards et al., 2014a; Edwards et al., 2014b), or that because sharing requires a much more extensive road-system it may be more likely than sparing to lead to forest degradation through fragmentation and potential impacts on forest flammability (Berenguer et al., 2021; Bousfield et al., 2021). Incorporating how these additional risks may impact biodiversity via changes in forest resilience, hunting pressures and subsequent dung availability is an important area for future research. Lastly, we did not project long-term ecological dynamics or profitability outcomes for scenarios. Sharing will likely extirpate low-density, valuable species across the entire concession, whereas sparing can better retain old-growth processes and species in unlogged portions. However, sparing is likely to have lower future financial returns, because it would rely on harvesting the remaining lower value merchantable trees instead of the next-most-valuable species (Castro et al., 2021; Piponiot et al., 2019a; Sist et al., 2021). Policies incentivising old-growth sparing should therefore be accompanied by wider forest management reforms that support more yield-sustaining post-logging silviculture (Cerullo and Edwards, 2019; Finlayson et al., 2022), and source greater wood volumes from purpose-grown plantations (Piponiot et al., 2019a; Sist et al., 2021).

4.1. Management implications and conclusions

Business-as-usual harvesting was up to 90 % more profitable than extreme sparing, with this higher profitability driven by more spatially extensive logging enabling harvesting of larger volumes of sparsely-distributed, high-value stems – a larger proportion of which remained unexploited within unlogged concession areas under sparing. These results suggest that active policy mechanisms, standards, or regulations would be needed to make spatially-concentrated logging operations (which benefit biodiversity) more commercially attractive than other harvesting regimes (Bousfield et al., 2021; Kleinschroth et al., 2019; Piponiot et al., 2019a; Sist et al., 2021).

To reconcile conservation and timber production, timber managers could reduce the costs of sparing through more sophisticated spatial planning than we tested in our analysis. Harvesting intensively in the most remunerative parcels increased the profitability of extreme sparing by 25 % by enabling greater exploitation of high-value, locally uncommon trees, with further cost-savings probable under more-mixed sparing scenarios. Governments could also provide subsidies or reductions in logging taxes for companies maintaining unlogged forest areas critical for biodiversity (Bousfield et al., 2021), whilst certification standards such as FSC could couple access to premium timber markets with sparing-favouring management plans (Bousfield et al., 2021). Ultimately, carbon-focused market mechanisms, such as REDD+ and the RIL-C agenda, will be critical for promoting land-sparing policies that demonstrably improve carbon outcomes (Derroire et al., 2021), including by reducing road networks (Cerullo and Edwards, 2019; Griscom et al., 2019; Piponiot et al., 2019b; Putz et al., 2019). Cost-effective carbon payments have the potential to reduce logging harvest intensities in the Brazilian Amazon (Bousfield et al., 2022) and promote more sustainable harvest practices in sub-Saharan Africa (Ndjondo et al., 2014); they could also play a role in promoting sparing-style logging harvests.

Future analyses should explore how sparing at different scales and in different spatial configurations would affect biodiversity, for example by assessing the conservation outcomes of sparing larger blocks of old-growth forest versus more fragmented approaches, which may target sparing to supplement old growth retention around already protected forest regions (e.g., around riparian buffers). However, achieving the largest conservation improvements to logging impacts under sparing will almost certainly require actions extending beyond single concessions. This may involve supporting the production of high-grade timber plantations on deforested lands under emerging restoration agendas (Sist et al., 2021), or intensifying production and granting concession licenses only in forest margins, leaving core areas protected (Piponiot et al., 2019a). However, where landscape production strategies include harvesting within natural forest concessions, our results suggest that practitioners striving to reconcile timber production with biodiversity conservation should pursue harvesting regimes that retain as much old growth forest as possible.

CRediT authorship contribution statement

Gianluca Cerullo: Funding acquisition, Writing – review & editing, Writing – original draft, Formal analysis, Investigation, Methodology, Conceptualization. **Filipe França:** Funding acquisition, Investigation, Methodology, Conceptualization, Supervision, Writing – review & editing. **Tom Finch:** Writing – review & editing, Investigation, Methodology. **Philip Erm:** Writing – review & editing, Methodology. **Hannah Griffiths:** Writing – review & editing, Investigation. **Julio Louzada:** Funding acquisition, Writing – review & editing. **Chris G. Bousfield:** Writing – review & editing, Investigation, Methodology. **Mike R. Massam:** Writing – review & editing. **Carlos A. Peres:** Writing – review & editing. **Jos Barlow:** Funding acquisition, Writing – review & editing. **Rhys E. Green:** Writing – review & editing, Methodology. **David P. Edwards:** Supervision, Writing – review & editing, Methodology, Conceptualization. **Andrew Balmford:** Supervision, Funding acquisition, Writing – review & editing, Methodology, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110065.

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