Disentangling the effects of habitat fragmentation and top-down trophic cascades on small mammal assemblages on Amazonian forest islands

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ABSTRACT

Habitat loss and fragmentation are widely acknowledged to affect species diversity. However, the pathways through which their effects are propagated through foodwebs, ultimately driving species diversity, are less well understood. We investigated to what extent the effects of habitat loss and fragmentation on small mammals in Central Amazonia are mediated by higher trophic levels, specifically mammal mesopredators and apex predators. We surveyed these three mammal groups across 25 islands surrounded by a landscape-scale gradient of forest cover within the Balbina Hydroelectric Reservoir, in addition to three adjacent continuous forest sites. We then applied Structural Equation Modelling based on apex-predator incidence and either the abundance or biomass of mesopredators and small mammals. Apex-predator incidence was positively affected by landscape forest cover, as well as mesopredators abundance and biomass. Small mammal abundance, but not biomass, was negatively affected by forest cover. Contrary to expectations, the negative effect of forest cover on small mammal abundance was not mediated by a decrease in mesopredator abundance nor incidence of apex-predators. Instead, small mammal increase is apparently favoured by the proliferation of the few persisting smaller-bodied species which can take advantage of augmented resources related to habitat degradation. The further increment in small mammal abundance in the absence or lower abundance of predators might be prevented by the resource availability characterising these evergreen forests. Mammal assemblages seem to be primarily regulated by bottom-up forces. While this suggests a delayed extinction debt in Amazonian forest islands, remaining biodiversity might be poorly resilient to additional habitat disturbances.

1. Introduction

Habitat loss and fragmentation typically involve a decrease in habitat size, increase in isolation (MacArthur and Wilson, 1967) and changes in habitat structure such as those promoted by edge effects (Louthan et al., 2015). Likewise, the amount of habitat available in the local landscape surrounding habitat patches also decreases (Fahrig, 2013). Although these twin processes are widely acknowledged to affect species diversity (Sala et al., 2000; Haddad et al., 2015), the mechanisms through which their effects are propagated on local foodwebs, ultimately influencing how species diversity is stabilized, are less well understood (Hagen et al., 2012).

Species interactions within fragmented forest landscapes tend to be particularly affected by the altered abundance and diversity of predators (Kruess and Tscharntke, 1994). Due to their low population densities and large spatial requirements (Carbone and Gittleman, 2002), apex predators are highly sensitive and often driven to local extinction as patch area decreases (Terborgh et al., 2001). The absence of apex predators likely moderates top-down forces (Estes, 1996), possibly releasing lower trophic levels, such as mesopredators, into higher abundances (Crooks and Soulé, 1999). As key features of habitat structure further deteriorate in patches embedded within highly fragmented

landscapes (Rocha-Santos et al., 2016), even mesopredators might undergo local extinction (Benchimol and Peres, 2015a). This would eventually culminate in a top-down trophic cascade, in which lower levels of the foodweb, such as small-bodied mammals, would then be released (Adler and Levins, 1994; Terborgh et al., 2006; Moore et al., 2022). Disentangling the contribution of habitat fragmentation from top-down forces can elucidate how efficient measures can be designed to maximise biodiversity persistence in such landscapes (Dyer and Letourneau, 2003; Hanna and Cardillo, 2014).

Biodiversity loss and community shifts are known to be particularly acute in insular fragmented landscapes created by the construction of hydroelectric dams, due to the elevated hostility of the open-water matrix for most terrestrial species (Jones et al., 2016). Notwithstanding, the ever-expanding hydroelectric sector remains a development priority in lowland tropical countries due to escalating renewable energy demands. This is disquieting not least because of the flat topography of many tropical forest regions and the large numbers of species therein. Forest islands created in the aftermath of damming further comprise a natural laboratory to understand mechanisms maintaining biodiversity in fragmented landscapes given their equally uniform matrix and convergent histories of anthropogenic disturbance (Diamond, 2001). One of the most iconic of these landscapes is the Balbina Hydroelectric Reservoir, located in central Brazilian Amazonia (Fearnside, 1989), which contains 3526 forest islands emerging across >400,000 ha of shallow water (Jones et al., 2021). Yet, the Guri Lake in Venezuela is among a well-studied hydroelectric reservoir in tropical forests (Jones et al., 2016). Local predator extinction on Guri islands promoted the hyper-abundance of herbivores, culminating in the

'ecosystem meltdown', characterised by rapid collapse of baseline ecosystem functioning (Terborgh et al., 2001, 2006). In addition, Gibson et al. (2013) recorded accelerated local species extinctions in the aftermath of habitat fragmentation in small mammal assemblages in the Chiew Larn Hydroelectric Reservoir, Thailand. These once diverse assemblages were reduced to only one hyperdominant rat species 33-years after damming (Moore et al., 2022).

In this study, we aim to disentangle the relative contribution of habitat fragmentation from top-down forces regulating assemblages of non-volant small mammals (rodents and marsupials) in the vast Balbina landscape. For this purpose, we investigated to what extent the effects of habitat fragmentation on the abundance and biomass of small non-flying mammals are mediated by higher trophic levels, namely mammal mesopredators (i.e., species that prey on small mammals) and apex predators (i.e., species that exert 'landscapes of fear' or prey on mesopredators and small mammals; Gallagher et al., 2017). We surveyed mammals across 25 variable-sized islands surrounded by varying amounts of forest cover, in addition to three adjacent continuous forest sites. Given that the remaining species diversity in fragmented landscapes could be explained by either the Island Biogeography Theory or the Habitat Amount Hypothesis (e.g., Bueno and Peres, 2019), we initially considered both of these scenarios. We then identified the scenario that best explains each of these mammal groups. Overall, we expected that small mammal abundance and biomass would be driven by both negative fragmentation effects and positive inter-trophic effects given an eventual process of predator release (Fig. 1). Along the gradient of fragmentation (i.e., smaller and more isolated habitat patches, or lower overall habitat amount), we expect apex-predators to undergo
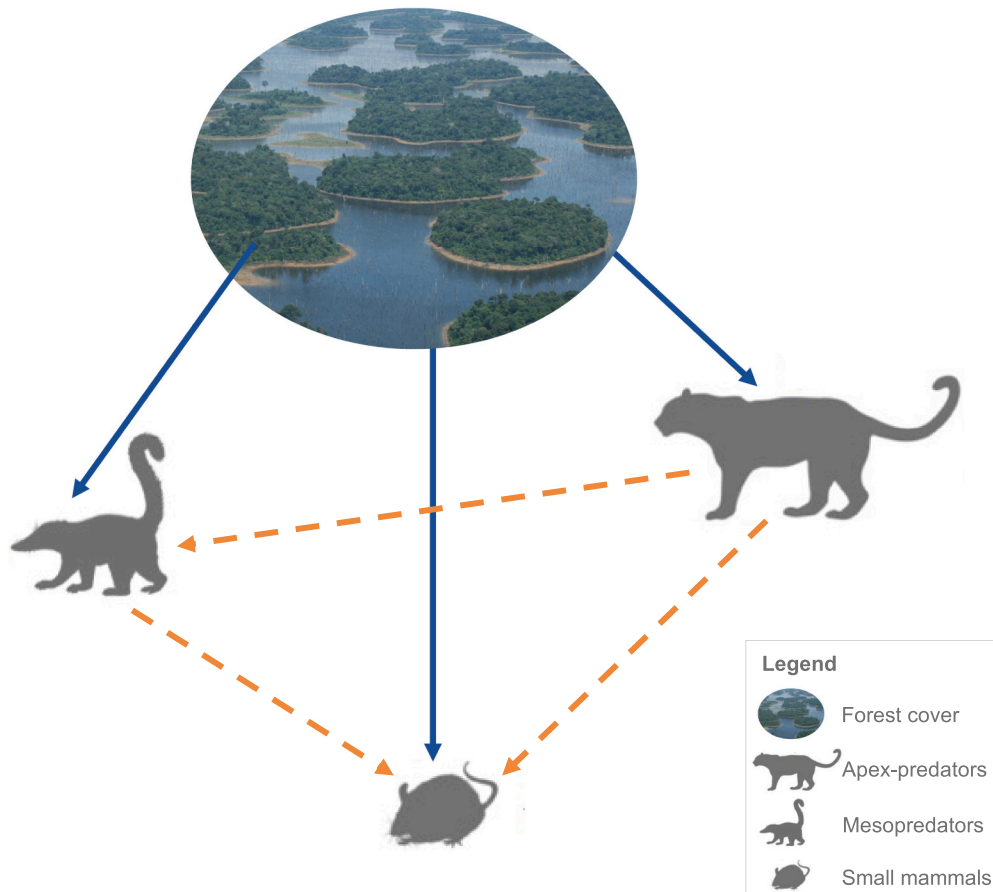

Fig. 1. Representation of the different pathways considered to explain small mammal abundance and biomass in the archipelagic Balbina landscape. These include the effects of habitat fragmentation on each mammal groups — apex-predators, mesopredators and small mammals (denoted by the blue arrows) — and the inter-trophic effects of fragmentation as mediated by the inter-trophic relationships (orange arrows). Solid and dashed lines denote the expected positive and negative relationships, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

local extinctions, resulting in an increase in the abundance and biomass of mesopredators. As a result, we expect mesopredators to decline in abundance or undergo local extinction in highly fragmented landscapes, thereby allowing small mammal abundance and biomass to increase.

2. Methods

2.1. Study area

The archipelagic Balbina landscape (centroid coordinates: 1°41′33″S, 59°38′57″W; Fig. 2a) was created in 1986, following the completion of a major dam on the Uatumã River, a left-bank tributary of the Amazon River. Within the 443,772-ha hydroelectric reservoir, a pristine forest area of 312,900 ha was flooded, and 3546 forest islands were created (Jones et al., 2021). Most islands consist of dense closed-canopy *terra-firme* forest (Fig. 2b). The mean annual temperature and rainfall in this region is 28 °C and 2376 mm, respectively (IBAMA, 1997). Surveys were carried out on 25 islands and three mainland continuous forest (CF) sites. Islands surveyed varied widely in size (0.55 to 1459 ha, mean ± SD: 197 ± 348 ha), and isolation distance to the nearest mainland CF site (10 to 11,885 m; 4042 ± 3260 m; Table S1). Landscape forest cover ranged between 9.2 and 100 % (72.7 ± 30.4 %) when considering 200-m buffers centred onto the centroid of each sampled island; between 3.0 and 97.6 % (50.6 ± 28.6 %) when buffer sizes were 800-m radii; between 3.4 and 100 % (54.5 ± 29.9 %) when buffer sizes were 900-m radii; and between 4.4 and 100 % (53.0 ± 28.9 %) when buffer sizes were 1000-m radii.

2.2. Mammal surveys

Mammals were sampled twice at each forest site (Fig. 2c) over two consecutive field seasons. From April to November 2014 and April to November 2015, small mammals were sampled along two continuous periods of 16 consecutive nights, using trapping transects. Each transect consisted of a set of nine live trap stations (hereafter, LTs), followed by an array of three pitfall-trap units. Each LT station was placed 20 m apart from each other and included two Sherman traps (23 × 9 × 8 cm, H. B. Sherman Traps, Inc., Tallahassee, Florida) and one wire mesh trap (30 ×

17.5 × 15 cm, Metal Miranda, Curitiba, Paraná). At each LT station, one trap was set on the ground, one in the understorey (~1.5 m high) and one in the (sub)canopy (>10 m high). Traps of different types were placed alternatively on the ground and in the understorey across consecutive stations, but only Sherman traps were placed in the canopy due to logistical limitations. At the forest canopy stratum, small mammals were sampled using an adaptation of the method described by Lambert et al. (2005). LTs were baited with a mix of bananas, peanut powder, sardines, and oak flocks. Pitfall-traps (100*L*) were also spaced apart by 20-m intervals and connected by a 50-cm high plastic fence that was buried 10 cm underground and included 10 m of overhanging fence farther extended beyond the two external pitfalls. Due to spatial restrictions on small islands, alternative smaller trapping plots were established therein. Thus, all islands smaller than 2 ha and those between 2 and 10 ha were sampled by trapping plots containing only three LT stations followed by an array of one pitfall, and six LT stations followed by an array of two pitfalls, respectively. All traps were inspected daily and whenever live captures could not be identified in the field during the first trapping season, a maximum of five voucher specimens per species per survey site were collected for further identification, and subsequently deposited at the Mammal Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), in Manaus, Brazil. All other individuals recorded were weighted and tagged (Fish and Small Animal Tag, size 1; National Band and Tag Co., Newport, Kentucky), so that any subsequent recaptures could be distinguished. Additionally, tissue samples were collected from all individuals recorded and deposited at the INPA Mammal Collection. However, we were not always able to identify at the species-level records of sympatric congeners of *Proechimys* spp. (*P. cuvieri* and *P. guyanensis*) and *Oecomys* spp. 1 (*O. roberti* and *O. bicolor*). Because these congeners are ecologically very similar (Jones et al., 2009), we refer to those taxa as "ecospecies." To streamline, we use hereafter "species" to refer to both species and ecospecies.

In this study, we considered the relatively large *Didelphis marsupialis* (>1.2 kg) as a mesopredator rather than a 'small mammal', as it is known to predate on other small mammal species (Jones et al., 2009). Accordingly, camera-trapping was used to detect *D. marsupialis*, which is more effective than live- or pitfall-trapping for this species (Palmeirim et al., 2019), similarly to other mesopredators of similar or larger body
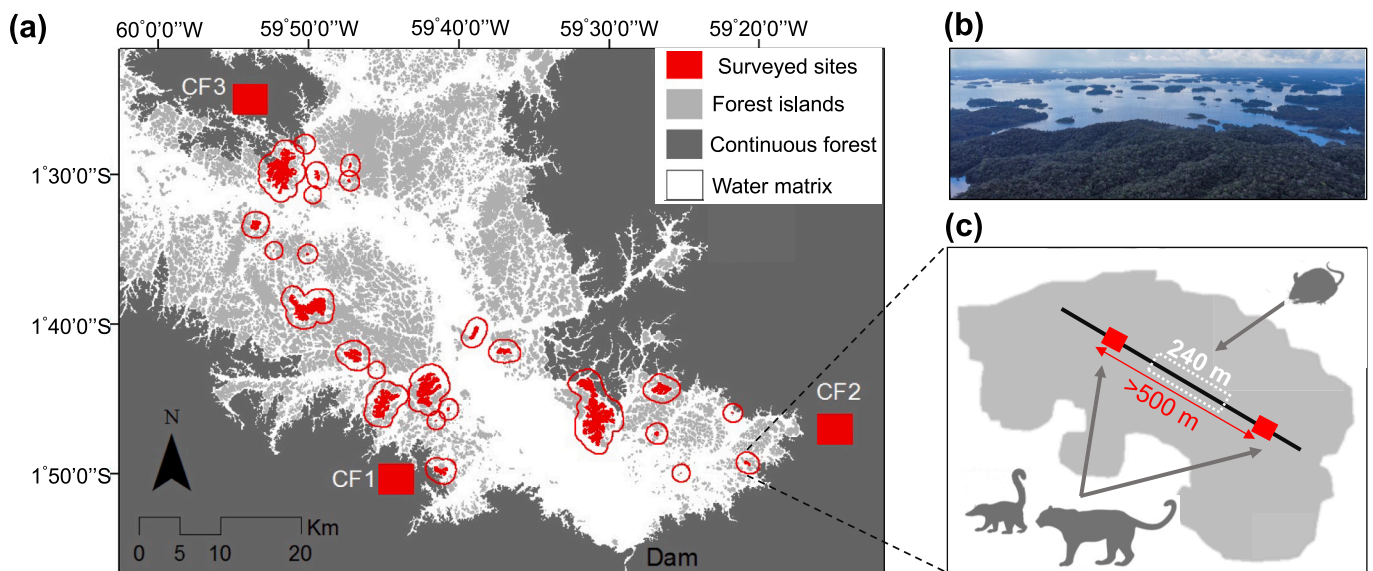

Fig. 2. (a) Surveyed sites within the Balbina Hydroelectric Reservoir of Central Brazilian Amazonia: 25 islands (in red and highlighted by a 1000-m buffer contour line) and three continuous forest sites (CF1, CF2 and CF3; indicated by red rectangles). (b) Aerial photograph of the Balbina landscape (photo credit: R. di Ponzio). (c) Illustration of the sampling methods and sampling effort at a small island on which predators and small mammals were surveyed using two camera-traps (red rectangles) and live- and pitfall-trapping along linear transects (white dashed rectangle), respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

size. We additionally excluded from subsequent analyses two Echimyidae—*Makalata didelphoides* and *Echimys chrysurus*—that were recorded only once during the study. Both species feed on seeds and foliage, in addition to some fruit (Patton et al., 2000), and consequently are rarely attracted to the bait used here.

Data on apex predator and mesopredator species were extracted from camera-trapping surveys on the entire medium- to large-bodied vertebrate fauna (Benchimol and Peres, 2015a). To do so, Reconyx HC500 Hyperfire digital camera traps were used over a 30-day period during each of two consecutive years between June 2011 and December 2012. The number of camera traps deployed per site varied according to island area, so that two to ten camera traps were deployed on each island, and 15 camera traps at each CF site (for details on sampling effort per site, Table S1). Camera traps were unbaited, spaced by at least 500 m (except on small islands), and placed 30–40 cm above ground. We configured all camera traps to obtain a rapid sequence of five images (< 1 s apart) of each animal, using 15-sec intervals between records. However, we only considered records of the same species as independent if intervals between photographs exceeded 30 min, or if different individuals could be recognized based on natural marks (see details in Benchimol and Peres, 2015a).

As apex-predators, we considered two felid hypercarnivores, *Puma concolor* and *Panthera onca*. As mesopredators, we considered the three felid species *Leopardus pardalis*, *Leopardus wiedii* and *Puma yaguaroundi*, the mustelid *Eira barbara*, the Procyonid *Nasua nasua*, and the large Didelphid *D. marsupialis*. As a proxy of apex-predator and mesopredator abundance per site, we considered the sum of independent records from those species obtained across all camera traps at that site divided by the sampling effort per site. We used the number of individuals per 100 trap-nights and the number of independent camera-trap records per 10 trap-nights for small mammals and predators, respectively. We summarise each species diet and body mass information, as well as our classification of trophic group in Table S2. We also assume that a 3-year gap between small- and large-bodied mammal surveys (between 24 and 27 years of island creation) would not significantly affect our results, as there were no severe local disturbances, including timber extraction and hunting, in the sampled sites between sampling occasions, which could have affected some populations.

2.3. Data analysis

2.3.1. Patch and landscape metrics

For each surveyed forest site, we calculated island *area*, the Euclidian distance from the nearest mainland continuous forest of each surveyed island (*dist*), and the Proximity Index (*prox*), following McGarigal et al. (2012), which considers both the area and isolation of each land mass within that buffer. Because previous studies used a 500-m radial buffer to predict both small (Palmeirim et al., 2018) and mid-sized to large mammal richness (Benchimol and Peres, 2015a) on the same islands, the *prox* metric considered this radius threshold in the preliminary analysis. Additionally, we obtained the proportion of forest cover within buffers centered onto the centroid of each sampled island, a metric related to the habitat amount that has been widely used in studies assessing fragmentation effects on biodiversity (see Fahrig, 2013). For this, multiple buffers should be considered to further evaluate the 'scale of effect', i.e., or identify the spatial scale that best fits the evaluated pattern. We considered buffer sizes ranging from 100 m to 1500 m radii. These metrics were obtained using a high-resolution RapidEye© satellite imagery in the ArcMap software (ESRI, 2018) (see Benchimol and Peres, 2015a for further details on imagery processing, and patch and landscape metrics). Because some of these metrics could not be obtained for the three continuous forest sites, we assigned these sites with values resembling "real-world" values. Thus, we assumed *area* to be equal to one order of magnitude (10-fold) larger than our largest island (i.e., 14,597 ha for Is25) (Palmeirim et al., 2022), *prox* to have the same value as the island with the highest *prox* value (i.e., 642932 for Is18). To

streamline, hereafter we use forest area to refer to the area of both island and CF sites.

2.3.2. Mammal metrics

Species abundance was given by the sum of the standardized abundance for all species of each group. Although small mammal surveys allowed us to identify each individual recorded, camera-trapping could not ensure distinction between individuals (except for those that could be distinguished based on natural marks). Yet, variation in abundance is expected to induce variation in detection probability (Royle and Nichols, 2003). In particular, we would expect smaller-bodied predators, specially at smaller forest sites, to pass more often in front of cameras, thereby being recorded more often. However, we (1) found the opposite trend: lower number of mesopredators records at smaller forest sites (Benchimol and Peres, 2015b), and (2) estimates of species occupancy were indeed very similar to the observed species occupancy for most predator species (Benchimol and Peres, 2015b). As such, while for small mammals we could use the number of individuals recorded as their abundance, for apex- and mesopredators, following Benchimol and Peres (2021), we used the number of independent camera-trapping records divided by the sampling effort per site as a proxy of species abundance. We however removed from any subsequent analyses an outlier characterised by a disproportionate abundance of *Didelphis marsupialis* (Fig. 2), likely corresponding to few animals at close proximity to a nest. Species biomass was obtained by multiplying the species-specific standardized abundance by their body mass at each site. Small mammal body mass was measured in situ, whereas body mass data for meso- and apex predators were extracted from Paglia et al. (2012). We scrutinized the distribution of each response variable, including the abundance and biomass of both small mammals and mesopredators. To do so, we analysed the histograms of each variable, in addition to the function *descdist* from the 'fitdistplus' R package (Delignette-Muller and Dutang, 2015). To achieve normality, we $\log_{10}$-transformed species abundance and biomass of small mammals.

2.3.3. Patch and landscape metrics selection

We first performed a 'scale of effect' analysis to select the 'best' *cover* buffer size to fit the abundance and biomass of small mammals and mesopredators (Jackson and Fahrig, 2015). This was done by plotting the Akaike Information Criteria corrected for small sample size (AICc) using Linear Models (LMs) (Burnham and Anderson, 2002). Due to the data distribution of apex-predator abundance and biomass, characterised by 43 % of zeros, we alternatively considered incidence (presence/absence) data for this mammal group to adjust the data distribution within the Generalised Linear Models (GLMs) framework, The corresponding GLM was therefore fitted with a binomial distribution. We performed models for each mammal metric considering one buffer size at a time (i.e., 100, 150, 200, 250, 300, 350, 400, 450, 500, 550, 600, 650, 700, 750, 800, 850, 900, 950, 1000, 1250 and 1500 m-radii). The 'best' buffer sizes of *cover* for small mammal abundance and biomass were either 150 m or 200 m (Fig. S1a and c), with the latter being selected for subsequent analyses as it allowed for more variation in the range of the *cover*. The 'best' *cover* buffer sizes for mesopredator abundance and biomass were 1000 m (Fig. S1b) and 900 m (Fig. S1d), respectively, while that of apex-predator incidence was 800 m (Fig. S1e).

Then, to select the best combination of predictors fitting our response variables, i.e., abundance and biomass of both small mammals and mesopredators, in addition to incidence of predators, we compared the AIC corrected for small sample sizes (AICc; Burnham and Anderson, 2002) for models including: (1) *area* ($\log_{10} x$) and *dist*, (2) *area* ($\log_{10} x$) and *prox* ($\log_{10} x$), and (3) *cover* at its 'best' scale of effect. While *dist* is mostly related to the Island Biogeography Theory (MacArthur and Wilson, 1967), we also considered *prox* as a metric of island isolation as that accounts for islands near the sampling site, from which also immigrants could be potentially sourced (McGarigal et al., 2012). Because

area and *prox* were highly correlated considering all 28 sampling sites, we repeated all models considering only islands, for which these two variables were no longer highly correlated as evidenced by the Pearson correlation test ($r < 0.70$). For this reason, models including *area* and *prox* were not considered when all 28 sites were included. As result, the model including only *cover* best fitted both small mammal metrics, whereas no model provided a better fit for both mesopredator metrics and apex-predator incidence (Table S3). We therefore retained *cover* in all subsequent analysis. Island area and landscape forest cover were positively correlated, with $r = 0.68$ for 200-m buffers, $r = 0.76$ for 800-m buffers, $r = 0.75$ for 900-m buffers, and $r = 0.74$ for 1000-m buffers.

2.3.4. Structural equation modelling (SEM)

We used piecewise SEM in which the path diagram is translated into a set of linear equations, which are evaluated individually, ensuring analyses can be carried out for smaller sample sizes (Lefcheck, 2016). We therefore framed a SEM model including (1) habitat fragmentation effects on apex-predators, (2) apex-predator and habitat fragmentation effects on mesopredators; and (3) mesopredator, apex-predator and habitat fragmentation effects on small mammals. We further inferred on the indirect effect of habitat fragmentation via mesopredators by multiplying the standardized coefficients of the effect of forest cover on both mesopredators and small mammals (Lefcheck, 2016). We ran our SEM model considering first standardized species abundance, and then standardized biomass. Given that neither standardized species abundance nor biomass were discrete variables but were normally distributed, we applied LMs. As an exception, we applied a GLM regarding

apex-predator incidence which was fitted with a binomial distribution. SEMs were carried out using the 'piecewiseSEM' R package (Lefcheck et al., 2016). The set of potential relationships among unconnected variables in the path diagram (i.e., conditional independence claims) comprise the basis set of each SEM. We examined the assumptions of each SEM, i.e., all important relationships are included in the basis set, by calculating their goodness-of-fit using the Shipley's test of directed separation on whether there were any missing relationships among unconnected variables (Shipley, 2000). Shipley's test was conducted by combining all *P*-values across the basis set into a test statistic, Fisher's C, which was <0.05 in both instances. All data analyses were performed in R (R Development Core Team, 2021).

3. Results

Overall, larger forest sites retained or accumulated higher numbers of mammal species (Fig. 3). At least one of the two apex predator species was present on 12 islands, including two islands smaller than 1.5 ha. Ocelot *L. pardalis* and common opossum *D. marsupialis* were the two most widely distributed mesopredators, while the remaining mesopredators only occurred at forest sites >71 ha. The rodent *Hylaeamys megacephalus* ($n = 18$ sites) and the marsupial *Philander opossum* ($n = 18$) were the two most ubiquitous small mammal species and occurred across the entire range of forest area, while seven species were restricted to only the largest islands (>193 ha) and continuous forest sites. However, as island size decreased, some of the persisting species showed increased abundance (e.g., *Marmosa murina*, *Oecomys* sp.1, *P. opossum*
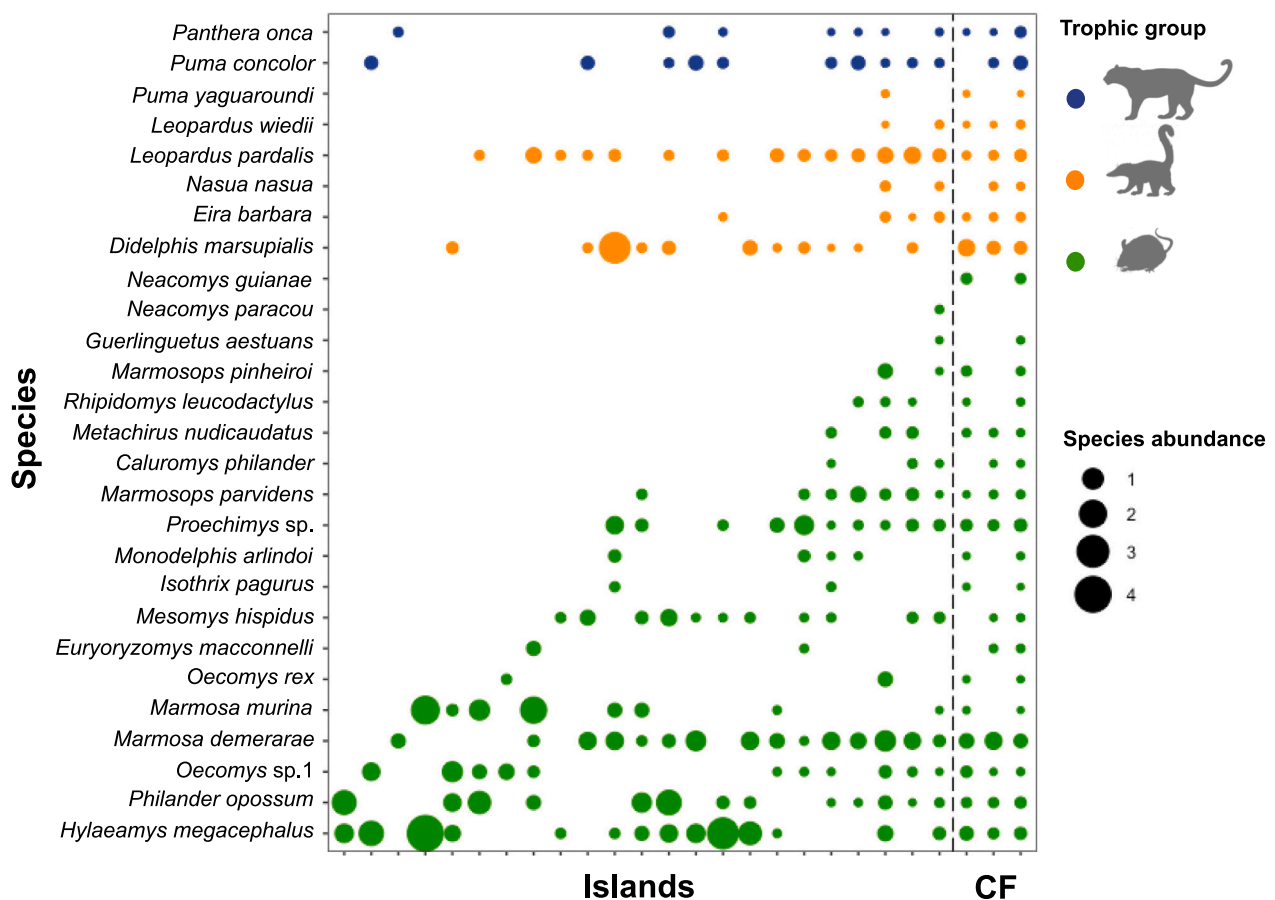

Fig. 3. Species-specific standardized abundance of mammal apex-predators (*blue*), mesopredators (*green*) and small non-volant mammals (*orange*) across the 25 islands and three mainland continuous forest sites surveyed in this study. Sites are ordered left to right from the smallest to the largest. Species are ordered from the least to the most ubiquitous (i.e., widely distributed). Standardized species abundances of apex- and mesopredators correspond to the number of camera-trap records per 10 camera trap-days, and those of small mammals to the number of individual captures per 100 trap-days. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and *H. megacephalus*) (Fig. 3).

At the landscape-scale, the abundance of small mammals decreased with forest cover, while that of mesopredators increased, as well as the presence of apex-predators (Fig. 4). In the context of the framed SEM model, the presence of apex-predators was positively affected by forest cover (*std. estimate* = 0.50). Mesopredators abundance was also positively affected by forest cover (std. estimate = 0.62) but remained unaffected by the presence of apex-predators (Fig. 5). Small mammal abundance was negatively affected by forest cover (*std. estimate* = −0.52) and the effect of mesopredators was positive but relatively weak (std. estimate = 0.36). The indirect effect of forest cover as mediated by mesopredators on small mammals was also relatively weak (*std. estimate* = 0.22). Also in this context, the presence of apex-predators did not affect small mammal abundance (*std. estimate* = −0.078). The same can be stated for any direct effects of mesopredators (*std. estimate* = 0.33) (Table S4; Fig. 5). Results were similar considering species biomass for mesopredators and small mammals (Table S4), apart from small mammal biomass which was unaffected by forest cover (Fig. S2).

4. Discussion

Local extinctions of apex predators are widely reported to inflate populations at lower trophic levels (Estes et al., 2011; Terborgh, 2015). Such top-down forces are considered by many as prevalent in modulating species diversity in natural ecosystems (Terborgh and Estes, 2013; Prugh et al., 2009), including insular tropical forest fragments (Terborgh et al., 2001). In the central Amazonian Balbina insular landscape, we observed that as landscape-scale forest cover decreased, the abundance of mesopredators decreased, while that of small mammals increased. However, any augmented small mammal populations resulted directly from negative forest cover effects, rather than indirectly via any tropic cascade such as mesopredator release.

Island area plays a primary role in modulating most vertebrate assemblages persisting in the Balbina insular landscape (Palmeirim et al., 2022), which is consistent with insular fragmented landscapes elsewhere (Jones et al., 2016). Typically, important limiting factors for species population sizes and colonization rates are the habitat area and degree of isolation (MacArthur and Wilson, 1967), or the amount of habitat cover (Fahrig, 2003). These factors increase the incidence of apex-predators as well as the number of mesopredator species at sites with higher forest cover (Benchimol and Peres, 2015a). Consequently, more mesopredators species translates into higher mesopredator abundance and biomass. A positive abundance-area relationship has been similarly observed for the remaining mid-sized to large vertebrate species occurring in Balbina (Benchimol and Peres, 2021). It is also possible
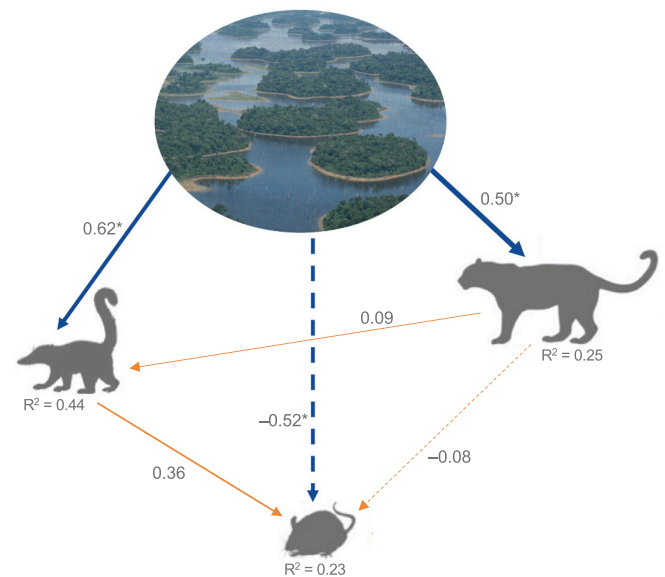

Fig. 5. SEMs denoting the effects of forest cover on apex-predator incidence, mesopredators abundance and small mammal abundance (blue arrows), and the inter-trophic relationships between each trophic group (orange arrows). For each relationship, we indicate the standardized coefficients (with asterisks indicating significant relationships: $P < 0.05$), and the coefficient of determination (R^2) for each response variable. Positive and negative pathways are represented by continuous and dashed lines, respectively, in which line thickness is scaled to illustrate the relative strength of the effects. Each trophic group and forest cover is represented by the same icon as in Fig. 1. This model met the piecewise SEM assumptions (*Fisher's C* = 3.847 with *P* = 0.986 and on 12 degrees of freedom). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that any joint effects of insularity and isolation may impose additional "fence effects", limiting dispersal and somehow also contributing to higher abundances (and biomass) at more isolated islands (Adler et al., 1986). Contrary to our expectations, however, mesopredator abundance was not negatively affected by apex predator incidence. This agrees with Pires et al. (2022), showing that terrestrial mammal predator-prey interaction networks across several Balbina islands are less prone to occur due to the low abundance of mammal species. Top-down regulation in this fraction of the foodweb may thus be relaxed, particularly on small islands.

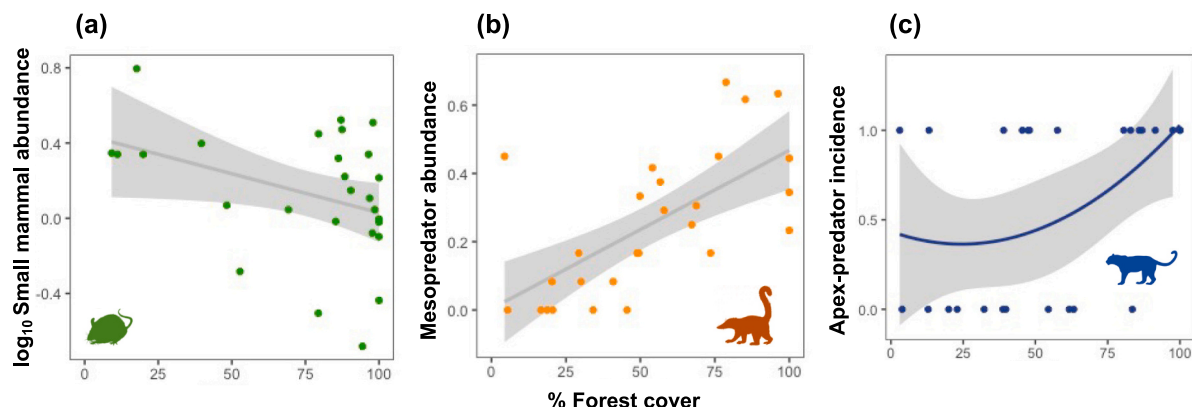The abundance and biomass of small mammal assemblages were

Fig. 4. Relationship between forest cover (%) and (a) small mammal abundance ($\log_{10} x$), (b) mesopredator abundance and (c) apex-predator incidence. Mesopredator abundances have been standardized as the number of camera-trap records per 10 camera trap-days; small mammal abundances were standardized as the number of individuals per 100 trap-days. For each group, forest cover was analysed considering its 'best' scale of effect, which was represented by 200 m, 1000 m, and 800 m radial buffers for small mammals, mesopredators and apex-predators, respectively. Lines represent the model adjusted for each relationship ($P < 0.05$), and shaded areas indicate the 95 % confidence region.

better explained by the overall habitat amount (cf. Fahrig, 2003). Forest cover further had a negative effect on small mammal abundance, which was not observed considering species biomass. The reduced subset of small mammal species persisting at the Balbina archipelago is comprised of matrix-tolerant species that can traverse the aquatic matrix (Palmeirim et al., 2018), and are, somewhat surprisingly, comparatively smaller bodied (Palmeirim et al., 2021a). This contributes to explaining the increase in small mammal numerical abundance, but not the aggregate biomass.

Small mammals have also been reported to increase in population abundance in other fragmented tropical forest landscapes (Glanz, 1990), including those in Amazonia (Malcolm, 1991; Palmeirim et al., 2020) and analogous insular fragments (Moore et al., 2022). In other cases, species abundances remained stable (Santos-Filho et al., 2012), with different species showing opposing trends (Pardini, 2004). At Balbina, while species-specific small mammal abundance was highly variable, sites surrounded by less extensive forest cover were consistently characterised by higher small mammal abundance (see Fig. 4a). Yet, our SEM approach showed that such increase in abundance was not due to indirect fragmentation effects through mesopredator release. This is contrary to our initial expectations given the overall importance of top-down mechanisms regulating species diversity (e.g., da Fonseca and Robinson, 1990; Colman et al., 2014). For instance, defaunation of medium to large mammals was linked to an increase in small mammal species diversity in a biome-wide analysis across the Brazilian Atlantic Forest (Bovendorp et al., 2019). The observed increase in abundance in this study was instead apparently directly driven by a decrease in landscape-scale forest cover. Generally, smaller forest islands, or landscapes with lower forest cover, are characterised by greater habitat degradation, likely mediated by intense edge effects (Benchimol and Peres, 2015c). It is therefore possible that small mammals are alternatively taking advantage of enlarged trophic and structural resource availability in less forested landscapes, which are also characterised by a higher degree of habitat degradation. Elsewhere in the Amazon, several small mammal species have been observed to respond positively to disturbed and edge-dominated habitats (Malcolm, 1991; Lambert et al., 2006). Moreover, small mammals that have somehow persisted at species-poor sites may undergo some level of density compensation, thereby further boosting their local abundance.

Notwithstanding, augmented small mammal populations in the absence or lower abundance of mesopredators could be limited by local carrying capacity. This may be related to the overall low forest habitat productivity in Balbina. Most small mammals in this study are largely herbivores, and primarily consume fruits, invertebrates, seeds, and small vertebrates, in this order of importance (Jones et al., 2009). Fruit availability at our Balbina sites, where the forest matrix is restricted to non-flooded *terra firme* forest, is almost certainly very seasonal, and thus unlikely to sustain large populations of small mammals, thereby precluding them from increasing in abundance (or biomass) even in the absence of their predators. Indeed, seasonality in mature fruit and seed production in this forest type has been reported elsewhere in Amazonian sites (Haugaasen and Peres, 2005), limiting vertebrate frugivore/granivore abundance therein (Haugaasen and Peres, 2007). Such bottom-up environmental limitations can also explain why the nest density of leaf-cutting ants failed to increase on small predator-free forest islands (Palmeirim et al., 2021b). Moreover, top-down control has been shown to be at best weak for mammal predator-prey interactions (Pires et al., 2022). In contrast, Terborgh et al. (2001) report hyperabundance of multiple herbivore taxa on forest islands at Lago Guri, Venezuela, which was attributed to release from predation. However, the semi-deciduous dry vegetation of Lago Guri (Terborgh et al., 2001) is typically subject to much higher levels of herbivory than our wet forest sites (Coley et al., 1985), eventually releasing herbivore guilds to hyper-abundance on predator-free islands.

Moreover, given the apparent lack of any predator effects on small mammal biomass, we likely failed to account for small mammal

morphological responses to any release from predation on small islands in this study. In contrast, rodents on reservoir islands in China rapidly became larger-bodied following habitat insularization, likely due to release from predation pressure (Li et al., 2021). On those same reservoir islands, habitat loss initially removed rodent predators, which then released rodent populations indicating top-down regulation, whereas bottom-up mechanisms on small islands precluded the increase in rodent abundance (Wang et al., 2020). In addition, given the expected high seasonality in mature fruit production at Balbina, it is possible that the likely seasonal resource-pulse further interacts with both bottom-up and top-down forces (Greenville et al., 2014), which could only be assessed by year-round monitoring of both mammals and their resources. Notwithstanding, it is possible that some of the predation effects may be expressed behaviourally rather than in demographic terms (Gallagher et al., 2017). Although we have provided insights on the extent to which small mammal responses to habitat fragmentation are mediated by their mammalian predators, we recommend that further studies should account for the temporal dimension to fully understand prey-predators dynamics (Estes et al., 2011).

4.1. Conservation implications

Our findings did not support the notion of predator-free Amazonian forest islands decaying to an 'ecological meltdown', which is characterised by rapid collapse of baseline ecosystem functioning induced by hyperabundance of certain guilds (herbivores: Terborgh et al., 2001, rodents: Moore et al., 2022). If ongoing processes at Balbina islands can be defined as an 'ecological meltdown', this would more likely be due to the severity of edge effects that increasingly degrade the vegetation structure of insular forests (Benchimol and Peres, 2015c). As such, the extinction debt that insular forest fragments continue to pay overtime may take longer at Balbina than at either the Guri Lake of Venezuela (Terborgh et al., 2001) or the Chiew Larn Reservoir of Thailand (Moore et al., 2022). Yet, the apparent strength of ongoing bottom-up mechanisms can further render these forest islands more susceptible to other major disturbances (Wang et al., 2020), such as wildfires and logging. Future hydroelectric dam blueprints across lowland tropical forests must therefore consider that newly created insular landscapes can only sustain reduced levels of biodiversity (Jones et al., 2016). Preserving vast expanses of continuous primary forests thus appears to be the best strategy to maintain the integrity of vertebrate assemblages, including both their apex-predators and mesopredators, and the ecosystem functions that they may exert.

Ethical approval

Author statement

The corresponding author confirms on behalf of all authors that during the preparation of this work the authors did not use any AI tool.

CRediT authorship contribution statement

Ana Filipa Palmeirim: Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Maíra Benchimol:** Writing – review & editing, Data curation. **Marcus V. Vieira:** Writing – review & editing, Supervision. **Carlos A. Peres:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated

Data availability

The data supporting the findings of this study are openly available in the supplementary materials of previous publications and will be additionally made available in the Dryad Digital Repository.

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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.2024.110594.

References

Adler, G.H., Levins, R., 1994. The island syndrome in rodent populations. Q. Rev. Biol. 69, 473–490.

Adler, G.H., Wilson, M.L., Derosa, M.J., 1986. Influence of island area and isolation on population characteristics of Peromyscus leucopus. J. Mammal. 67, 406–409.

Benchimol, M., Peres, C.A., 2015a. Widespread forest vertebrate extinctions induced by a mega hydroelectric dam in lowland Amazonia. PloS One 10, e0129818.

Benchimol, M., Peres, C.A., 2015b. Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. Biol. Conserv. 187, 61–72.

Benchimol, M., Peres, C.A., 2015c. Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. J. Ecol. 103, 408–420.

Benchimol, M., Peres, C.A., 2021. Determinants of population persistence and abundance of terrestrial and arboreal vertebrates stranded in tropical forest land-bridge islands. Conserv. Biol. 35, 870–883.

Bovendorp, R.S., Brum, F.T., McCleery, R.A., Baiser, B., Loyola, R., Cianciaruso, M.V., Galetti, M., 2019. Defaunation and fragmentation erode small mammal diversity dimensions in tropical forests. Ecography 42, 23–35.

Bueno, A.S., Peres, C.A., 2019. Patch-scale biodiversity retention in fragmented landscapes: reconciling the habitat amount hypothesis with the island biogeography theory. J. Biogeogr. 46, 621–632.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Inference: A Practical Information-theoretic Approach, 2nd edition. Springer-Verlag, New York, USA.

Carbone, C., Gittleman, J.L., 2002. A common rule for the scaling of carnivore density. Science 295, 2273–2276.

Coley, P.D., Bryant, J.P., Chapin III, F.S., 1985. Resource availability and plant antiherbivore defense. Science 230, 895–899.

Colman, N.J., Gordon, C.E., Crowther, M.S., Letnic, M., 2014. Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. Proc. R. Soc. B Biol. Sci. 281, 20133094.

Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563–566.

da Fonseca, G.A., Robinson, J.G., 1990. Forest size and structure: competitive and predatory effects on small mammal communities. Biol. Conserv. 53, 265–294.

Delignette-Muller, M.L., Dutang, C., 2015. fitdistrplus: an R package for fitting distributions. J. Stat. Softw. 64, 1–34.

Diamond, J., 2001. Damned experiments! Science 294, 1847–1848.

Dyer, L.A., Letourneau, D., 2003. Top-down and bottom-up diversity cascades in detrital vs. living food webs. Ecol. Lett. 6, 60–68.

ESRI, 2018. ArcMap 10.1. Environmental Systems Research Institute Inc., Redlands, CA, USA.

Estes, J.A., 1996. Predators and ecosystem management. Wildl. Soc. Bull. 24, 390–396.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Wardle, D. A., 2011. Trophic downgrading of planet Earth. Science 333, 301–306.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. J. Biogeogr. 40, 1649–1663.

Fearnside, P.M., 1989. Brazil's Balbina Dam: environment versus the legacy of the pharaohs in Amazonia. Environ. Manag. 13, 401–423.

Gallagher, A.J., Creel, S., Wilson, R.P., Cooke, S.J., 2017. Energy landscapes and the landscape of fear. Trends Ecol. Evol. 32, 88–96.

Gibson, L., Lynam, A.J., Bradshaw, C.J., He, F., Bickford, D.P., Woodruff, D.S., Bumrungsri, S., Laurance, W.F., 2013. Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. Science 341, 1508–1510.

Glanz, W.E., 1990. Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama. Four Neotropical Rainforests 287–313.

Greenville, A.C., Wardle, G.M., Tamayo, B., Dickman, C.R., 2014. Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. Oecologia 175, 1349–1358.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052.

Hagen, M., Kissling, W.D., Rasmussen, C., De Aguiar, M.A., Brown, L.E., Carstensen, D. W., Olesen, J.M., 2012. Biodiversity, species interactions and ecological networks in a fragmented world. Adv. Ecol. Res. 46, 89–210.

Hanna, E., Cardillo, M., 2014. Island mammal extinctions are determined by interactive effects of life history, island biogeography and mesopredator suppression. Glob. Ecol. Biogeogr. 23, 395–404.

Haugaasen, T., Peres, C.A., 2005. Tree phenology in adjacent Amazonian flooded and unflooded forests 1. Biotropica 37, 620–630.

Haugaasen, T., Peres, C.A., 2007. Vertebrate responses to fruit production in Amazonian flooded and unflooded forests. Biodivers. Conserv. 16, 4165–4190.

IBAMA, 1997. Plano de Manejo Fase I: Reserva Biológica do Uatumã. Eletronorte/ IBAMA. Brasília/DF/Brazil. Retrieved from. http://www.icmbio.gov.br.

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob. Ecol. Biogeogr. 24, 52–63.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Purvis, A., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: ecological archives E090-184. Ecology 90, 2648.

Jones, I.L., Bunnefeld, N., Jump, A.S., Peres, C.A., Dent, D.H., 2016. Extinction debt on reservoir land-bridge islands. Biol. Conserv. 199, 75–83.

Jones, I.L., Saldanha Bueno, A., Benchimol, M., Palmeirim, A.F., Storck-Tonon, D., Peres, C.A., 2021. Using relict species-area relationships to estimate the conservation value of reservoir islands to improve environmental impact assessments of dams. In: Matthews, T.J., Triantis, K.A., Whittaker, R.J. (Eds.), The Species-Area Relationship: Theory and Application. Ecology, Biodiversity and Conservation. Cambridge Univ. Press, 2021, pp. 417–437.

Kruess, A., Tscharntke, T., 1994. Habitat fragmentation, species loss, and biological control. Science 264, 1581–1584.

Lambert, T.D., Malcolm, J.R., Zimmerman, B.L., 2005. Variation in small mammal species richness by trap height and trap type in southeastern Amazonia. J. Mammal. 86, 982–990.

Lambert, T.D., Malcolm, J.R., Zimmerman, B.L., 2006. Amazonian small mammal abundances in relation to habitat structure and resource abundance. J. Mammal. 87, 766–776.

Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579.

Lefcheck, J., Byrnes, J., Grace, J., 2016. Package 'piecewiseSEM'. R package version, 1.

Li, J., Dirzo, R., Wang, Y., Zeng, D., Liu, J., Ren, P., Ding, P., 2021. Rapid morphological change in a small mammal species after habitat fragmentation over the past half-century. Divers. Distrib. 27, 2615–2628.

Louthan, A.M., Doak, D.F., Angert, A.L., 2015. Where and when do species interactions set range limits? Trends Ecol. Evol. 30, 780–792.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Press Princeton, USA.

Malcolm, J.R., 1991. The Small Mammals of Amazonian Forest Fragments: Pattern and Process. PhD dissertation,. Department of Zoology, Gainesville, Florida, USA.

McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Retrieved from. http://www.umass.edu/landeco/research/fragstats/fragstats.html. (Accessed 5 June 2017).

Moore, J.H., Palmeirim, A.F., Peres, C.A., Ngoprasert, D., Gibson, L., 2022. Invasive rat drives complete collapse of native small mammal communities in insular forest fragments. Curr. Biol. 32, 2997–3004.

Paglia, A.P., Da Fonseca, G.A., Rylands, A.B., Herrmann, G., Aguiar, L.M., Chiarello, A. G., Patton, J.L., 2012. Lista Anotada dos Mamíferos do Brasil 2a Edição/annotated checklist of brazilian mammals. Occas. Pap. Conserv. Biol. 6, 1–82.

Palmeirim, A.F., Benchimol, M., Vieira, M.V., Peres, C.A., 2018. Small mammal responses to Amazonian forest islands are modulated by their forest dependence. Oecologia 187, 191–204.

Palmeirim, A.F., Benchimol, M., Peres, C.A., Vieira, M.V., 2019. Moving forward on the sampling efficiency of neotropical small mammals: insights from pitfall and camera trapping over traditional live trapping. Mamm. Res. 64, 445–454.

Palmeirim, A.F., Farneda, F.Z., Vieira, M.V., Peres, C.A., 2021a. Forest area predicts all dimensions of small mammal and lizard diversity in Amazonian insular forest fragments. Landsc. Ecol. 36, 3401–3418.

Palmeirim, A.F., Benchimol, M., Leal, I.R., Peres, C.A., 2021b. Drivers of leafcutter ant populations and their inter-trophic relationships in Amazonian forest islands. Ecosphere 12, e03518.

Palmeirim, A.F., Emer, C., Benchimol, M., Storck-Tonon, D., Bueno, A.S., Peres, C.A., 2022. Emergent properties of species-habitat networks in an insular forest landscape. Sci. Adv. 8, eabm0397.

Palmeirim, A.F., Santos-Filho, M., Peres, C.A., 2020. Marked decline in forest-dependent small mammals following habitat loss and fragmentation in an Amazonian deforestation frontier. PLoS One 15, e0230209.

Pardini, R., 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. Biodivers. Conserv. 13, 2567–2586.

Patton, J.L., Da Silva, M.N.F., Malcolm, J.R., 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. Bull. Am. Mus. Nat. Hist. 2000, 1–306.

Pires, M.M., Benchimol, M., Cruz, L.R., Peres, C.A., 2022. Terrestrial food web complexity in Amazonian forests decays with habitat loss. Curr. Biol. https://doi.org/10.1016/j.cub.2022.11.066.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., Brashares, J.S., 2009. The rise of the mesopredator. Bioscience 59, 779–791.

R Development Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051- 07-0.

Rocha-Santos, L., Pessoa, M.S., Cassano, C.R., Talora, D.C., Orihuela, R.L., Mariano-Neto, E., Cazetta, E., 2016. The shrinkage of a forest: landscape-scale deforestation leading to overall changes in local forest structure. Biol. Conserv. 196, 1–9.

Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence–absence data or point counts. Ecology 84, 777–790.

Sala, O.E., Stuart Chapin, F.I.I.I., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Santos-Filho, M., Peres, C.A., Da Silva, D.J., Sanaiotti, T.M., 2012. Habitat patch and matrix effects on small-mammal persistence in Amazonian forest fragments. Biodivers. Conserv. 21, 1127–1147.

Shipley, B., 2000. A new inferential test for path models based on directed acyclic graphs. Struct. Equ. Model. 7, 206–218.

Sikes, R.S, 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J. Mammal. 97, 663–688. Animal Care, Use Committee of the American Society of Mammalogists.

Terborgh, J.W., 2015. Toward a trophic theory of species diversity. Proc. Natl. Acad. Sci. 112, 11415–11422.

Terborgh, J., Estes, J.A. (Eds.), 2013. Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. Island press.

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., et al., 2001. Ecological meltdown in predator-free forest fragments. Science 294, 1923–1926.

Terborgh, J., Feeley, K., Silman, M., Nuñez, P., Balukjian, B., 2006. Vegetation dynamics of predator-free land-bridge islands. J. Ecol. 94, 253–263.

Wang, R., Zhang, X., Shi, Y.S., Li, Y.Y., Wu, J., He, F., Chen, X.Y., 2020. Habitat fragmentation changes top-down and bottom-up controls of food webs. Ecology 101, e03062.