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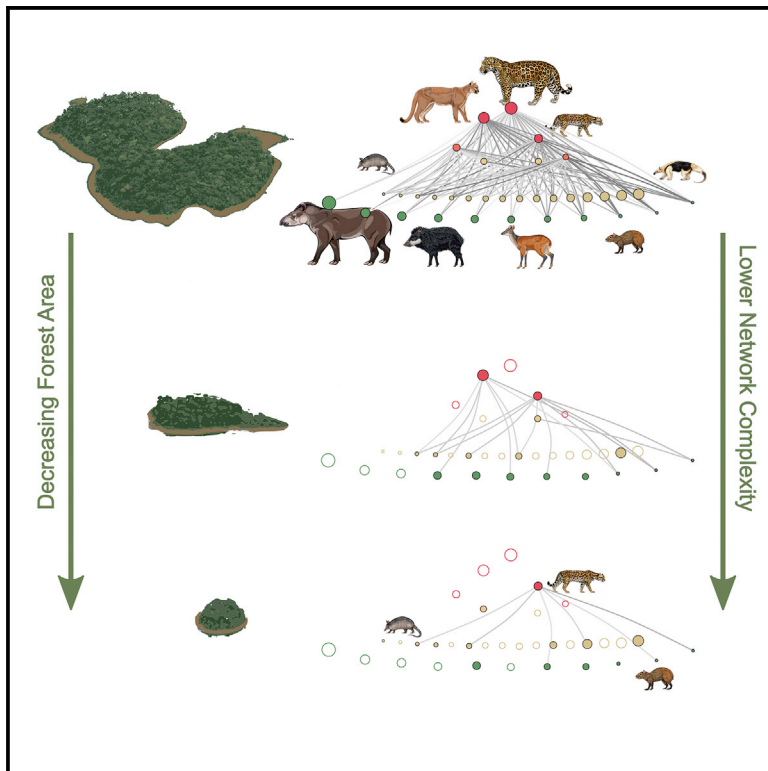
Terrestrial food web complexity in Amazonian forests decays with habitat loss

Graphical abstract

Highlights

- Functional extinctions have changed the fauna of land-bridge islands in the Amazon

- The complexity of predator-prey networks decays with decreasing forest area

- Several species have no potential predators or fewer prey on small forest islands

- Forest loss in the Amazon generates simplified dysfunctional food webs

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In brief

Investigating the vertebrate fauna of islands formed by a reservoir in Amazonia, Pires et al. learn how interaction networks change with forest size. Their results indicate that abundance declines on small islands reduce network complexity and disrupt trophic structure. These results show that small forest remnants host dysfunctional food webs.

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Terrestrial food web complexity in Amazonian forests decays with habitat loss

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SUMMARY

The conversion of natural ecosystems into human-modified landscapes (HMLs) is the main driver of biodiversity loss in terrestrial ecosystems.[1–3] Even when species persist within habitat remnants, populations may become so small that ecological interactions are functionally lost, disrupting local interaction networks.[4,5] To uncover the consequences of land use changes toward ecosystem functioning, we need to understand how changes in species richness and abundance in HMLs[6–8] rearrange ecological networks. We used data from forest vertebrate surveys and combined modeling and network analysis to investigate how the structure of predator-prey networks was affected by habitat insularization induced by a hydroelectric reservoir in the Brazilian Amazonia.[9] We found that network complexity, measured by interaction diversity, decayed non-linearly with decreasing smaller forest area. Although on large forest islands (>100 ha) prey species were linked to 3–4 potential predators, they were linked to one or had no remaining predator on small islands. Using extinction simulations, we show that the variation in network structure cannot be explained by abundance-related extinction risk or prey availability. Our findings show that habitat loss may result in an abrupt disruption of terrestrial predator-prey networks, generating low-complexity ecosystems that may not retain functionality. Release from predation on some small islands may produce cascading effects over plants that accelerate forest degradation, whereas predator spillover on others may result in overexploited prey populations. Our analyses highlight that in addition to maintaining diversity, protecting large continuous forests is required for the persistence of interaction networks and related ecosystem functions.

RESULTS

Faunal surveys showed that the studied landscape contains a rich assemblage of terrestrial and arboreal vertebrates, with five carnivores, two opportunistic omnivores, and more than 20 potential prey species, including ungulates, rodents, xenarthrans, primates, and terrestrial birds.[9] Using network models,[10,11] we generated potential interaction networks with realistic trophic structures in which predators feed on species at lower trophic levels according to body size relationships. Thus, large predators such as the jaguar (*Panthera onca*) are more likely to prey on ungulates and xenarthrans, whereas smaller predators such as the jaguarundi (*Herpailurus yagouaroundi*) and omnivores such as the tayra (*Eira barbara*) are more likely to prey on terrestrial birds and rodents (Figure 1). Next, we assessed the extent to which patch and landscape metrics influence the structure of those networks. We expected that sites with reduced forest area would exhibit disrupted interaction networks with reduced interaction diversity and interaction evenness and lower numbers of interactions per species. We also expected networks on small forest islands would be flattened, exhibiting low predator-prey ratios and reduced mean trophic level.

Accounting for differences in species occurrence and detection rates across sites, we found that there is an apparent forest area threshold of around 100 ha, above which local networks become more representative of the overall regional network (Figure 1). The overall structure of interaction networks changed considerably with forest area. The diversity of potential interactions increased substantially with area, from fewer than 10 expected interactions on small islands (forest area < 100 ha) to more than 30 on large islands and mainland forest areas (nonlinear regression: $F_{37,2} = 144.83$, $r^2 = 0.88$, p < 0.001; Figure 2A; Table S1). Fewer interactions imply less connected networks, such that the expected network connectance on sites with forest area smaller than 100 ha ($C = 0.02 \pm 0.03$) was nearly 10 times lower than the expected connectance on larger forest sites
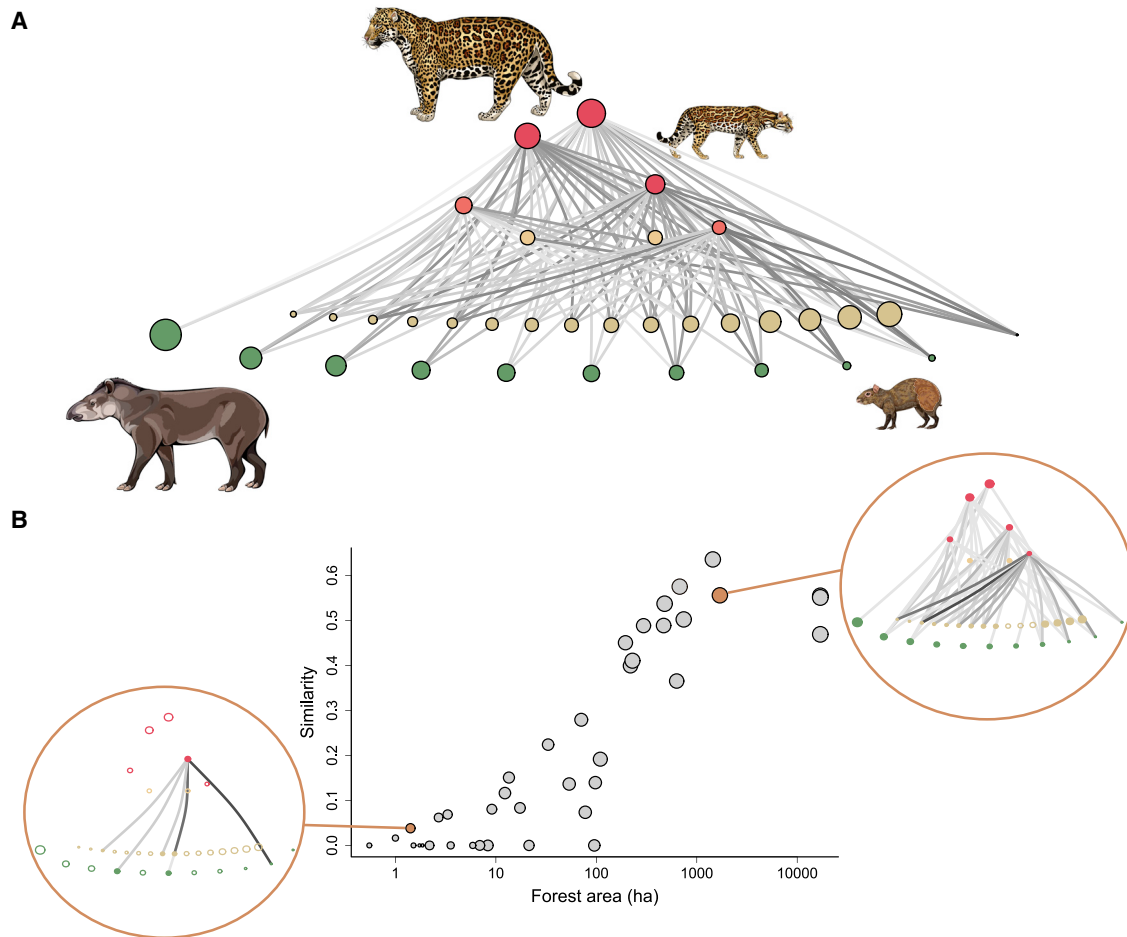
Figure 1. Predator-prey interaction network

(A) Potential interaction network considering the regional pool of species and example of potential networks for sites with variable forest area. Node size scales with species body mass, node color, and position vary with trophic level and the shade of links varies with interaction probability, with darker links representing more likely interactions.

(B) The plot shows the similarity between the regional network and local networks weighted by relative detection rates as a function of forest area. Circle size scales with species richness. The two example networks represent potential networks for two sites (highlighted with different colors in the plot) with either small (left) or large (right) forest area. Empty nodes in the example networks correspond to species that were not recorded at those two sites.

(C = 0.19 ± 0.6). This increase in interaction diversity partly occurs due to an increase in the number of interactions, but interaction evenness also increased with forest area (non-linear regression: $F_{37,1}$ = 70.95, r^2 = 0.79, p < 0.001; Figure 2B; Table S1), meaning that a wider and more balanced spectrum of interactions is more likely to occur on larger forest sites. Sites with low forest area were either predator-free or contained prey populations linked to only one potential predator, whereas they were linked to 3–4 potential predators on sites with greater forest area (Figures 2C and 2D). Similarly, the mean number of prey species per predator ranged from fewer than 5 on sites with small forest area to more than 10 on large forest sites.

These differences in community composition resulted in clear divergences in the trophic structure of networks at sites with varying forest area. Predator-prey ratios and mean trophic level were widely variable across sites with little remaining forest, from assemblages that completely lacked predators to others where only predators with no co-occurring potential prey were

recorded. Large forest islands and continuous forest sites, however, converged into similar predator-prey ratios (approximately 0.2; Figure 2E) and similar average trophic levels (approximately 2.4; Figure 2F). We found little effect of island proximity to continuous forest on network structure (Table S1).

These changes in expected networks occur because sites with larger forest area are more species-rich and also retain greater abundances, both of which raise the interaction probability for most predator-prey species pairs (Figure 3A). Considering interaction patterns at the species level, we found that many species would have no potential interactions at several sites where they were recorded (Figure 3B). For instance, large-bodied mammals such as giant anteaters (*Myrmecophaga tridactyla*), white-lipped peccaries (*Tayassu pecari*), and lowland tapirs (*Tapirus terrestris*) were effectively predator-free in nearly 40% of all sites where they occurred (Figure 3B). The absence of interactions may occur either because predators have not been recorded with their potential co-occurring prey or because
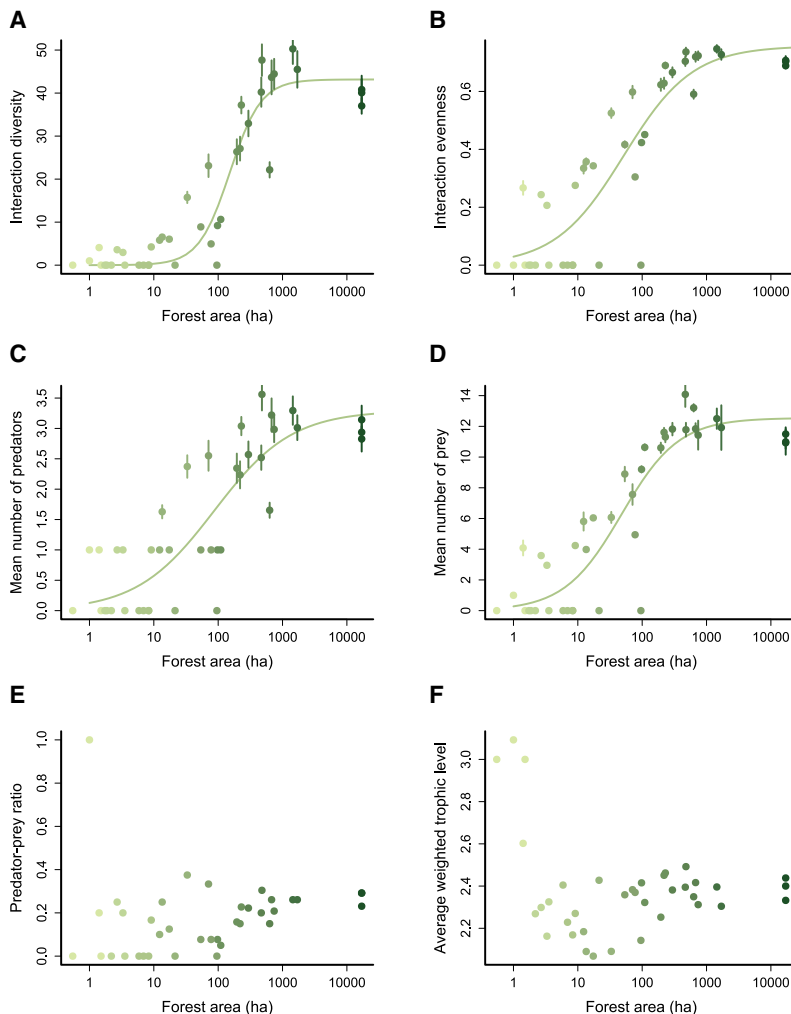
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Figure 2. Structure of predator-prey networks

(A–F) Variation in different structural descriptors of predator-prey networks as a function of forest area within surveyed forest sites. Circles represent the mean and error bars the standard deviation for the metrics computed for each of 100 potential networks generated per site. The color gradient follows forest area, and the three darkest circles represent mainland forest sites. Curves represent the model with highest fit (see Table S1).

performed extinction simulations and estimated the similarity between the networks obtained using actual records and those obtained from simulations. A neutral extinction model, in which extinction probability on islands was proportional to species relative abundance in continuous forest areas, generated networks that were very dissimilar from those inferred from observations, especially on small islands (Figure S1). This extinction model tended to underestimate the frequency of interactions involving species that were detected at low rates in continuous forest areas, such as ocelots, acouchis, and large terrestrial birds but were present on most islands (Figure S1). Another model where the predator occurrence probability was proportional to prey availability also performed badly in reproducing the networks on small islands, underestimating the occurrence of some interactions but overestimating others (Figure S1).

DISCUSSION

The Balbina island system is an emblematic quasi-experimental case study showing the consequences of habitat loss and fragmentation for biodiversity.[12,13] The multiple islands formed at the same time but containing varying levels of forest cover have already been shown to host different assemblages of trees,[14] invertebrates,[15–17] birds,[18] and mammals,[9,19] with greater risks of local extinction on small islands.[9] Here, we show how these habitat-related effects extend to interaction networks. We found that network complexity, measured here mainly by the diversity of interactions, decreased non-linearly with remaining forest area as a consequence of changes in both species richness and abundance. On small forest islands, networks had fewer potential interactions, with many species lacking their habitual predators or potential prey. We also found that although sites retaining large forest areas tend to converge into the same trophic structure expected to be found on the mainland, small islands often hosted idiosyncratic networks that failed to retain the structural properties found on large islands and mainland continuous forest sites. These effects of habitat availability on the structure of interactions networks have three main implications.

First, our analyses show that habitat loss in Amazonian forests results not only in reduced species diversity[9,19] but also in an overall simplification of ecological networks as interactions are lost. The non-linear relationship between network structural

their relative abundances were so low that interactions have been functionally lost. Conversely, all prey species on sites with larger forest area had at least one potential predator (logit regression: $\beta = 1.16 \pm 0.46$, *deviance* = 9.11, p = 0.002; Figure 3C). Although all predators had at least one potential prey where they occurred (Figure 3B), prey availability also increased with forest area (Figure 3D). However, predators were not detected on some islands containing relatively high prey availability; indeed, except for the ocelot, *Leopardus pardalis*, which attained higher relative abundances where prey availability was higher, prey availability was not a good predictor of either the relative abundance or presence/absence of potential predators (Table S2).

We also analyzed the structure of the metanetwork formed by all study sites and each potential pairwise interaction. This metanetwork has a core-periphery structure (Figure 4A) that gives rise to a nested pattern (NODF = 51.75; $NODF_{null}$ = 14.6 ± 1.1; p < 0.001), wherein large forest islands and mainland sites hosted most potential interactions, whereas only a nested subset of the most common interactions occurred on small islands. To examine whether the interaction networks on variable-sized forest sites could emerge from simple extinction rules, we
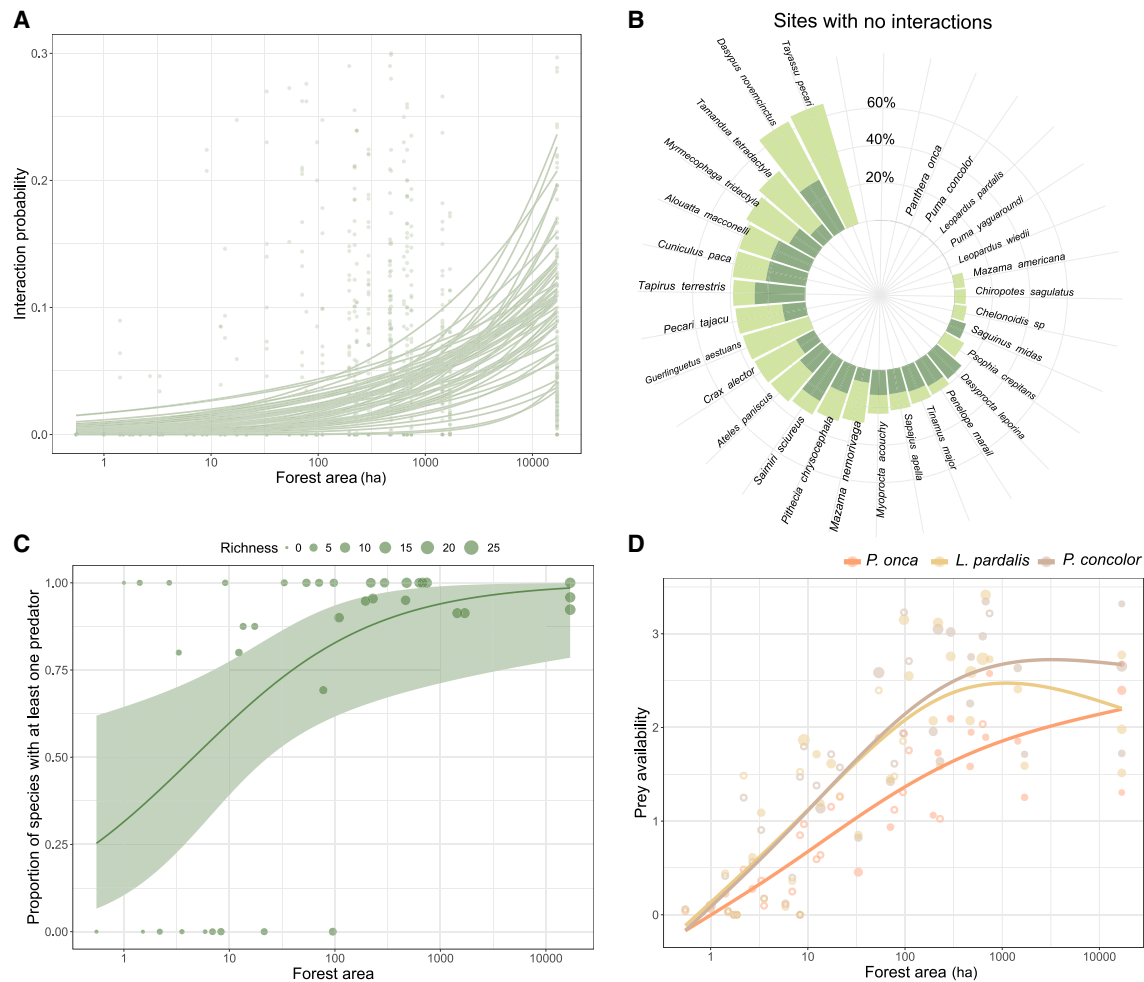
Figure 3. Species-level interaction patterns within islands and mainland sites

(A) Variation in the probability of pairwise interactions between potential predator-prey species with forest area. All trend lines, representing every possible combination of predator-prey species pairs, show increasing interaction probability.

(B) Percentage of sites (bar height) where species have been detected, but pairwise interaction probabilities were below 0.05 (dark bars) or 0.10 (light bars). Missing bars indicate that a particular species had potential interactions within all sites.

(C) Proportion of species with at least one predator as a function of forest area.

(D) Prey availability for the three largest felid predators in the region. Circle size is proportional to the relative abundance of each predator across sites. Open circles represent the prey availability for sites where predators were absent (see Table S2).

metrics and forest area suggests that there is a minimum habitat remnant size required to maintain the integrity of interaction networks. Such non-linear relationships between network structure and habitat area have been predicted by theoretical work[20] and were recently shown for different types of empirical networks in the temperate region.[4] Here, we show this phenomenon also occurs in networks describing vertebrate interactions in the world's largest tropical forest biome. A threshold effect with abrupt transitions in diversity in response to habitat reduction and fragmentation happens when multiple species respond similarly to habitat loss.[21,22] In the case of networks, abrupt structural changes may occur because species that are less sensitive to habitat loss help to maintain network structure under moderate levels of habitat reduction.[23,24] However, as habitat area is further diminished, those interactions forming the core of the

network may be lost,[25] resulting in a sudden disruption in structure. This process is supported by the structural arrangement we found for the metanetwork, in which there was a shared set of interactions common to most sites, but several interactions were only likely at sites containing large forest areas, a pattern also detected for plant-frugivore interactions in fragmented landscapes.[26]

We also found that although predator-prey ratios and mean trophic levels tended to converge on sites with greater forest area, the trophic structure of networks on small islands was highly variable. This suggests that although ecological processes shape the interaction networks on large islands and mainland sites, idiosyncratic features governing the species composition of small forest islands resulted in unique and likely dysfunctional simplified systems at different sites. Over half
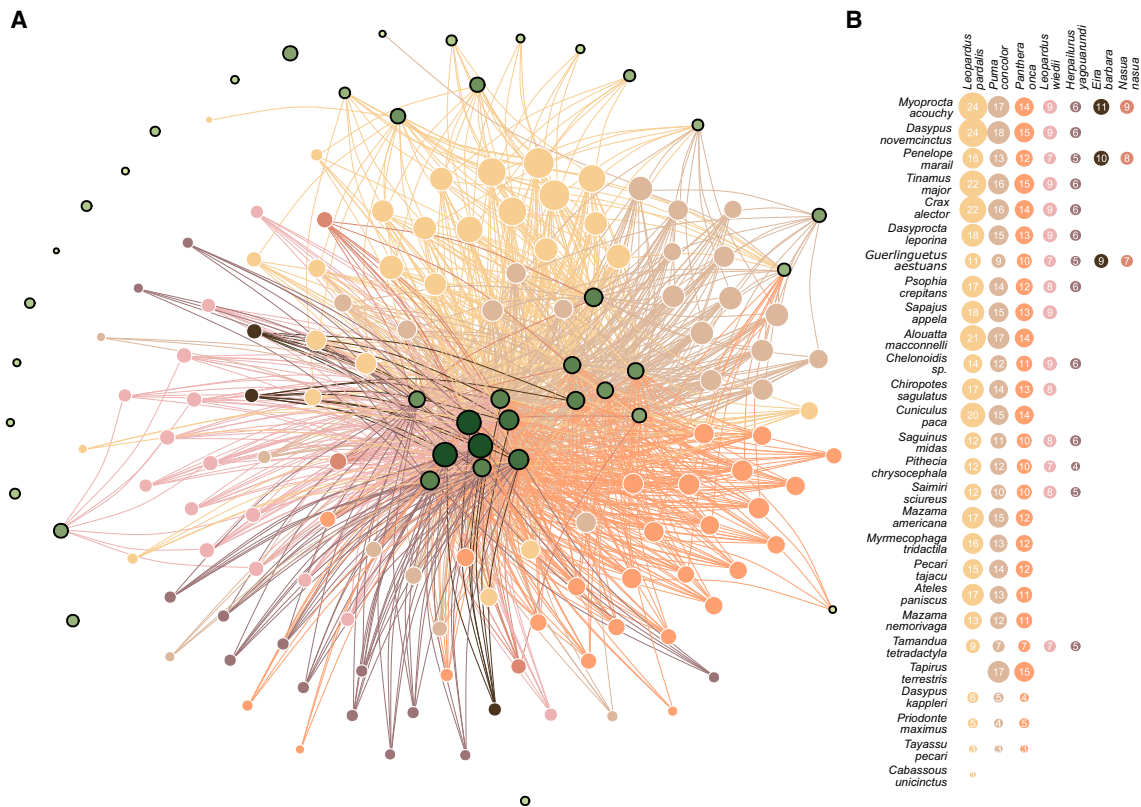
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Figure 4. Interaction frequency across islands and mainland sites

(A) Metanetwork representing each pairwise interaction and the islands on which they are likely to occur. Green nodes represent sites and node size and color corresponds to forest area, with darker colors representing sites with larger forests. All other nodes represent pairwise interactions, and colors indicate the predator species as shown in the matrix. Nodes disconnected from the network represent sites with no potential interactions.

(B) Matrix showing the frequency of occurrence of each interaction, measured as the number of sites where predator-prey interactions are likely to occur.

(50.3%) of all 3,546 islands in the Balbina Reservoir have less than 10 ha of forest and only 184 islands, about 5%, have more than 100 ha of remaining forest,[9] which indicates that the vast majority of the islands can no longer sustain functional interaction networks.

Second, our results show that many species generally lack predators at small islands or their interactions are much less likely to occur because local predator abundance is low. This suggests that top-down regulation may be relaxed at those sites. Release from predation may result in over-inflated populations at sites where the remaining prey species are not strongly limited by resource availability. Even if populations on small islands are partially limited due to resource limitation, in the absence of top-down control, populations may attain higher abundances than expected based on the remaining habitat area.[27] This appears to be the case of the nine-banded armadillo (*Dasypus novemcinctus*) and the red acouchi (*Myoprocta acouchy*), which were found at higher densities on small islands compared with larger islands and mainland sites.[9] A previous study in the same system[28] also reported that habitat-generalist rodents attained high abundances on small islands, which could result from either relaxed predation pressure or competitive release. Habitat degradation and release from predation may eventually result in more extreme cases of faunal collapse

as happened at Chiew Larn Reservoir in Thailand, where smaller island fragments became dominated and eventually completely monopolized by an opportunistic hyperabundant rodent.[29,30]

The consequences of predator-free environments may cascade to other trophic levels, affecting processes such as forest regeneration. On the land-bridge islands of Lago Guri, for instance, release from predation of leaf-cutter ants, howler monkeys, and rodents reduced the recruitment of canopy trees, changing the structure of the vegetation on small islands.[31] Although scatter-hoarding rodents such as acouchis and agoutis can be important secondary seed dispersers,[32] at high densities, they may end up producing a net negative effect on seedling recruitment due to high rates of seed predation and cache pilferage.[33,34] Thus, release from predation on small islands may have consequences for vegetation structure, promoting further changes in the remaining habitat.

Third, the converse may also happen, and predators may overexploit prey populations on some islands. Predators such as pumas, jaguars, and ocelots were often recorded on sites with low prey availability. These species can often traverse the open-water matrix,[19] and individuals may occasionally hunt on small islands over short residence times. However, area-sensitive prey species that cannot establish sufficiently large

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populations on resource deprived sites with little forest area may be overhunted during transient pulses of predation events. Such spillover predation may link predator-prey dynamics of isolated islands[35,36] and can be particularly harmful to prey populations when the landscape configuration allows predator movement but restricts that of prey.[37] This has been reported for other island systems where insular prey populations are small and prey diversity is low,[38] thereby partially explaining the idiosyncratic composition of small islands.

Small habitat remnants may have high conservation value, especially in highly modified landscapes.[39] However, our results show that sites retaining small to intermediate forest areas in a fragmented landscape in the Amazon not only host species-poor ecological communities but are also composed of interaction networks with reduced complexity that may not be able to retain functionality. These findings have implications for our understanding of the consequences of human impacts in Amazonian forests, which have both intensified and proliferated in the last four decades. Deforestation has been an escalating threat for Amazonian biodiversity, and deforestation rates have soared in the past few years, such that even the most pristine areas are now threatened by the expansion of cattle pastures, cropland, logging, and mining.[40,41] As habitat loss and fragmentation spreads, several subregions of the Amazon may end up as collections of small forest fragments hosting dysfunctional food webs. Understanding these changes in food web structure is an important step toward developing effective conservation planning that preserves the structural and functional properties of ecological systems.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.11.066.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Survey data	figshare	https://doi.org/10.6084/m9.figshare.21623676
Software and algorithms		
R Statistical Software	R Project	https://www.r-project.org
Contributed R packages	Comprehensive R Archive Network (CRAN)	https://cran.r-project.org
R Code	figshare	https://doi.org/10.6084/m9.figshare.21623676

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed to and will be fulfilled by the lead contact, Mathias M Pires (piresmm@unicamp.br).

Materials availability

The study did not generate new unique reagents.

Data and code availability

- All data reported in this paper has been deposited at figshare and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- All original code has been deposited at figshare and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study area

This study was conducted in a set of 37 variable-sized forest islands and three mainland continuous forest sites located within and adjacent to one of the largest hydroelectric impoundments on Earth – the Balbina Dam. Created in 1986, the reservoir area of 4,437 km^2 encompasses 3,546 forest islands in the central state of Amazonas. In 1990, most of the reservoir and a vast tract of adjacent mainland continuous forests became effectively protected with the creation of the Reserva Biológica do Uatumã, the largest Biological Reserve in Brazil. Given the large number of islands created simultaneously and surrounded by a homogeneous open-water matrix, the Balbina archipelago represents an excellent quasi-experimental landscape to test ecological hypotheses. Furthermore, islands and continuous forest sites are effectively protected from anthropogenic disturbances, including logging and hunting.[19]

We carefully selected 37 forest islands to be surveyed, which ranged widely in size (from 0.83 to 1690 ha) and isolation across the reservoir. Islands were selected based on two cloudless georeferenced 30-m resolution Landsat ETM+ images (230/061 and 231/061; year 2009). In addition, we also selected three widely distributed undisturbed continuous forest sites (CFs) in the adjacent mainland area. All sampling sites were spaced by at least 1 km from each other.[9,19]

METHOD DETAILS

Faunal surveys and abundance estimates

We carried out field surveys of midsized to large vertebrate species using line-transect censuses and camera trapping between June 2011 and December 2012. We first established line-transects on each sampling site; one to five variable-length transects were cut within each island, according to their size and shape, to cover a representative extent of the islands. Three parallel 4-km linear transects, separated from each other by 1 km, were established at each CF. Line-transect surveys were conducted by two observers on foot at a constant speed (~1.0 km/h) following a standardized protocol.[42] We conducted eight line-transect surveys on each sampling site, separated by intervals of at least 30 days, minimizing potential effects of time of day and seasonality. Line-transect surveys were conducted in the mornings (06:15h - 10:30h) and afternoons (14:00h – 17:30h) and were discontinued during rainy weather. We also deployed digital camera traps (CTs, Reconyx HC 500 Hyperfire) on all transects, which were active 24h/day over a 30-day period

in each year (2011 and 2012). We deployed two to ten CTs at each island (mean [SD] = 4.38 [3.21]), according to island size, and 15 CTs at each CF site, spaced by at least 500 m (except for small islands). CTs were unbaited, and placed off-trails and 30-40 cm above ground. We considered records of the same species as independent if intervals between photos were ≥ 30 min, or if different individuals could be identified. Our total survey effort was: 1,168 km of line-transect censuses and 12,420 CT-days (mean [SD] = 310.5 [251.83], range = 120-900 CT days/site) based on 207 camera-trapping stations. Further details can be found in Benchimol & Peres.[19] Abundance estimates were calculated considering species-specific detection rates, considering either line-transect census (number of individuals or groups detected per 10 km walked) or camera trapping (i.e. number of independent photo captures per 10 trap-nights).[9] We acknowledge it would be naïve to assume that these are unbiased estimates of actual local abundance, especially due to variation in detectability across species. Yet, it is reasonable to assume that variation in detection rate for the same species across sites is correlated with variation in local abundances. We therefore assume that the likelihood of interactions between any pair of species increases when they both accrue higher detection rates.

Spatial metrics

For each of the sampled islands and CFs, we obtained a set of local, patch and landscape metrics. Using high-resolution RapidEye© satellite images from our study period, we conducted a semi-supervised classification in ArcMap (version 10.1) to obtain four land use types (closed-canopy forest, open-canopy forest, bare ground, and water). At the patch scale, we calculated island area, total forest area (i.e., excluding bare ground), closed-canopy forest area, nearest distance to a continuous forest site, and island shape [Perimeter:Area (P:A) ratio]. At the landscape scale, we considered multiple buffers (250 m, 500 m and 1000 m) outside the perimeter of each island and mainland forest sites and quantified the percentage of both total forest cover and closed-canopy forest within the buffer, and a proximity index modified from McGarigal et al.[43] (see details in Benchimol and Peres[44]). Because total forest area was highly correlated with other metrics except distance to CFs, we focused on those two predictors in our analyses.

Building interaction networks

To construct predator-prey interaction networks based on the quantitative composition of vertebrate assemblages, we used a probabilistic approach instead of assuming a fixed network topology. Because predator-prey interactions are highly determined by body mass relationships,[45,46] especially among terrestrial vertebrates,[47] we used a modelling approach whereby interaction probabilities are first estimated as a function of body mass and then weighted by relative abundances.[48] We obtained interaction probabilities between co-occurring species using a statistical model where the probability of an interaction between predator j and prey i is a function of their body mass ratios[10,11]:

$$P_{ij} = \frac{e^{\alpha + \beta log\left(\frac{m}{M}\right) + \gamma log^2\left(\frac{m}{M}\right)}}{1 + e^{\alpha + \beta log\left(\frac{m}{M}\right) + \gamma log^2\left(\frac{m}{M}\right)}} \quad \text{(Equation 1)}$$

where m is the body mass of prey i, M is the body mass of predator j, and α, β and γ are free parameters that determine how body-mass ratios and interaction probabilities are related. The parameter values used in the analyses are shown in Table S3. The resulting function has a non-linear form where the interaction probability is high around a certain optimal body-mass ratio, which may vary for different predator species, but overall decreases for prey that are too small or too large relative to their predators. To parameterize the model, we used parameter values obtained by fitting the models to dietary data of each of the predator species in this study from several sites across the entire Neotropical realm.[49] These models have a high success rate in predicting general resource use patterns despite the spatial variation in each species' diets.[11] Assuming interactions are also dependent on encounter rates, interaction probabilities were weighted by the product of relative abundances of each species, so that a particular interaction was more likely in those sites where the species involved were detected more frequently, whereas interactions between low-abundance species were rare. Because arboreality reduces primate predation risk induced by cursorial predators, we also down-weighted the interaction probability between predators and all primate species by setting an upper bound of 0.3, corresponding to the maximum frequency of occurrence of primates in the diets of terrestrial carnivores according to a recent compilation on the diets of all neotropical carnivorans.[49]

QUANTIFICATION AND STATISTICAL ANALYSIS

Characterizing network structure

We characterized the structure of the reconstructed interaction networks representing each insular and continuous sampling site using a set of network metrics. First, to better understand how considering local abundances may change the overall network structure, we computed the similarity between the networks representing each site and the regional potential network, which depict all potential interactions that are unweighted by relative abundances. We computed dissimilarity using the approach proposed by Poisot et al.[50] but using the quantitative Bray-Curtis dissimilarity index as implemented in the function *betalinkr* from the *bipartite* R package.[51] To examine how network complexity and connectivity differed across sites we computed interaction diversity (the effective number of expected interactions), interaction evenness (which measures how evenly distributed interaction probabilities are), network connectance (the proportion of expected interactions over all possible interactions), and the average expected number of predators (prey) per prey (predator) for each network, i.e., the average degree or number of links across all predators/prey in the network. To describe

the trophic structure of predator-prey networks we recorded the predator-prey ratio, based on the observed species checklist of each site and the effective mean trophic level of each network by summing the species' trophic levels, computed using the *TrophInd* function from the R package *NetIndices*,[52] weighted by the local detection rate of each species. Thus, the effective trophic level increases when predator species richness is high and predators are abundant relative to their prey. To test how patch and landscape metrics affected network structure, we tested the fit of linear and nonlinear models with the metrics above as response variables and forest area within each site and isolation distance from the mainland as predictors. These results are presented in Table S1.

To understand how variable interaction patterns at the species level were across sites, we recorded the expected number of interactions for each species at each sampling site and computed the frequency of sites at which a species had been observed but had no expected interactions (assuming a threshold of $P < 0.01$ or 0.05 to count an interaction as unlikely). We also estimated prey availability for each predator i at each site k as: $v_{i,k} = \sum_j P_{ij} N_{j,k}$, where P_{ij} is the pairwise interaction probability and $N_{j,k}$ is the relative abundance of prey j. Then we used generalized linear models to evaluate if predator relative abundance and occurrence varied with prey availability while controlling for forest area. These results are presented in Table S2.

Structure of the sites metanetwork

We also analyzed the structure of the metanetwork representing which pairwise interaction that would likely occur at each site.[26] To characterize structure, we computed the degree of each interaction as the number of sites within which that pairwise interaction would occur as well as the network nestedness using a quantitative nestedness index.[53] We fixed the order of the matrix used to compute nestedness, from the sites with largest forest area to the smallest, so that we could assess the degree to which the interaction sets of sites with reduced forest area were nested within the interaction sets of large sites containing larger forest area. To test for the significance of the nested pattern we used a null model approach, building null networks for which the probability that interactions are assigned to a certain site is proportional to the frequency of the interaction and the number of interactions estimated for that site (null model 2[54]).

Extinction simulations

To test whether local assemblages and therefore the interaction networks on sites with varying forest area could emerge from simple extinction rules, we performed extinction simulations under two different scenarios. In the first, islands retain the same number of species detected in the surveys, but species are randomly sampled according to their baseline detection rate in continuous forest areas in the mainland. This simulates a neutral extinction process where extinction risk is high for rare species and low for common ones. We then assigned species the same relative abundances found for the original set of species on each island while retaining the relative abundance rank of the sampled species in continuous forest areas. Therefore, simulated assemblages retain the richness and variation in detection rates in all replicates but may contain different sets of species. In the second model, we fixed the number of prey and predator species to be the same as originally recorded on each island. The sampling process of prey species obeys the same criteria described above, but predators are selected according to prey availability, so that the simulated systems retain a certain set of potential prey with lower extinction risk and the predators that have greater access to prey. We ran 100 replicates for each model, built the potential network for each replicate, and computed the similarity between simulated networks and those inferred based on the actual field surveys. To better understand the degree to which simulated systems differ from real-world observations, we computed the mean frequency of interactions under the simulated scenarios and then calculated the difference between the frequency of interactions expected from field surveys and under each extinction scenario. These results are presented in Figure S1. We performed all analyses and simulations using R[55] and all original code is available at figshare (https://doi.org/10.6084/m9.figshare.21623676).