Drivers of leafcutter ant populations and their inter-trophic relationships in Amazonian forest islands

ANA FILIPA PALMEIRIM [ID],[1,]† MAÍRA BENCHIMOL [ID],[2] INARA R. LEAL,[3] AND CARLOS A. PERES [ID][1,4]

[1]*School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ UK*
[2]*Laboratório de Ecologia Aplicada à Conservação, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado km 16, Ilhéus, BA CEP 45662-900 Brazil*
[3]*Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego, s/ no, Recife, PE CEP 50670-901 Brazil*
[4]*Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil*

Abstract. Under habitat loss and fragmentation, the intensity of local ecological processes involving species interactions changes pervasively, accelerating local species extinctions, and disrupting essential ecosystem functions. We addressed this issue by examining the direct population drivers of apex predators (five felid species), armadillo mesopredators, leafcutter ants (*Atta sexdens* and *Atta cephalotes*), and the indirect effects mediated by their inter-trophic relationships in a ~25-yr-old land-bridge island system formed by a hydroelectric dam in the Central Amazon. These trophic groups and pioneer tree abundance were surveyed across 34 variable-sized islands and three continuous forest sites. Leafcutter populations were characterized in relation to their occurrence, colony density, and proportion of inactive colonies, and for each leafcutter response, we considered the direct and/or indirect effects of forest area on each trophic group. Leafcutter occupancy was best explained by the direct model, colony density by either the direct or the indirect model, and proportion of inactive colonies by an indirect model via the effects of pioneer tree abundance. The direct forest area effects were positive for apex predators and leafcutter occupancy, but negative for armadillos and pioneer trees. Yet leafcutter colony density declined in increasingly larger forest areas. The absence or low abundance of apex predators on small islands released armadillo hyper-abundance, which contrary to expectation from top-down control, covaried positively with leafcutter colony density. Finally, the indirect model showed that leafcutter colonies were more active under higher pioneer tree abundances. That leafcutter density increases on smaller islands whenever present is likely attributed to the hyper-abundance of pioneer plants and canopy gaps. Although apex predators apparently suppressed armadillos, the remaining fraction of the food web seems to be controlled by bottom-up mechanisms most likely related the overall low foliage palatability typical of wet evergreen forests. Our findings can be used to inform the long-term viability of forest ecosystems affected by hydropower development in lowland Amazonia.

Key words: bottom-up forces; evergreen forest; habitat loss and fragmentation; herbivorous insects; island systems; top-down forces; trophic cascades; tropical forest.

† **E-mail:** anafilipapalmeirim@gmail.com

INTRODUCTION

Under habitat loss and fragmentation—typically involving reduced habitat area, increased isolation, and edge effects (Fahrig 2003, Ewers and Didham 2007)—the intensity of local ecological processes concerning species interactions changes pervasively, accelerating local species extinctions, and disrupting essential ecosystem functions (Crooks and Soulé 1999, Tylianakis

et al. 2008). Understanding the mechanisms driving species responses across food webs has become imperative given the escalating pace of ecosystem alterations in the Anthropocene (Tylianakis et al. 2008, Estes et al. 2011, Terborgh 2015).

In fragmented landscapes, top-predators, due to their low population densities and large spatial requirements (Carbone and Gittleman 2002), are highly susceptible to local extinctions (Lomolino et al. 1989, Woodroffe and Ginsberg 1998). In their absence, top-down forces become more relaxed (Hairston et al. 1960, Estes 1996) and intermediate trophic levels, such as mesopredators, are released into higher abundances (Crooks and Soulé 1999). As habitat conditions further deteriorate, all large predators may eventually be extirpated from forest remnants, triggering first-order consumers (e.g., herbivorous insects and rodents) to proliferate, which may lead to the population collapse of the lowest levels of the food web (Adler and Levins 1994, Terborgh et al. 2006), culminating in a top-down trophic cascade (Estes et al. 2011). Alternatively, in resource-limited environments, intraguild species interactions may be more intense, so that competition (e.g., for prey or nesting sites) negates their release from predators (Gruner 2004). In this case, the effects of resource depletion often promote a bottom-up cascade in which lower trophic levels propagate upward to nonadjacent higher levels (Hunter and Price 1992, Kagata and Ohgushi 2006). Disentangling the strengths of either of these top-down or bottom-up forces in driving species responses under habitat loss and fragmentation is therefore required to inform appropriate landscape management (Wright et al. 1994, Patten and Bolger 2003). Yet, despite the vast literature on the relative importance of bottom-up vs top-down forces (Hunter and Price 1992, Walker and Jones 2001), only a few studies have investigated these mechanisms in fragmented tropical forest ecosystems (but see Morante-Filho et al. 2016, 2018, Hernández-Ruedas et al. 2018, Wang et al. 2020).

In disturbed Neotropical forest habitats, colony density of the herbivorous leafcutter ants, *Atta* spp. (hereafter, leafcutters; Weber 1972, Fowler et al. 1989) typically increases (Leal et al. 2014). Such proliferation is due to the relaxation of either top-down forces, due to the lack of

predators, mostly armadillo species (Rao 2000, Terborgh et al. 2001), and leafcutter parasitoids (Almeida et al. 2008). Alternatively, bottom-up mechanisms, given the newly augmented pioneer tree abundance (Falcão et al. 2011; i.e., leafcutters' preferred trophic resource: Wirth et al. 2003) or canopy gaps, favor the availability of leafcutter nesting sites (Vasconcelos 1990, Vieira-Neto and Vasconcelos 2010). Under such novel conditions, leafcutters negatively affect the structure and composition of local tree assemblages (Leal et al. 2014), either due to direct landscaping effects from nesting (Corrêa et al. 2010, Meyer et al. 2013) or herbivory (Rao et al. 2001, Terborgh et al. 2006, Urbas et al. 2007). Indeed, these fungus-growing ants can remove biomass from 50% of all plant species in the colony's foraging area, including 15% of the standing leaf crop each year (Wirth et al. 2003).

Here we investigated the relative strength of top-down vs bottom-up forces driving apex predator, mesopredator, and leafcutter populations. To do so, we considered a tetra-trophic system comprised of the abundance of apex predators (felid species), mesopredators (dasypodid armadillo species), leafcutter ants (*Atta sexdens* and *Atta cephalotes*: Vasconcelos 1988, Nogueira 2009), and the basal area density of adult pioneer trees, all of which were surveyed within 34 forest islands and three continuous forest sites within an archipelagic landscape. In particular, leafcutters were alternately examined considering their site occupancy (presence/absence), colony density, and degree of activity (proportion of inactive colonies). We then used a network approach to examine the relative strength and sign of both direct and indirect effects of fragmentation-related metrics, further hypothesizing three alternative operational models (Fig. 1). The strengths of top-down or bottom-up mechanisms are indicated by either predator-mediated indirect effects, or both direct habitat effects and the indirect effects mediated by foliage resource availability provided by pioneer trees. With more intensive levels of habitat modification, we expect declines in apex predator abundance to result in higher armadillo abundances, which in turn should exert stronger top-down negative control of leafcutter colonies (Rao 2000, Terborgh et al. 2001; Hypothesis 1). Alternatively, if bottom-up forces are dominant,
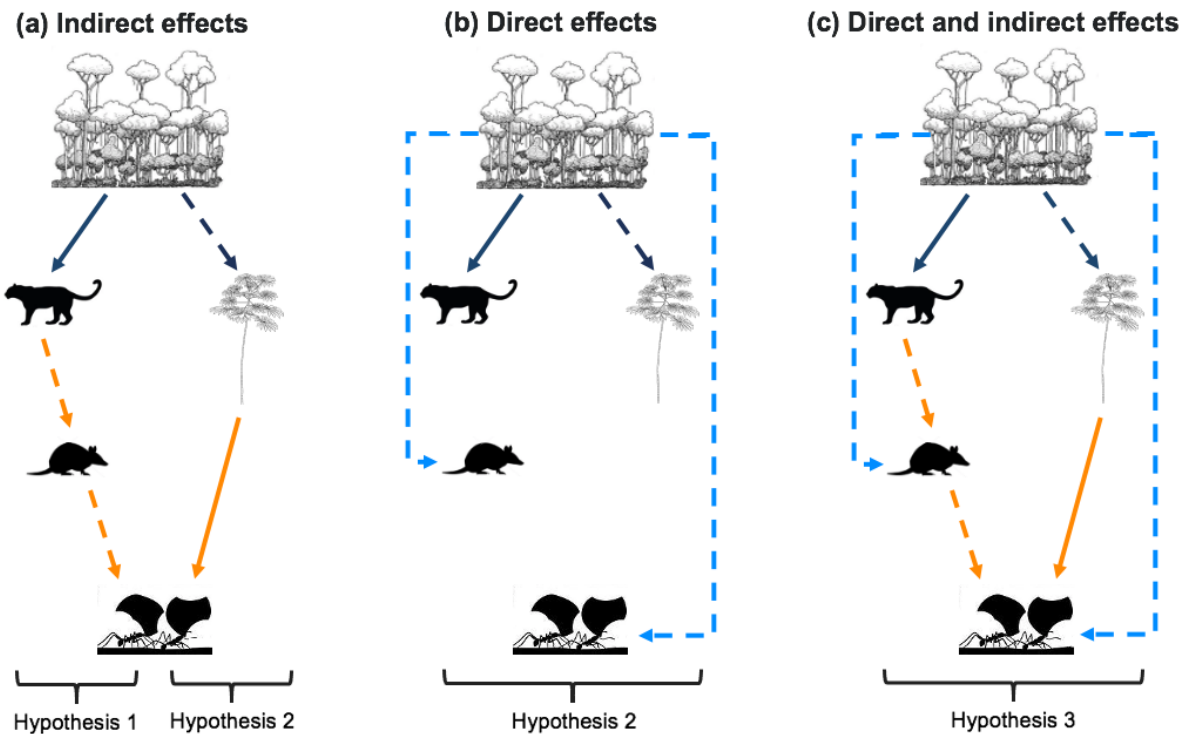
Fig. 1. Three alternative models explaining apex predator, mesopredator, and leafcutter ant population metrics at the Balbina archipelagic landscape: (a) indirect effects of habitat fragmentation-related metrics (forest area, isolation, and fire severity), (b) direct effects, and (c) both direct and indirect effects. Dark blue arrows represent the direct effects of forest area on apex predators and pioneer trees. Yellow arrows represent the indirect area effects on leafcutter ants, via both apex predators and mesopredators (Hypothesis 1) or via pioneer trees (Hypothesis 2). Light blue arrows represent the direct effects of forest area on mesopredators and leafcutter ants (Hypothesis 2). Hypothesis 3 corresponds to a combination of Hypotheses 1 and 2 and is represented in (c). Positive and negative hypothesized pathways are represented by continuous and dashed lines, respectively. In each model, we indicate the hypothesis supporting each pathway (see main text for a detailed description of each hypothesis).

we expect leafcutter colonies to benefit from smaller forest sites, which are characterized by stronger edge effects and hyper-abundance of pioneer trees (Benchimol and Peres 2015*a*; Hypothesis 2). In addition, if both top-down and bottom-up forces operate concomitantly, leafcutters are expected to be negatively affected by increased mesopredator abundance and positively affected by reduced forest area or higher pioneer tree availability (Wirth et al. 2007; Hypothesis 3). We also investigated how leafcutters use both insular and continuous forest habitat across a wide gradient of habitat degradation and landscape contexts in the Central Amazon. Given their typically positive responses to human-induced disturbance (Leal et al. 2014), we expected higher densities of leafcutter colonies at degraded forest sites, such as forest edges and small forest islands. We further discussed our results in light of local phytophysiognomic context—wet evergreen forest—against a backdrop of those reported from a dry semi-deciduous forest island system (Rao 2000, Terborgh et al. 2001).

MATERIAL AND METHODS

Study area

This study was carried out in 34 forest islands and three mainland continuous forest (CF) sites in the Balbina Hydroelectric Landscape (1°48′ S, 59°29′ W; Fig. 2), located in the central Brazilian

Amazon. The Balbina Dam was built in 1986 downstream of terrains of undulating topography along the Uatumã River, a left bank tributary of the Amazon River. This dam created a vast 443,772-ha reservoir, where 312,900 ha of primary forest were inundated and the former hilltops were converted into 3546 land-bridge islands (FUNCATE/INPE/ANEEL 2000). As a compensatory policy, part of the reservoir and a large continuous forest area on the left bank of the Uatumã River were legally protected in 1990 by the 942,786-ha Uatumã Biological Reserve, Brazil's largest protected area in this category. Selected forest islands within the reservoir were never connected to any other landmass and have not been subject to logging nor hunting, but many islands experienced understory fires during the El Niño drought of late-1997 to early-1998 (Benchimol and Peres 2015*a*). Mean annual temperature and rainfall in this region are 28°C and 2376 mm, respectively. Islands and the neighboring continuous forest sites consist of dense closed-canopy evergreen upland (terra firme) forest on predominantly oxisol and podzolic soils characterized by low fertility (IBAMA 1997).

We pre-selected 34 forest islands according to their size, degree of isolation, and spatial distribution, so that a wide spectrum of island configurations could be sampled across the entire reservoir. Surveyed islands were at least 1 km apart from one another, with island size ranging from 0.55 to 1685 ha (mean ± SD: 227 ± 396 ha; Appendix S1: Table S1) and isolation distances to the nearest mainland varying from 44 to 13,217 m (4562 ± 3969 m); CF sites were widely distributed throughout the reservoir and placed between 200 and 1500 m from the nearest lake margin (Fig. 2). Sampling was carried out between June 2011 and December 2012, under research permit No. 12344-1 issued by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/MMA).

Predator surveys

Data on apex predator and mesopredator species abundance were extracted from camera-trapping surveys on the entire medium- to large-bodied vertebrate fauna (Benchimol and Peres 2015*b*). To do so, Reconyx HC500 Hyperfire digital camera traps were used over a 30-d period
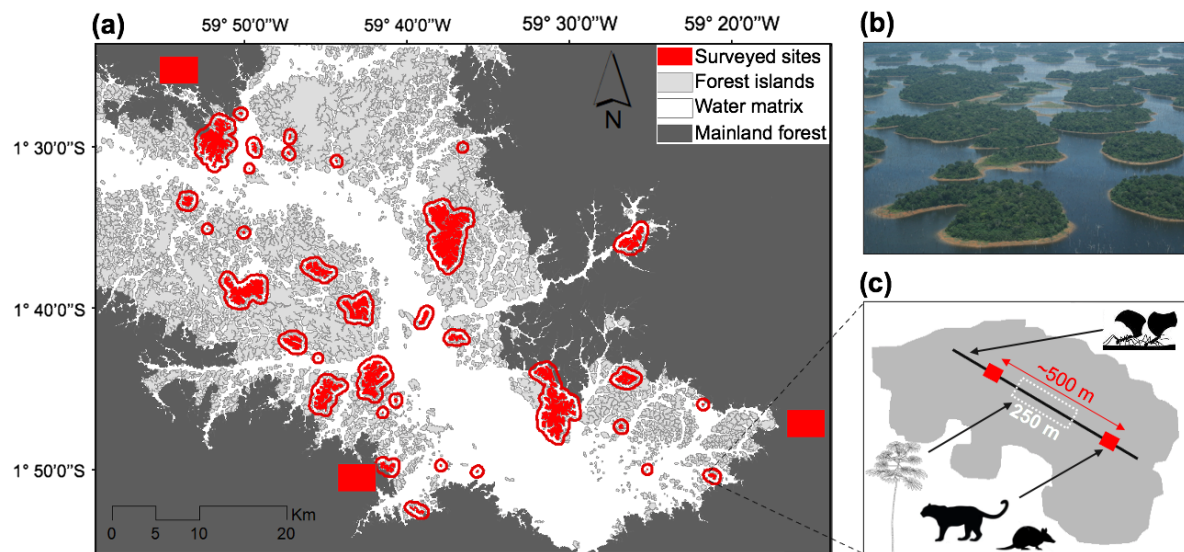

Fig. 2. (a) Surveyed forest sites within the Balbina Hydroelectric Dam Landscape in central Brazilian Amazonia: 34 islands (in red and highlighted by a 500 m buffer) and three continuous forest sites (indicated by red rectangles). (b) Aerial view of the Balbina forest archipelago (photo credit: E. M. Venticinque) including the open-water matrix. (c) Sampling design used at each survey site: transects surveying leafcutter ants, camera-trapping to survey apex predators and mesopredators and vegetation plots to inventory pioneer trees; vegetation plot size and distance between camera traps are indicated in the figure.

during each of two consecutive years. 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, see Appendix S1: 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 five photograph sequence of each animal recorded, using 15-s 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 on the basis of natural marks (see details in Benchimol and Peres 2015b). As apex predators, we considered the following native hypercarnivores, all of which felids: *Leopardus pardalis* ($N = 170$ records, 24 sites), *Puma concolor* ($N = 95$, 18 sites), *Panthera onca* ($N = 29$, 14 sites), *Leopardus wiedii* ($N = 19$, 9 sites), and *Puma yagauroundi* ($N = 8$, 6 sites); and, as mesopredators, the two dasypodid (armadillo) species: *Dasypus novemcinctus* ($N = 799$, 37 sites) and *Dasypus kappleri* ($N = 28$, 6 sites). Apex predator and mesopredator abundance per site are defined as the sum of independent records from those species obtained across all camera traps at that site. Prior to analysis, predator abundance was standardized (per 319 trap nights) according to sampling effort considering the average effort per site. As the number of records was used as a proxy of predator abundance, we hereafter refer to such camera trap records as individuals to improve text flow.

Leafcutter ant surveys

Leafcutters were surveyed using line-transect censuses, in which two observers walked slowly (1 km/h) along an established transect and searched for all nests of leafcutter colonies located within 10 m on either side of the transect (Wirth et al. 2007). Our surveys were focused on adult colonies (i.e., colonies that have already reproduced which usually happens ~5 yr after colony establishment (Hölldobler and Wilson 1990), which are conspicuous and easily detected (Perfecto and Vandermeer 1993). Given the likely higher number of ants in adult colonies, those are also expected to have a proportionally higher impact on the ecosystem (Wetterer 1994). Each detected colony was classified as either active (i.e., with ants) or inactive (i.e., without ants). One to five variable-length transects were established within each island, according to island size and shape so that a representative island area could be covered. On each CF site, we established three parallel 4-km linear transects spaced apart by at least 1 km. A total of 81 transects were surveyed, ranging from 0.5 to 4.0 km in length (mean ± SD = 2.71 ± 3.32 km), amounting to an overall census area of 217 ha (Appendix S1: Table S1). At each sampling site, two species of leafcutters (*A. cephalotes* and *A. sexdens*: Vasconcelos 1988, Nogueira 2009) were characterized in terms of occurrence (presence/absence of active and inactive colonies), colony density (number of active and inactive colonies/ha), and proportion (%) of inactive colonies. Inactive colonies correspond to those that had either migrated, died, or were not foraging at the time of sampling. This provided additional information on the local leafcutter occupancy.

Pioneer tree inventory

Data on pioneer trees were obtained from floristic inventories carried out within 87 quarter-hectare vegetation plots located at varying distances from the forest edge (mean ± SD = 294 ± 507 m, range = 28–3169). On each island and CF site, we inventoried one to four 0.25-ha forest plots according to island size (Appendix S1: Table S1). Island plots were always spaced by ≥50 m from the nearest forest edge to avoid possible edge effects. All live trees ≥10 cm in diameter at breast height (DBH) within each plot were measured, tagged, and identified to species level by an expert botanist (for details on floristic surveys, see Benchimol and Peres 2015a). Based on 118 tree species classified as pioneers (Benchimol and Peres 2015a), we considered their basal area density (m^2/ha) in each plot, or the mean value among plots if more than one plot had been surveyed in the same site.

Landscape, patch, and habitat quality metrics

We considered a set of landscape, patch, and local metrics as indicators of the degree of forest habitat loss, isolation, and degradation of each surveyed site. At the landscape scale, we considered the Proximity index ($\log_{10} x$; McGarigal et al. 2012) and the linear distance to continuous forest ($\log_{10} x$). At the patch scale, we considered

island area ($\log_{10}$ x) and shape ($\log_{10}$ x), and degree of fire severity as a forest habitat quality metric. Fire severity was scored based on the extent to which each forest site had been affected by surface fires and the number of charred trees and height of char marks on each tree (Benchimol and Peres 2015*a*) (for a detailed explanation on each metric, see Appendix S1: Table S2). Because patch and landscape variables could not be readily obtained for continuous forest settings, we assigned their metrics to closely approximate real-world values (i.e., assuming zero isolation and area one order of magnitude larger than the largest island surveyed; see detailed explanation in Appendix S1: Table S2). Within each survey site, we further subdivided each line-transect used to survey leafcutter ant colonies into 100-m transect segments, which were further characterized in terms of the Euclidian distance between their centroids and the nearest forest edge.

Data analysis

We first examined the relationship between each trophic level—apex predators, mesopredators, leafcutters, and pioneer trees—and island size ($\log_{10}$ x), using generalized linear models (GLM) fitted with a Gaussian distribution, across all 37 survey sites. To streamline, hereafter we use forest area to refer to both island and CF sites. Prior to analysis, we scrutinized the distribution of each response variable, while apex predator abundance, mesopredator abundance, pioneer tree basal area density, and leafcutter colony density were $\log_{10}$-transformed. In subsequent analyses, explanatory variables were previously standardized ($x = 0$, $\sigma = 1$) to place coefficient estimates onto the same scale.

To account for any potential edge effect, we first analyzed patch and landscape characteristics of all sites where leafcutter colonies were detected. This analysis was carried out within leafcutter-occupied sites across 100-m transect segments. Of the 14 sites where leafcutters were detected, we excluded two small islands (André and Torém) in which only one 100-m transect segment was used to survey leafcutters, thereby precluding replication within those islands. We obtained 56 and 624 segments where colonies were either present or absent, respectively. To account for overinflated zeros in our sample within each surveyed site, we

restricted the number of segments where colonies were absent by randomly selecting three times as many zero segments as those where colonies were detected, except for three islands in which the number of occupied segments was higher than the number of unoccupied segments. We therefore selected 131 segments where colonies were missing (Appendix S1: Table S3). To examine the factors affecting colony habitat selection, we related the presence/absence data for all transect segments to a set of fragmentation-related variables including segment edge distance and, at the site-level, forest patch area and isolation, given by the proximity index and linear distance to continuous forest. Due to the high pairwise correlation between variables ($r < 0.75$), we retained only edge distance and proximity index. We then performed generalized linear mixed models (GLMMs) using a binomial distribution, while considering site identity as a random term to account for natural variability in site-scale environmental settings.

We then examined the direct and indirect habitat effects on leafcutter assemblages based on a tetra-trophic system using a structural equation modelling (SEM) technique. Structural equation modellings are characterized by paths representing hypothesized causal relationships between variables, which can appear as both predictors and responses (Shipley 2000). For this reason, SEMs are particularly useful in testing and quantifying indirect or cascading effects that could otherwise be overlooked by any single model (Grace et al. 2007). Here we used a piecewise SEM in which the path diagram is translated to a set of linear equations, which are evaluated individually, allowing analyses to be carried out for smaller sample sizes (Lefcheck 2016). We built three different SEMs representing each hypothetical scenario: direct, indirect, and both effects (Fig. 1). To do so, we compiled a list of structured equations, each of which consisted of one GLM relating one of the four trophic groups with a habitat variable and/or another trophic group, depending on whether the direct, indirect, or both effects were considered. However, in GLMs explaining apex predator abundance and pioneer tree basal area density (response variables), landscape, patch, and habitat quality metrics (explanatory variables) were consistently included regardless of the model (i.e., direct, indirect, or

both). Generalized linear models were fitted using a binomial distribution with a logit-link function (for leafcutter occurrence) or Gaussian distribution (all other cases). Each SEM was further alternately fitted with either one of the leafcutter metrics. All 37 sampling sites were included in the analysis considering leafcutter occurrence, whereas only a subset of 14 sites (where leafcutters were detected) were included in those analyses considering either colony density or proportion of inactive colonies. Structural equation modellings were carried out using the piecewiseSEM R package (Lefcheck et al. 2016).

To improve statistical inference given overall limitations in sample size, we opted to include only one habitat variable in each SEM at a time. In SEMs including leafcutter occurrence across all sites, forest area ensured a much higher explanatory power of each trophic group compared to those obtained when any of the other environmental variables were considered (i.e., proximity index, distance to continuous forest, shape, and fire severity; Appendix S1: Table S4). For simplicity, we present the results obtained considering only forest area. Moreover, as sample sizes were particularly limited for SEMs including either colony density or proportion of inactive colonies ($N = 14$), we analyzed the predator effects on leafcutter assemblages separately from the pioneer tree effects. To do so, we build two SEMs of three and two trophic levels, respectively, representing the direct, indirect, and both effects.

In piecewise SEM, the goodness-of-fit is assessed using Shipley's test of directed separation on whether or not there are any missing relationships among unconnected variables (Shipley 2000). The set of potential relationships among unconnected variables in the path diagram (i.e., conditional independence claims) constitutes the basis set. Shipley's test is conducted by combining all P values across the basis set into a test statistic, Fisher's C. Because the goodness-of-fitness cannot be assessed in a saturated model (i.e., without unconnected variables), in SEMs targeting the effect of pioneer trees on leafcutter colony density and proportion of inactive colonies, we added a second environmental variable. We therefore selected fire severity because it substantially affects pioneer tree abundance (Benchimol and Peres 2015*b*).

Fisher's C statistic can be further used to obtain an Akaike's information criterion value extended to small sample sizes (AIC_c; Shipley 2013). To evaluate model fitting, we ordered the three models (direct, indirect, and both) obtained for each of the leafcutter metrics according to their AICc. Models whose ΔAICc values are less than 3 are generally considered to have substantial support; models whose ΔAICc are between 3 and 7 are considered to present considerably less support; and those whose ΔAICc are >10 have essentially no support relative to the best model of the set (Burnham and Anderson 2010). All data analyses were performed in R (R Development Core Team 2017).

Results

Considering all apex predators, at least one felid species was recorded in 78% ($N = 29$) of all 37 survey sites ($N = 321$ records), exhibiting a maximum abundance per site of 19.1 individuals across multiple species (mean ± SD: 6.7 ± 5.8). Armadillos were ubiquitous across all sites ($N = 827$ records) at variable abundances averaging 29.4 ± 31.5 individuals (range = 2.7–178.1). The abundance of pioneer trees was also highly variable, with basal area densities per site ranging from 2.4 to 20.8 m^2/ha (8.8 ± 4.4 m^2/ha). Leafcutter colonies were absent from 23 islands, and a total of 84 colonies were detected on 11 islands and all three CF sites. The overall colony density per site was relatively low, ranging from 0 to 1.4 colonies/ha (0.15 ± 0.34 colonies/ha).

Apex predator abundance was increasingly higher in larger forest areas (Fig. 3a), but no changes were observed in armadillo mesopredator abundance (Fig. 3b) and, conversely, pioneer tree basal area density was higher on smaller islands (Fig. 3c). The leafcutter incidence probability increased toward larger forest areas (Fig. 3d). However, considering only those sites where leafcutters did occur ($N = 14$), colony density decreased with forest area (Fig. 3e), but no trend was observed considering the proportion of inactive colonies (Appendix S1: Table S5). On occupied sites, leafcutter colonies were more likely to be detected at 100-m transect segments near forest edges (β = −0.385, $P = 0.026$, Table 1), but this relationship was relatively weak (conditional $R^2 = 0.06$; Appendix S1: Fig. S1).
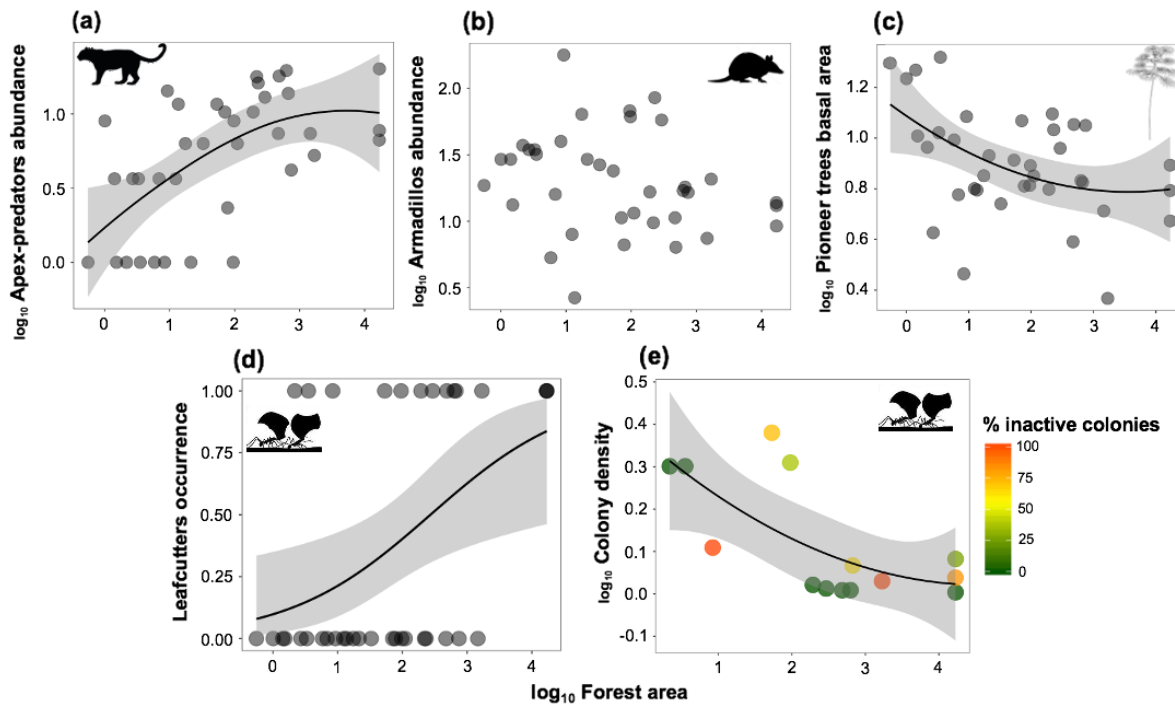
Fig. 3. Relationship between (a) standardized abundance of apex predators ($\log_{10}x$), (b) standardized abundance of mesopredators ($\log_{10}x$), (c) basal area density of pioneer trees (m^2/ha; $\log_{10}x$), and (d) occurrence of leafcutter ants (P/A of colonies) and forest area ($\log_{10}x$) across all 34 surveyed islands and three mainland continuous forest sites in the Balbina landscape. (e) Relationship between leafcutter colony density (number of colonies/ha; $\log_{10}x$) and forest area ($\log_{10}x$) considering only sites were leafcutters were detected ($N = 14$); circles are color-coded according to the proportion of inactive colonies. Lines indicate the model adjusted for the strongest relationships ($P < 0.05$), and shaded areas represent the 95% confidence region.

Considering leafcutter occurrence across all 34 forest sites, the direct model best fitted the data (lowest AIC$_c$), while the indirect model failed to meet the required SEM assumptions (Table 2). According to the direct model, as forest area increased, apex predator abundance increased ($\beta = 0.56$, $P = 0.003$), basal area density of pioneer trees decreased ($\beta = -0.43$, $P = 0.008$), and the occurrence probability of leafcutters increased ($\beta = 0.52$, $P = 0.016$; Fig. 4a).

Considering the effects of first- and second-order predation on leafcutter colony density within the range of leafcutter-occupied sites ($N = 14$), our data were best fitted by the direct model (AIC$_c$ = 90.37), and, to a lesser extent, by the indirect model (93.98; Table 2). In terms of the direct model, forest area positively affected apex predator abundance ($\beta = 0.69$, $P = 0.007$) but negatively affected armadillo abundance

Table 1. Generalized linear mixed model (GLMM) explaining leafcutters colony incidence (presence/absence) at 100-m transect segments distributed across 12 surveyed sites where leafcutters have been detected.

Model parameter	Estimate	SE	z	P
Intercept	−0.899	0.169	−5.329	<0.0001
Edge distance	−0.385	0.173	−2.225	0.026
Proximity index	0.250	0.161	1.550	0.121

Notes: Data includes 56 transect segments with ≥1 leafcutter colony recorded and 131 randomly selected transect segments with no colonies detected. Transect segments were characterized in terms of their distance to the forest edge and Proximity index. Transect segments were further nested within survey sites (random variable).

($\beta = -0.62$, $P = 0.020$) and leafcutter colony density ($\beta = -0.64$, $P = 0.014$; Fig. 4b). In terms of the indirect model, higher apex predator abundance apparently suppressed armadillo

Table 2. Results from piecewise structural equation model (SEM) on candidate models considering the direct and indirect effects or both.

Model	C	P	df	AIC$_c$	K
Leafcutter occurrence (N = 37)					
Direct and indirect	6.974	0.323	6	58.82	14
Direct	11.853	0.458	12	50.10	11
Indirect†	18.912	0.041	10	66.16	12
Leafcutter colony density (log$_{10}$ x; N = 14)					
Predator effects					
Direct and indirect	2.013	0.366	2	168.1	11
Direct	7.819	0.252	6	90.37	9
Indirect	8.851	0.182	6	93.98	9
Pioneer tree effects					
Direct and indirect	0.035	0.983	2	44.90	8
Direct	1.762	0.779	4	36.78	7
Indirect†	11.661	0.029	4	59.88	7
Percentage of inactive leafcutter colonies (N = 14)					
Predator effects					
Direct and indirect	1.636	0.441	2	165.5	11
Direct	7.583	0.27	6	89.54	9
Indirect	5.341	0.501	6	81.69	9
Pioneer tree effects					
Direct and indirect	1.823	0.768	4	46.5	8
Direct	7.352	0.118	4	49.82	8
Indirect	1.823	0.768	4	36.92	7

Notes: SEMs built considering leafcutter ant occurrence (N = 37 sites), leafcutter colony density (N = 14 sites), and proportion of inactive colonies (N = 14 sites). Effects of predators and pioneer trees were fitted in separate SEMs considering leafcutter colony density and proportion of inactive colonies. Within each SEM, models were fitted using a Gaussian distribution, except for the model including leafcutter occurrence which was fitted using a binomial distribution with a logit-link function. C statistics, degrees of freedoms (df), and P values are related to the Fisher test assessing the independence claims of the basis set. Akaike information criterion for small samples values (AIC$_c$) is a diagnostic of model fit and K corresponds to the number of parameters included in each model. Best fit model(s) are indicated in boldface for both considerably high support (ΔAIC$_c$ < 3, in which ΔAIC$_c$ = AICc$_i$ − AIC$_{cmin}$, i = ith model) and less support (3 < ΔAIC$_c$ < 7).

† This model did not meet the piecewise SEM assumptions.

abundance (β = −0.67, P = 0.009) which was positively related to leafcutter colony density (β = 0.51, P = 0.060; Fig. 4b). The effect of pioneer tree basal area density was also best supported by the direct effect of forest area (Table 2; Appendix S1: Fig. S2a). Moreover, neither the occurrence nor the colony density of leafcutters were related to any diversity measure of pioneer trees (Appendix S1: Table S6). Effects of pioneer trees on leafcutters were only detected when considering the proportion of inactive colonies. According to the indirect model that best fitted the data (Table 2), pioneer trees had a negative effect on the proportion of inactive colonies (β = −0.61, P = 0.020; Fig. 4c). Predator effects were also expressed by the indirect model, but no effects on the proportion of inactive colonies were detected (Appendix S1: Fig. S2b).

DISCUSSION

Across the range of forest sites in Balbina, bottom-up mechanisms exerted a pivotal role in structuring leafcutter populations, as seen by the strong support from models on the direct effects of forest area including both leafcutter occurrence and colony density, and the indirect model showing the effects of pioneer trees on the proportion of inactive colonies. Nevertheless, considering leafcutter colony density, the effects of apex predators on armadillos and those on leafcutters further supported the data, yet to a lesser extent. Accordingly, apex predators were either missing or rare on small islands, releasing armadillo hyper-abundance, at least partly due to weak top-down effects. Yet armadillos apparently failed to control leafcutter colony density
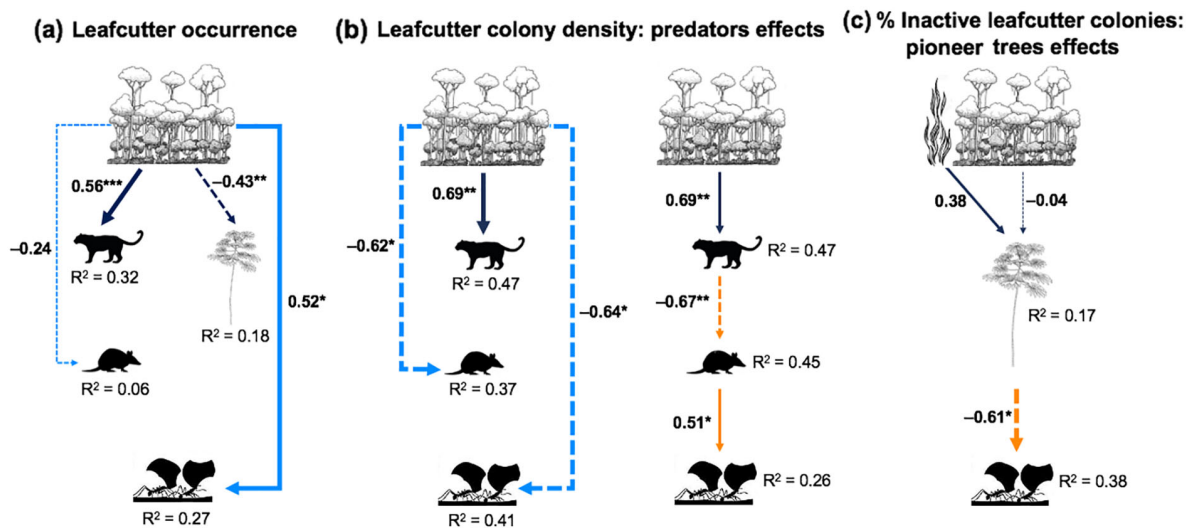
Fig. 4. Best SEMs obtained considering (a) the occurrence of leafcutters (P/A of colonies), including the effects of both predators and pioneer trees within the same SEM (N = 37 sites); (b) leafcutter colony density (colonies/ha), including predator effects and considering only sites where leafcutters were present (N = 14); and, (c) proportion of inactive leafcutter colonies including pioneer tree effects across 14 sites where leafcutters were recorded. In each model, we indicate the standardized coefficients for each relationship, with asterisks indicating significant relationships (*approx. P < 0.05; **P < 0.01; ***P < 0.001), and the coefficient of determination (R^2) for each response variable. Positive and negative pathways are represented by continuous and dashed lines, respectively, which line thickness scaled to illustrate the relative strength of effects.

even where they were highly abundant, as shown by their overall positive relationship, thereby ruling out the hypothesis of any top-down mechanism controlling this fraction of the food web.

Leafcutter drivers

Previous studies have shown that leafcutter colonies typically benefit from forest habitat disturbance (Leal et al. 2014, Tabarelli et al. 2017). Leafcutter colony density drastically increases on both small forest islands in archipelagos elsewhere (Rao 2000, Terborgh et al. 2001) and near edges in forest fragments surrounded by a terrestrial matrix (Wirth et al. 2007, Dohm et al. 2011, Silva et al. 2012). Contrary to our expectations, leafcutter occurrence throughout the Balbina archipelago was limited by forest island area, but additionally boosted by high availability of pioneer trees, their preferred host plants (Farji-Brener 2001, Wirth et al. 2003, Falcão et al. 2011), rather than being suppressed by high armadillo abundance, their direct nest predators (Testa et al. 2019).

Small islands suppressed leafcutter occupancy (i.e., colonies were >40% more likely to occur on islands >100 ha). The conspicuous absence of leafcutters from all four smallest islands (<2.17 ha), in addition to another 19 variable-sized islands, may well be due to their prior absence from those hilltop forest locations during the pre-inundation period. This could be attributed to the overall low leafcutter colony density prior to the dam, as suggested by the extremely low colony density observed in undisturbed CF sites surveyed in the mainland. Leafcutter occupancy probability was increasingly higher on larger islands. This hypothesis is further supported by similarly low leafcutter colony densities in other large tracts of undisturbed primary rainforest in the Amazon (Vasconcelos 1988, Jaffe and Vilela 1989). Because these forests are dominated by old-growth shade-tolerant plant species, the available biomass of palatable foliage is relatively low (Farji-Brener 2001, Wirth et al. 2003), further limiting leaf harvesting and cultivation of the symbiotic fungal gardens on which leafcutters depend (Howard et al. 1988).

Leafcutter selection of suitable food plants is an extraordinarily complex process that involves the assessment of multiple plant traits, environmentally induced factors, and the individual foraging history and motivational status of both the ants and their fungi (see review in Leal et al. 2014). However, leaf longevity and regeneration strategy are strongly correlated with palatability not only to leafcutters (Farji-Brener 2001, Wirth et al. 2003) but also herbivorous insects in general (Southwood et al. 1986). Therefore, shade-tolerant evergreen plants, by investing more heavily in effective chemical defense mechanisms, are likely to be comparatively less palatable than deciduous or semi-deciduous and pioneer plants, which experience higher rates of herbivory (Coley et al. 1985, Pringle et al. 2011). Moreover, leafcutter density in mature forests might be further suppressed by the low availability of treefall canopy gaps, limiting the suitability of leafcutter nest-sites which require a minimum level of direct sunlight on their nest-heaps (Vasconcelos 1990, Vieira-Neto and Vasconcelos 2010). In a fragmented landscape ~200 km from Balbina (Biological Dynamics of Forest Fragment Project, BDFFP) that shares a similar floristic composition, leafcutter colony density is low in both forest fragments and continuous forests, with *A. sexdens* being absent in fragments smaller than 13 ha (Vasconcelos 1988, Dohm et al. 2011). Overall, bottom-up mechanisms that apparently operated prior to damming continue to determine the current distribution of leafcutters across the Balbina archipelagic landscape. It is possible that any resource limitation still reduces colonization events, which are now further deterred by the inhospitable aquatic matrix.

The rampant augmentation of leafcutters in disturbed habitats is boosted by the typically high availability of pioneer trees, representing an abundant resource (Urbas et al. 2007, Leal et al. 2014). At Balbina, although leafcutter colony density remained relatively low and was unrelated to pioneer tree abundance, leafcutter colony activity was higher at sites containing higher pioneer tree abundances. In addition, leafcutter colonies were more often detected near forest edges, where the availability of pioneer trees was also disproportionally higher (Benchimol and Peres 2015*a*). Fast-growing pioneer trees are usually poorly defended against herbivores (Coley

et al. 1985) and comprise the preferred resource of leafcutter ants (Farji-Brener 2001, Wirth et al. 2003, Falcão et al. 2011). For example, leafcutters are known to adjust their foraging trail networks according to pioneer plant availability (Silva et al. 2013) and even alter their diet along forest edges, where the defoliation of pioneer trees is greater than in forest interiors (Falcão et al. 2011). Moreover, leafcutters are also known to be affected by either army ants and parasitoid phorid flies (Feener and Brown 1993). In Balbina, army ants have been extirpated from small islands (at least <3 ha) but were frequently recorded at nearby mainland forest sites (Nogueira 2009). Therefore, army ant predation may have contributed to suppress leafcutter density only at larger forest sites (Rao 2000). Parasitoids phorid flies influence leafcutters foraging rhythms and their decline along desiccated forest edges is known to further contribute to the elevated leafcutter densities therein (Almeida et al. 2008). At Balbina, however, the abundance of parasitic phorids was similar between small islands and continuous forest sites and therefore unlikely to affect leafcutter density (Nogueira 2009).

Limitations due to the field protocol used may have biased data on leafcutters. Indeed, our sampling design primarily aimed to obtain robust samples of mammal and tree assemblages at each surveyed site. For this reason, sampling effort was nearly proportional to the forest area of each surveyed site and covered both edge (<100 m from the edge) and core habitats (>100 m). Therefore, as leafcutters were more likely to establish their nests near forest edges (Wirth et al. 2007, Dohm et al. 2011, Silva et al. 2012), our surveys may have underestimated leafcutter density, eventually resulting in false negatives. However, overall sampling intensity was much higher on small forest islands (i.e., a transect covers almost the entire island). False negatives are thus more likely to arise at larger forest sites, further reinforcing the positive relationship with forest area. Moreover, edge effects induced a compositional decay of tree assemblages within 100 m of the nearest forest edge, including higher abundance of pioneer trees (Benchimol and Peres 2015*a*). This type of disturbed habitat, further referred to as edge-dominated habitat, occupies most of the area of all

islands surveyed (e.g., >60% of islands smaller than 50 ha are comprised of edge-dominated habitats; Appendix S1: Table S7). As such, although we did not concentrate our sampling effort on island edges, the predominant edge-dominated habitat of even central areas of small islands provides a similarly suitable habitat for leafcutters. This also suggests that false negatives were more likely at larger forest areas than at small islands.

Apex predator and armadillo drivers

The importance of the indirect model when considering leafcutter colony density was favored by the smaller subset of forest areas included in the dataset. Indeed, analyses excluding small islands (0.5–2.17 ha) and considering only the 14 leafcutter-occupied forest sites, ensured detection of relevant inter-trophic relationships. First, mesopredators apparently compensated for the decline in apex predator abundance, illustrating the relaxation of top-down forces further consistent with several processes of defaunation under human–habitat disturbance (Estes et al. 2011, Dirzo et al. 2014). However, mesopredator abundance was positively related to leafcutter colony density. The positive association between these trophic groups suggests that armadillo abundance may benefit from high leafcutter density, which in turn depended on pioneer tree abundance. In fact, it is possible that limited island replication may have precluded better performance of the model representing both direct and indirect effects due to higher number of parameters and thus higher AIC_c. The adjustment of armadillo abundance according to leafcutter density may suggest a bottom-up cascade according to which higher abundance of pioneer trees increases leafcutter ant colony density and in turn armadillo mesopredators. However, apex predators did not benefit from higher armadillo abundance likely due to the stronger area effects that limit population size of apex predators (Benchimol and Peres 2015b, 2020). Overall, bottom-up cascades may be rare but has been detected in other terrestrial ecosystems (Teder and Tammaru 2002, Gratton and Denno 2003). For instance, the accumulation (or dilution) of plant defensive materials by herbivorous insects is known to provide a mechanistic basis for bottom-up cascades (Kagata and Ohgushi 2006).

Balbina vs. Guri Lakes

Leafcutter colony density increased on smaller forest islands, provided that those were occupied. However, elevated leafcutter densities on smaller islands were relatively modest compared to that observed on 10-yr-old land-bridge islands formed within the Lago Guri hydroelectric reservoir in Venezuela (Rao 2000, Terborgh et al. 2001, Fig. 5). In fact, the relationship between leafcutter occupancy and island size was opposite at those two archipelagic landscapes. At Guri, the aberrant hyper-proliferation of leafcutters (in addition to other folivores such as iguanas and howler monkeys) on small forest islands was attributed to local predator extirpation, as validated by a manipulative cage experiment measuring predation on *Atta* colonies (Rao 2000). Insular forests at Lago Guri, however, consist of semi-deciduous dry vegetation (Terborgh et al. 2001), which are subject to much higher levels of herbivory than wet forests (Coley et al. 1985). The apparently much higher community-wide
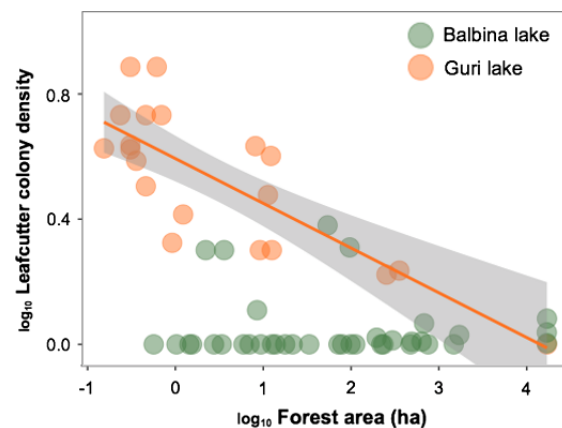

Fig. 5. Relationship between leafcutter ant colony density (ha^{-1}) (log$_{10}$ x) and forest area (log$_{10}$ x) at both the Balbina and Guri hydroelectric reservoirs. Leafcutters were sampled in 34 islands and three continuous forest (CF) sites at Balbina, and 19 islands and one CF site at Guri. CF sites at both Balbina and Guri were fitted with an approximate area of 16,879 ha, one order of magnitude higher than the largest island at Balbina. Data on leafcutter ants from Guri were extracted from Rao (2000). For Guri, line represents the adjusted model, and shaded area represents the 95% confidence region. Leafcutters were not detected at islands at zero colony density.

foliage palatability (i.e., higher digestibility of fungal cultivars) at Guri therefore likely removes a major bottom-up limitation in leafcutter densities on islands. This is supported by similar abundance releases observed for other herbivore guilds at Guri (Terborgh et al. 2001) that we never observed for any herbivore mammal at Balbina (Palmeirim et al. 2018, Benchimol and Peres 2020). We suspect that the absence of leafcutters, especially on smaller islands at Balbina, is due to the overall low leafcutter density in evergreen wet forests, which is further explained by the limited availability of suitable trophic resources (i.e., phytochemically suitable foliage that can be fed to underground ant gardens). Indeed, leafcutter densities at BDFFP were boosted within 50 m of forest edges but was limited to 17-fold increases compared to the pre-fragmentation scenario (max. ~2 colonies/ha, Dohm et al. 2011). This is consistent with our observations at Balbina (max. 1.4 colonies/ha) but much lower than the observed densities at Guri (max. 6.7 colonies/ha, Rao 2000). These contrasting trajectories of herbivorous vertebrate and invertebrate guilds between the Guri (a dry forest) and Balbina (a wet forest) hydropower reservoirs further indicate that these two systems are under predominantly different trophic dynamics characterized by strong top-down mechanisms at Guri, but not necessarily at Balbina. Moreover, dry forest trees and shrubs occurring on Guri islands are exposed to an additional hydrological stress. Given leafcutter's preference for plants under hydric stress (Meyer et al. 2006, Ribeiro-Neto et al. 2012), such condition may provide inherently more abundant resources for leafcutters and their fungal cultivars, contributing to their much higher densities therein. Increased leafcutter densities along forest edges have also been attributed to elevated hydric stress in plants occupying these marginal habitats (Silva et al. 2018).

Conservation implications

Selective defaunation at high trophic levels can result in wholesale shifts in the structure of ecosystems through relaxation of top-down forces (Terborgh et al. 2001, Estes et al. 2011, Dirzo et al. 2014). In Balbina, this was the case of apex predators that undergo local extinctions from smaller forest sites, thereby releasing

armadillo abundance, as indicated by the partially supported indirect model. Nevertheless, the positive relationship between armadillo abundance and leafcutter colony density suggests prevailing bottom-up, rather than top-down, forces. The modest observed increases in leafcutters and other herbivore guilds at Balbina likely contributed to decelerating the ecological meltdown processes predicted for these hyper-disturbed habitats (Terborgh et al. 2001). Moreover, the different mechanisms of population control acting in contrasting wet and dry forest types have major implications to the fate of herbivore guilds (Wright et al. 1994, Terborgh et al. 2001), with further consequences on ecosystem functioning (Leal et al. 2014).

Overall, the clear prevalence of bottom-up mechanisms renders isolated land-bridge islands more susceptible to other major disturbances detrimentally affecting forest dynamics, including timber extraction and the ravages of climate change (Wang et al. 2020). Our findings indicate that setting-aside large tracts of undisturbed primary tropical forest are the only insurance to maintain the integrity of terrestrial food webs and ecosystem functioning, particularly in evergreen Amazonian forests. Our results should be additionally considered in general guidelines informing the justification for hydropower development in lowland tropical forests.

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