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Loss of endangered frugivores from seed dispersal networks generates severe mutualism disruption

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Many tropical seed-dispersing frugivores are facing extinction, but the consequences of the loss of endangered frugivores for seed dispersal is not well understood. We investigated the role of frugivore endangerment status via robustness-to-coextinction simulations (in this context, more accurately described as robustness-to-partner-loss simulations) using data from the Brazilian Atlantic Forest biodiversity hotspot. By simulating the extinction of endangered frugivores, we found a rapid and disproportionate loss of tree species with dispersal partners in the network, and this surprisingly surpassed any other frugivore extinction scenario, including the loss of the most generalist frugivores first. A key driver of this pattern is that many specialist plants rely on at-risk frugivores as seed-dispersal partners. Moreover, interaction compensation in the absence of endangered frugivores may be unlikely because frugivores with growing populations forage on fewer plant species than frugivores with declining populations. Therefore, protecting endangered frugivores could be critical for maintaining tropical forest seed dispersal, and their loss may have higher-than-expected functional consequences for tropical forests, their regeneration processes, and the maintenance of tropical plant diversity

1. Introduction

The growing number of vertebrate species at risk of extinction threatens biodiversity and ecosystem health by compromising key interactions between species—such as seed dispersal by fruit-eating animals—that are critical for the functioning of natural ecosystems [1–5]. Tropical forest ecosystems are among the most vulnerable to negative effects following vertebrate species losses, particularly because the majority of tropical plant species rely on frugivores for animal-mediated seed dispersal [6,7]. Seed dispersal by frugivores is critical for forest regeneration. Gut passage often benefits seeds and speeds germination for many species [8,9], in addition to facilitating seed deposition into favourable microhabitats [10]. Dispersal of seeds is also considered a key aspect of maintaining plant diversity in tropical forests as it allows seeds and seedlings to escape density-dependent mortality concentrated under parent plants [11,12] and plays an important role in maintaining genetic diversity and gene flow across the landscape [13–15]. Interactions between frugivores and the fruiting species they consume create complex mutualistic networks that structure and maintain the diversity and regeneration processes of tropical forest plant communities [16,17]. Understanding how these networks disassemble following the loss of species currently most in danger of extinction is key to understanding how tropical forests will be affected by anthropogenic environmental change.

In mutualistic networks, simulations of robustness-to-partner-loss (often called 'robustness-to-coextinction' simulations because partner losses are often predicted to cause eventual coextinctions) are used to analyse the effects of a single extinction on another species' secondary removal from the network

caused by the loss of all its interaction partners [18–23]. To date, nearly all studies on the robustness of seed-dispersal networks to plants experiencing the total loss of disperser mutualists as a secondary consequence of frugivore extinctions come from networks restricted to avian frugivores [24], despite the critical importance of a diverse suite of non-avian seed dispersers across the tropics [25–28]. Additionally, because body size is positively related to gape width and consequently diet breath [24,29], and because many large-bodied animals are threatened with extinction [7,23,30], the majority of studies investigating the consequences of frugivore losses for seed-dispersal networks have focused on predictions that follow simulated extinctions of only large-bodied, avian frugivores [24,29,31]. However, body size is not always predictive of network centrality [24,32–34] and recent work has drawn attention to disproportionate focus being placed on body size as an indicator of network role [35,36]. A key knowledge gap is understanding the threat posed to seed-dispersal networks of the removal of the frugivore species most likely to be lost: those currently at risk of extinction, regardless of taxonomic group. This is underscored by existing work on avian seed-dispersal - networks that suggests that endangered frugivores can be particularly highly connected species and thus may have a disproportionately large impact on network robustness [33]. As the loss of endangered frugivores reflects the most immediate realistic scenario of disperser loss that tropical forests are faced with, assessing the effects of their loss on seed-dispersal networks is an urgent conservation concern.

Here we explore how current trends in frugivore species losses will affect the structure of a neotropical plant–frugivore network in the Brazilian Atlantic Forest, one of the most biodiverse and also most threatened ecosystems in the world [37]. We used the most complete seed dispersal interaction dataset available for any tropical ecosystem [38], a record of 8320 interactions between plant and frugivore species from multiple taxonomic groups. To understand the role of endangered frugivore species in this species-rich network and to better anticipate consequences of their losses for ecosystem functioning, we simulated frugivore losses as predicted by endangerment status and analysed the effects of removals on network robustness to secondary plant species' losses of the function of their seed dispersal mutualism following frugivore partner extinctions. We then evaluated if the effects of removing species according to extinction risk differ from scenarios predicted by the sequential top-to-bottom removal of: (1) frugivores with the highest body masses, as is frequently evaluated in studies assessing seed-dispersal network robustness (e.g. [23]); (2) the most generalist frugivores (i.e. those frugivores that interact with the highest number of plant species), which has traditionally been used as a 'worst-case scenario' of species losses in mutualistic networks (e.g. [19]); and (3) a random removal scenario, which represents a null-model approach. To investigate the potential for interaction compensation by frugivores less affected by (or even benefitting from) current global change patterns, we also analysed how population growth trends, in addition to endangerment status, relate to species' centrality within the network.

We hypothesized that scenarios of species removals both by endangerment status and by body size would be more deleterious for network robustness to seed-dispersal mutualism loss relative to a randomized species removal sequence. We expected this because large-bodied vertebrates tend to have wider diet breadths and often a higher vulnerability to anthropogenic environmental change. At the same time, we expected that the worst-case scenario would be removing the most-connected frugivores first. We also hypothesized that endangerment status may be a positive predictor of a species' network centrality—measured here as network degree—because extinction risk is, in part, a function of species' traits (such as body mass) that may also relate to determinants of a species' network centrality, such as diet breadth. The results of these simulations can benefit conservation efforts by improving our understanding of the functional roles of endangered species [20].

2. Methods

(a) Dataset

We used the largest and most comprehensive dataset available of frugivory interactions (pairwise foraging events between animal species and plant species) to construct our binary network. Data were collated by Bello *et al.* from 166 published and unpublished sources [38]. The dataset spans 55 years of frugivore foraging observations in the Brazilian Atlantic Forest, a rapidly shrinking biodiversity hotspot of critical conservation concern [39–41]. A total of 8320 interactions are described in the dataset between 331 vertebrate species (232 birds, 90 mammals, 5 fish, 1 amphibian and 3 reptiles) and 788 plant species.

We used IUCN classifications [42] as markers of species endangerment. Species in the network dataset that were either data-deficient or unevaluated were omitted from all analyses ($n = 22$ omitted species: 1 ungulate, 4 bat, 5 fish, 1 rodent, 1 reptile and 10 bird species; see electronic supplementary material, table S1 for list of omitted frugivores).

(b) Geographical scales

We ran all analyses described below both at the biome scale (for the entire Atlantic Forest) and also at the ecoregion scale, using ecoregions defined by the Brazilian Ministry of the Environment and Instituto Brasileiro de Geografia e Estatistica [43]. We limited our ecoregion analyses to the three regions with the largest number of frugivory observations within the Atlantic Forest biome (and therefore the most completely characterized networks): (1) *cerrado* savannah/forest mosaic (377 observations between 55 plant and 91 frugivore species); (2) *mata caducifolia* (566 observations between 129 plant and 84 frugivore species); and (3) *Serra do Mar* (1741 independent frugivory observations between 246 plant and 173 frugivore species). Other ecoregions had fewer than 155 observations and are not included in our ecoregion-scale analysis to avoid using relatively small sample sizes. The cerrado ecoregion is the driest of the four and hosts a mix of multiple vegetation forms along a continuum of dry savannah grassland to dense deciduous and semi-deciduous woodlands [44]. The mata caducifolia is a seasonal deciduous tropical forest in which many trees lose their leaves in the dry season [45]. The Serra do Mar ecoregion has a moist subtropical climate and hosts tropical montane forests stretching along the Serra do Mar mountain range along Brazil's southern coast [37,46].

(c) Simulations of frugivore extinctions and secondary plant losses from the network

We used deterministic topological coextinction models [18,19] to assess robustness to species losses from the network following the extinctions of their seed-dispersing partners. We sequentially removed frugivores from the network and assessed secondary consequences for plants by quantifying species left without

network partners. We use the term 'secondary plant losses' to mean plant species that become disconnected from the network following the loss of all of their seed-dispersing partners. Once this occurs, a plant has essentially lost access to the ecosystem function of its seed dispersal mutualism, changing what will guide its dispersal and regeneration processes in the future. This approach has been used to draw predictions regarding the persistence of plant populations once they have lost their dispersers, a scenario generally presumed to induce stronger negative density-dependent mortality and decreased regeneration success [47], with the most extreme prediction being future extinction. However, coextinction of plant species following the loss of their seed dispersal mutualists has never been documented. Rather, the deterministic topological coextinction model approach is more realistically interpreted in this context as a metric for measuring the functional consequences of seed disperser extinction on the plant community. We interpret our results from the perspective that losing frugivores constitutes the elimination of a powerful mutualism with a broad set of functional consequences that occur well before the extreme endpoint of plant species' coextinctions. To assess the relative effects of future frugivore extinction scenarios, we simulated losing frugivore species in the order of: (1) their risk level to extinction in the near future; (2) decreasing body mass (a simulation of ecological downsizing, which is broadly observed in tropical forests [7]); (3) most to least connected within the network (degree, often considered a worst-case scenario [19]); and (4) random species loss as a null model scenario [18,19,23]. We ran 1000 iterations of removals of random species and used bootstrapping to obtain a mean estimate and 95% confidence intervals. We repeated this process for the scenario of losing the most endangered frugivores species from the network first, with random resampling within each endangerment category (e.g. multiple species belong to the IUCN Critically Endangered category, so the simulations sequentially removed randomly selected Critically Endangered species until all of the species from that category had been removed, then repeated that process in the next most endangered IUCN category (Endangered), and so on. We divided the Least Concern IUCN category into four groups, which we removed in the order: those with (1) declining population numbers; (2) stable population numbers; (3) increasing population numbers; and (4) those with unknown population trends (29 species across the whole biome).

(d) Relationships between endangered frugivores and specialist trees

To gain a better understanding of mechanisms shaping relationships in the network between endangered frugivores and secondary plant losses of their seed dispersers in the network, we investigated if the most specialized trees (those visited only by one frugivore) are more likely to be visited by an endangered frugivore than chance alone would predict. To do this, we conducted a permutation test by building a null distribution of expected values for the proportion of endangered frugivores visiting specialist trees, if endangered and non-endangered frugivores visited trees irrespective of specialist status. Our null distribution was based on 9999 permutations of the proportion of overall observed interactions in the network that involved endangered frugivores and then compared the observed value (that is, the proportion of endangered frugivores that are visiting specialist trees) with that distribution to determine if the observed value surpassed the top 5% of expected values (i.e. $p < 0.05$). This is a one-tailed test as we had the *a priori* hypothesis that we are seeing a higher number of interactions of specialist plants with endangered frugivores than we would expect by chance.

(e) Relationships between frugivore extinction risk level and network centrality

We calculated the network degree for each species as the cumulative number of species in the other trophic level with which they interacted. In other words, the degree of a frugivore is the number of plant species whose fruit it consumes. Degree is a widely used centrality metric to reflect a species' role in maintaining overall network connectivity [48]. We analysed relationships between frugivore degree and extinction risk level at the biome scale using generalized linear models with negative binomial errors. For our response variable (degree) to agree with model assumptions (specifically negative binomial errors), we subtracted 1 from all degree values in order for the transformed data's distribution to include zeros. For all species for which interaction data existed (regardless of native or non-native status), we divided extinction risk level into two levels: 'higher risk' and 'lower risk' based on if the species was categorized as Least Concern (LC) by the IUCN (the 'lower risk' category); or alternatively at a risk level greater than LC (the 'higher risk' category), which includes Near Threatened (NT), Vulnerable (VU), Endangered (EN) and Critically Endangered (CR). We ran a second negative binomial model using frugivore population growth trends rather than IUCN-based extinction-risk-level groupings. Population trends are typically updated prior to official IUCN endangerment status updates and can be an earlier indicator of species' future trajectories.

We examined the relationships between frugivore diet breadth and endangerment level and population growth trend by comparing frugivore mean degrees. At the ecoregion scale, however, the number of frugivore species within many of the heightened extinction risk and population trend categories is low (e.g. the cerrado only has three frugivore species left that are in the 'higher risk' endangerment category) and thus we did not run models at this scale because of the very small sample sizes (see electronic supplementary material, table S2 for species counts per category).

3. Results

(a) Network robustness to secondary plant losses from the network following simulated frugivore extinction scenarios

At the biome scale, simulated extinction of endangered species first yields an initial and severe drop in the number of plant species with seed-disperser partners, and this outcome is worse than any other frugivore loss scenario in terms of secondary plant losses (figure 1a,b). While body mass and degree eventually surpass the severity of the endangered species loss scenario, this occurs only after the loss of all Critically Endangered, Endangered and Vulnerable frugivores, at which point approximately 28% of all plant species have already lost their dispersers in our simulations. This pattern is largely consistent at the ecoregion scale as well (figure 1c–h).

(b) Endangered frugivores and specialist tree associations

A total of 54.7% of the specialist plants (degree = 1) are only visited by endangered frugivores in the biome-scale network (table 1), despite endangered frugivores only making up approximately 14% of the frugivores and approximately 17% of the interactions in the network. Our
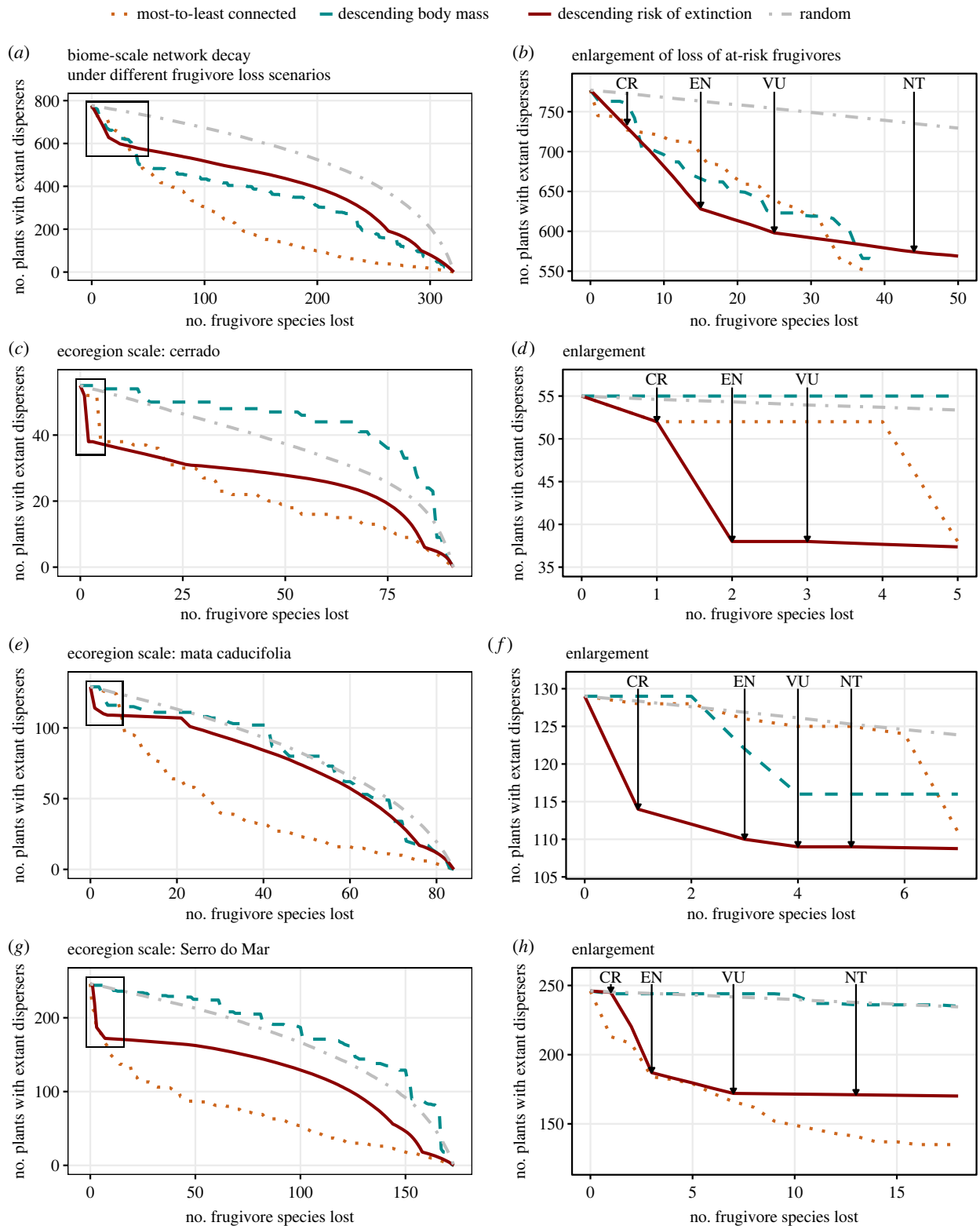
Figure 1. Frugivore loss simulations and the number of corresponding tree species left without interaction partners (seed dispersers) in the network at the biome and ecoregion scales. The y-axis shows the number of plant species with extant dispersers. The x-axis shows the number of frugivore species remaining in the network. The left column (plots (a, c, e, g)) show each frugivore loss scenario until the entire network has collapsed. The right column (plots (b, d, f, h)) are enlargements showing the subset of the simulated removals that correspond to losing all frugivores at risk of extinction (those above Least Concern IUCN status). Enlargements are annotated to indicate points beyond which all frugivores belonging to each risk category have been lost (note the cerrado has no Near Threatened (NT) species). The four simulated frugivore extinction scenarios shown are the sequential elimination of species based on: highest-to-lowest degree (as a potential worst-case scenario); largest-to-smallest body mass; random removals (mean of 1000 scenarios); and extinction risk level, in order from Critically Endangered (CR), Endangered (EN), Vulnerable (VU), to Near Threatened (NT). Within each endangerment category, we randomized species loss orders 1000 times, after which frugivores were sequentially removed from the Least Concern category, starting with those with populations that are declining, followed by stable, increasing, and unknown population trends. Upper and lower 95% CIs not visible owing to small size.

permutation test was strongly statistically significant ($p = 0.0001$) and indicated that specialist plants are interacting much more with endangered frugivores than expected by chance. Similarly, specialist trees at the ecoregion scale were largely dependent on endangered frugivores for dispersal (table 1).

Table 1. Proportion of specialist plants (listed here by degree or number of frugivore species, from 1—plants reliant on only a single frugivore species—to 5 frugivores) that are *exclusively* dispersed by endangered frugivores (grouped as all frugivores categorized as at greater risk of extinction than the LC category).

ecoregion	degree (no. frugivore partners)	no. plant species	no. species dispersed solely by endangered frugivores	proportion plants dispersed solely by endangered frugivores
Atlantic Forest biome	1	285	156	0.55
	2	120	37	0.31
	3	55	4	0.07
	4	44	5	0.11
	5	37	1	0.03
Serra do Mar	1	103	61	0.59
	2	38	10	0.26
	3	19	3	0.16
	4	19	1	0.05
	5	10	0	0.00
cerrado	1	30	17	0.57
	2	4	0	0.00
	3	0	0	0.00
	4	0	0	0.00
	5	0	0	0.00
mata caducifolia	1	58	19	0.33
	2	28	1	0.04
	3	8	0	0.00
	4	6	0	0.00
	5	5	0	0.00

(c) Centrality of at-risk frugivore species

Frugivores with higher extinction risks trended toward feeding on a greater diversity of fruiting plant species (i.e. had greater degree values in the network on average) than frugivores currently at a lower risk for extinction (figure 2), though this relationship was not statistically significant at the biome scale ($p = 0.25$) and appears qualitatively consistent at the ecoregion scales (figure 2c); we did not run models at ecoregion scale owing to small sample sizes.

Similarly, at the biome scale, frugivores with decreasing population sizes tended to forage on more plant species than those with increasing population trends ($p = 0.08$, figure 2b). This trend appears to be mirrored in most of the ecoregions (figure 2d).

4. Discussion

Leveraging the largest and most taxonomically comprehensive seed dispersal network available to date for a tropical system, we show here that across taxonomic groups (birds, arboreal mammals, terrestrial mammals), endangered species play a disproportionately large role in maintaining network structure in the Atlantic Forest, one of the most critically threatened and biodiverse ecosystems on the planet [39–41]. We report three key and novel findings from our models simulated probable future frugivore extinctions that shed light on the ecological roles of endangered animals and the ecosystem-level consequences of their losses. First, we show that at the biome and ecoregion scales, seed dispersal networks in this system are predicted to experience a rapid and outsized loss of tree species from the network if frugivores that are currently in danger of extinction are lost. At the biome scale, these secondary plant losses exceed even those predicted to follow the loss of the most-connected frugivores first, which has traditionally been considered a mutualistic network's worst-case scenario of loss. Second, this sharp pattern of secondary plant losses appears to occur because the frugivore species at a higher risk of extinction tend to interact with more tree species, particularly specialized tree species, than those at lower risk of extinction risk. Third, our results do not support the existence of functional redundancy between endangered dispersers and those currently increasing in abundance. Instead, we found that frugivore species with growing populations forage on significantly fewer plant species than frugivores with declining populations. When taken together, our results indicate that protecting endangered species will be critical for maintaining connectivity in tropical forest plant–frugivore networks and that the loss of endangered species may have higher-than-expected negative implications for tropical forest ecosystems by severely disrupting seed dispersal services and causing ecosystem function loss, potentially damaging the long-term reproductive success of animal-dispersed trees.

Surprisingly, in the Atlantic Forest network, we find that a sharp initial plummet in plant species driven by the loss of endangered frugivores surpasses secondary plant seed-dispersal mutualism losses predicted by the degree-based species removal scenario as well as the random-based and body mass-based removal scenarios. At the biome scale, we see over a quarter of plant species lost (approx. 28%)
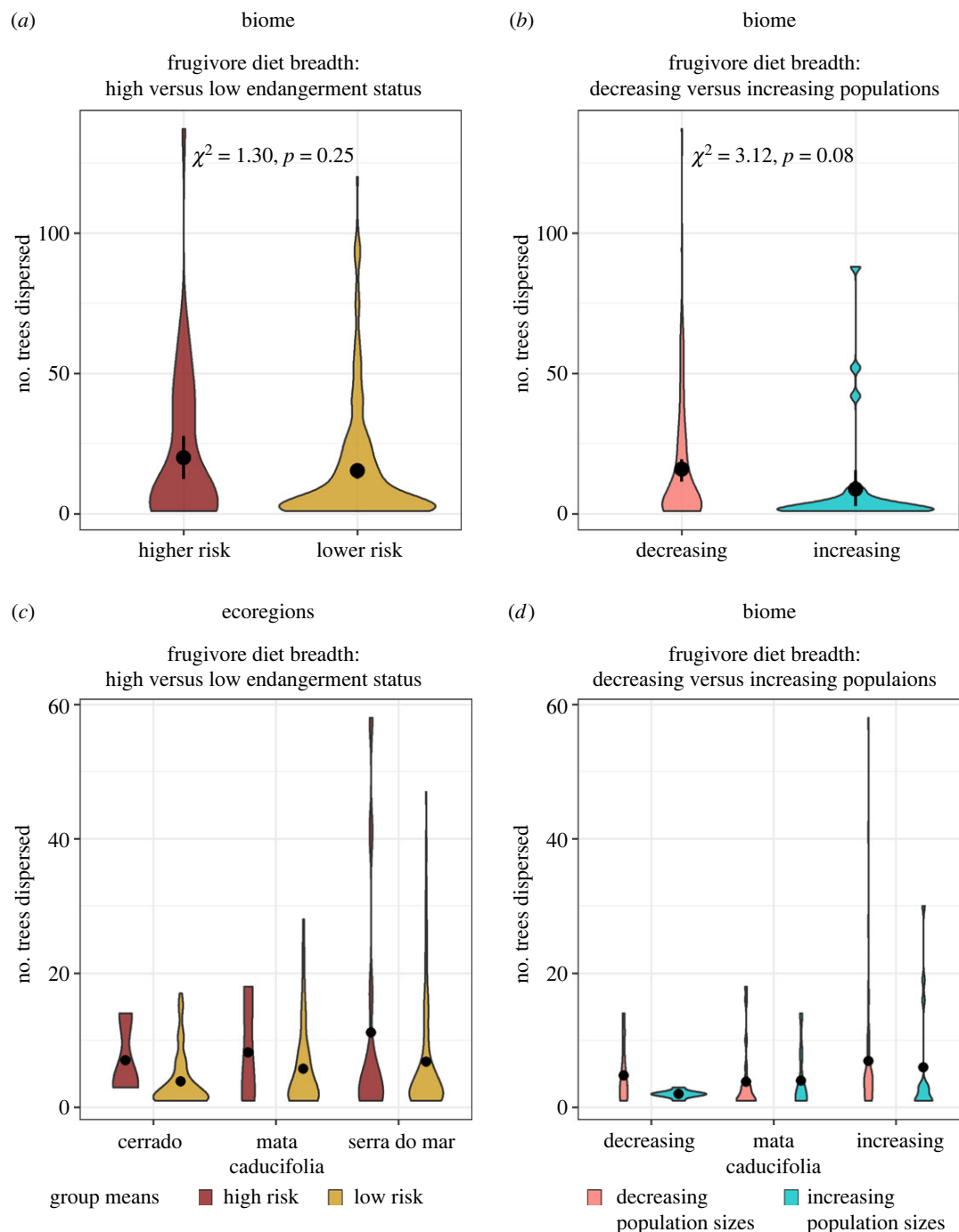
Figure 2. Violin plots showing relationships between frugivore degree and (*a*) extinction risk level and (*b*) global population trends. Widthof violin plots shows relative distribution of sample sizes. Bars show 95% confidence intervals (CI) around the means (shown as black circles), calculated from 1000 bootstrap iterations estimated from a negative binomial distribution using thefunction 'bootstrapnb' from the 'degreenet' package [49]. At the ecoregion scale, the degree of each frugivore species and group means (black circles) are plotted for each group of (*c*) frugivores at higher versus lower risk of extinction and (*d*) frugivores with decreasing versus increasing population trends. CIs are not included in (*c*) and (*d*) because the numbers of frugivore species within many of the extinction risk and population trend categories at the ecoregion scale are prohibitively low.

(figure 1*a*,*b*) from the network following the removal of all endangered and vulnerable frugivores, which comprise a relatively small portion of frugivores in the network (approx. 14%). This trend is largely mirrored at the ecoregion scale (figure 1*c*–*h*) and contradicts earlier predictions that selective removal of species with the highest degree from mutualistic networks will result in the largest secondary plant species losses [18,19,23,50]. Instead, our approach reveals an unexpected worst-case scenario of what is in fact also the most likely and realistic scenario of losing frugivores currently at risk of extinction.

The probable mechanism driving the steep plant-loss curves that follow the simulated extinctions of frugivores

at risk of extinction is the existence of a large portion of specialist trees in these networks that rely heavily on endangered frugivores. This is supported by our finding that frugivore partners of specialist trees are disproportionately species with a heightened extinction threat (as opposed to species of Least Concern). In fact, among highly specialized trees (those with just a single documented disperser species, *n* = 285 tree species) in this network, over half are only known to be dispersed by frugivores at risk of extinction. These findings run counter to the idea that endangered species tend to be more specialized than their abundant counterparts and that hyper-generalist species are also those most common in

a system [51]. Perhaps the wide-ranging nature of many endangered frugivores (e.g. primates, large birds) increases their likelihood of interacting with a larger number of specialist and/or rare plant species. Given that this is the most expansive characterization of the seed dispersal network in the tropics in existence, this is a surprising result with substantial conservation implications.

At the ecoregion scale, we also find sharp secondary plant losses following the simulated extinctions of endangered frugivores (figure 1c–h) and, as with the biome scale network, the underlying mechanism appears to be a disproportionate dependence of specialist trees on at-risk frugivores. In the ecoregion-level data, 33 to 59% of the most specialized trees (species with just one documented disperser) rely exclusively on frugivores with heightened extinction risks (table 1).

The non-random loss of functionally unique animal species sweeping across the tropics due to hunting, habitat loss and other anthropogenic activities has prompted questions about the potential for species unaffected or benefitted by defaunated conditions to ecologically compensate for species being lost [52–54]. There is no conclusive answer regarding the potential of the generally smaller-bodied, smaller-ranging species to fill the seed dispersal roles of the frugivores that systems are losing. Some existing studies indicate that exotic species and those robust to human disturbance (often rodents facilitating short-distance secondary dispersal) can compensate for the loss of traditionally dominant frugivores from networks, although dispersal distances and plant population connectivity are still diminished under such scenarios [55–58]. More often, studies have found low functional redundancy between frugivore species negatively affected versus those that thrive in response to anthropogenic disturbances, resulting in little to no effective compensation for the loss of seed dispersal services [54,59–63]. Here, we add to our understanding of this topic by examining relationships between species' network degrees—frugivore diet breadths—and their endangerment or population growth status. Our results indicate a trend in which species that are increasing in abundance have smaller diet breadths and as such are not able to fill the network roles of species that are declining, which appear to be the more generalist frugivores. This is consistent with other recent work [53,54] suggesting that tropical seed dispersal networks affected by defaunation are losing connectivity.

Our results underscore the need for further related research as this dataset—though it is the most comprehensive seed dispersal network data available to date for a tropical forest system—does not provide insights into differences in either seed dispersal effectiveness or interaction strength (i.e. it only provides information on presence or absence of interactions). Additionally, these data do not incorporate the fact that fruiting tree species can vary in their dependence on dispersers (e.g. intraspecific variation in susceptibility to conspecific density-dependent mortality and differences in

benefits gained from frugivore gut passage could affect predictions from our model approach of secondary consequences for plants following disperser extinctions). Further, sampling across ecoregions within the Atlantic Forest biome is currently uneven, and as such, we were only able to assess a small subset of ecoregions separately. It is also possible that rare trees could appear as specialists in this dataset because their full seed dispersal network has not yet been comprehensively sampled. Similarly, the importance of endangered frugivores as dispersers of specialist trees may be inflated by this meta-analysis approach if animals that are of higher conservation concern have diets that have been more thoroughly documented compared with non-endangered species in the network. As a final caveat to consider in future studies, bats are underrepresented both in this dataset and in most seed dispersal network studies but may be another major taxonomic component of networks currently at risk due to human activities [64,65].

Our findings indicate that frugivores currently most at risk of being lost from the Atlantic Forest biome play outsized roles in maintaining network connectance and are the sole frugivore dispersers for a large portion of the specialist trees within this system. Particularly given the global conservation importance and vulnerability of the Brazilian Atlantic Forest (both a conservation and biodiversity hotspot), we urge more consideration in seed dispersal network studies be given to the role of endangered animals across taxa (especially incorporating species beyond birds) in maintaining ecosystem functioning. Given that current species extinction rates are over 100 times greater than background rates and 16–33% of all vertebrates species are estimated to be threatened or endangered—most of which are in tropical forests—it is an urgent priority to evaluate the ecological roles and importance filled by at-risk species both for our conceptual understanding of ecosystem functioning and for informing conservation efforts [3,66,67].

References

1. Peres CA, Emilio T, Schietti J, Desmoulière SJM, Levi T. 2016 Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. Proc. Natl Acad. Sci. USA 113, 892–897. (doi:10.1073/pnas.1516525113)

2. Young HS, McCauley DJ, Galetti M, Dirzo R. 2016 Patterns, causes, and consequences of Anthropocene defaunation. Annu. Rev. Ecol. Evol. Syst. 47, 333–358. (doi:10.1146/annurev-ecolsys-112414-054142)

3. Ceballos G, Ehrlich PR, Dirzo R. 2017 Biological annihilation via the ongoing sixth mass extinction

signaled by vertebrate population losses and declines. *Proc. Natl Acad. Sci. USA* **114**, E6089–E6096. (doi:10.1073/pnas.1704949114)

4. Fricke EC, Ordonez A, Rogers HS, Svenning J-C. 2022 The effects of defaunation on plants' capacity to track climate change. *Science* **375**, 210–214. (doi:10.1126/science.abk3510)

5. Teixido AL, Fuzessy LF, Souza CS, Gomes IN, Kaminski LA, Oliveira PC, Maruyama PK. 2022 Anthropogenic impacts on plant-animal mutualisms: a global synthesis for pollination and seed dispersal. *Biol. Conserv.* **266**, 109461. (doi:10.1016/j.biocon.2022.109461)

6. Howe HF, Smallwood J. 1982 Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* **13**, 201–228. (doi:10.1146/annurev.es.13.110182.001221)

7. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. 2014 Defaunation in the Anthropocene. *Science* **345**, 401–406. (doi:10.1126/science.1251817)

8. Traveset A. 1998 Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspect. Plant Ecol. Evol. Syst.* **1**, 151–190. (doi:10.1078/1433-8319-00057)

9. Rogers HS, Cavazos BR, Gawel AM, Karnish A, Ray CA, Rose E, Thierry H, Fricke EC. 2021 Frugivore gut passage increases seed germination: an updated meta-analysis. *bioRxiv*, 2021.10.12.462022. (doi:10.1101/2021.10.12.462022)

10. Razafindratsima OH, Dunham AE. 2015 Assessing the impacts of nonrandom seed dispersal by multiple frugivore partners on plant recruitment. *Ecology* **96**, 24–30. (doi:10.1890/14-0684.1)

11. Janzen DH. 1970 Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528.

12. Connell JH. 1971 On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of populations* (eds PJ Den Boer, G Gradwell), pp. 298–312. Wageningen, The Netherlands: PUDOC.

13. Browne L, Ottewell K, Karubian J. 2015 Short-term genetic consequences of habitat loss and fragmentation for the neotropical palm *Oenocarpus bataua*. *Heredity* **115**, 389–395. (doi:10.1038/hdy.2015.35)

14. Giombini MI, Bravo SP, Sica YV, Tosto DS. 2017 Early genetic consequences of defaunation in a large-seeded vertebrate-dispersed palm (*Syagrus romanzoffiana*). *Heredity* **118**, 568–577. (doi:10.1038/hdy.2016.130)

15. Carvalho CdS, García C, Lucas MS, Jordano P, Côrtes MC. 2021 Extant fruit-eating birds promote genetically diverse seed rain, but disperse to fewer sites in defaunated tropical forests. *J. Ecol.* **109**, 1055–1067. (doi:10.1111/1365-2745.13534)

16. Bascompte J, Jordano P. 2007 Plant-animal mutualistic networks: the architecture of biodiversity. *Ann. Rev. Ecol. Evol. Syst.* **38**, 567–593. (doi:10.1146/annurev.ecolsys.38.091206.095818)

17. Bascompte J, Jordano P. 2013 *Mutualistic networks*. Princeton, NJ: Princeton University Press.

18. Dunne JA, Williams RJ, Martinez ND. 2002 Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* **5**, 558–567. (doi:10.1046/j.1461-0248.2002.00354.x)

19. Memmott J, Waser NM, Price MV. 2004 Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B* **271**, 2605–2611. (doi:10.1098/rspb.2004.2909)

20. Brodie JF, Aslan CE, Rogers HS, Redford KH, Maron JL, Bronstein JL, Groves CR. 2014 Secondary extinctions of biodiversity. *Trends Ecol. Evol.* **29**, 664–672. (doi:10.1016/j.tree.2014.09.012)

21. Losapio G, Schöb C. 2017 Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. *Funct. Ecol.* **31**, 1145–1152. (doi:10.1111/1365-2435.12839)

22. Briggs H, Ayers CA, Armsworth PR, Brosi BJ. 2019 Testing how antagonistic interactions impact the robustness of plant-pollinator networks. *J. Pollinat. Ecol.* **25**, 69–77. (doi:10.26786/1920-7603(2019)540)

23. Donoso I, Sorensen MC, Blendinger PG, Kissling WD, Neuschulz EL, Mueller T, Schleuning M. 2020 Downsizing of animal communities triggers stronger functional than structural decay in seed-dispersal networks. *Nat. Commun.* **11**, 1582. (doi:10.1038/s41467-020-15438-y)

24. Escribano-Avila G, Lara-Romero C, Heleno R, Traveset A. 2018 Tropical seed dispersal networks: emerging patterns, biases, and keystone species traits. In *Ecological networks in the tropics: an integrative overview of species interactions from some of the most species-rich habitats on earth* (eds W Dáttilo, V Rico-Gray), pp. 93–110. Cham, Switzerland: Springer International Publishing.

25. Fragoso JMV, Silvius KM, Correa JA. 2003 Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology* **84**, 1998–2006. (doi:10.1890/01-0621)

26. Nuñez-Iturri G, Howe HF. 2007 Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. *Biotropica* **39**, 348–354.

27. Heymann EW, Culot L, Knogge C, Noriega Piña TE, Tirado Herrera ER, Klapproth M, Zinner D. 2017 Long-term consistency in spatial patterns of primate seed dispersal. *Ecol. Evol.* **7**, 1435–1441. (doi:10.1002/ece3.2756)

28. Sales L, Culot L, Pires MM. 2020 Climate niche mismatch and the collapse of primate seed dispersal services in the Amazon. *Biol. Conserv.* **247**, 108628. (doi:10.1016/j.biocon.2020.108628)

29. Naniwadekar R, Chaplod S, Datta A, Rathore A, Sridhar H. 2019 Large frugivores matter: insights from network and seed dispersal effectiveness approaches. *J. Anim. Ecol.* **88**, 1250–1262. (doi:10.1111/1365-2656.13005)

30. Bovo AAA, Ferraz KMPMB, Magioli M, Alexandrino ER, Hasui É, Ribeiro MC, Tobias JA. 2018 Habitat fragmentation narrows the distribution of avian functional traits associated with seed dispersal in tropical forest. *Pers. Ecol. Conserv.* **16**, 90–96. (doi:10.1016/j.pecon.2018.03.004)

31. Vidal MM, Pires MM, Guimarães PR. 2013 Large vertebrates as the missing components of seed-dispersal networks. *Biol. Conserv.* **163**, 42–48. (doi:10.1016/j.biocon.2013.03.025)

32. Schleuning M *et al.* 2014 Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecol. Lett.* **17**, 454–463. (doi:10.1111/ele.12245)

33. Vidal MM, Hasui E, Pizo MA, Tamashiro JY, Silva WR, Guimarães PR. 2014 Frugivores at higher risk of extinction are the key elements of a mutualistic network. *Ecology* **95**, 3440–3447. (doi:10.1890/13-1584.1)

34. Mello MAR, Rodrigues FA, Costa LdF, Kissling WD, Şekercioğlu ÇH, Marquitti FMD, Kalko EKV. 2015 Keystone species in seed dispersal networks are mainly determined by dietary specialization. *Oikos* **124**, 1031–1039. (doi:10.1111/oik.01613)

35. Acevedo-Quintero JF, Saldaña-Vázquez RA, Mendoza E, Zamora-Abrego JG. 2020 Sampling bias affects the relationship between structural importance and species body mass in frugivore-plant interaction networks. *Ecol. Compl.* **44**, 100870. (doi:10.1016/j.ecocom.2020.100870)

36. Ong L, McConkey KR, Campos-Arceiz A. 2022 The ability to disperse large seeds, rather than body mass alone, defines the importance of animals in a hyper-diverse seed dispersal network. *J. Ecol.* **110**, 313–326. (doi:10.1111/1365-2745.13809)

37. Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009 The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv.* **142**, 1141–1153. (doi:10.1016/j.biocon.2009.02.021)

38. Bello C *et al.* 2017 Atlantic frugivory: a plant–frugivore interaction data set for the Atlantic Forest. *Ecology* **98**, 1729. (doi:10.1002/ecy.1818)

39. Martinez D, Hirota M, Ponzoni F, Rosa M. 2018 *Atlas dos remanescentes florestais da Mata Atlântica: mapeamento dos sistemas costeiros*. doi:10.13140/RG.2.2.21653.55522

40. de Santana RO, Delgado RC, Schiavetti A. 2020 The past, present and future of vegetation in the Central Atlantic Forest Corridor, Brazil. *Remote Sens. Appl.: Soc. Environ.* **20**, 100357. (doi:10.1016/j.rsase.2020.100357)

41. Galetti M *et al.* 2021 Causes and Consequences of Large-Scale Defaunation in the Atlantic Forest. In *The atlantic forest: history, biodiversity, threats and opportunities of the mega-diverse forest* (eds MCM Marques, CEV Grelle), pp. 297–324. Cham, Switzerland: Springer International Publishing.

42. IUCN. 2021 The IUCN Red List of Threatened Species. See (https://www.iucnredlist.org)

43. IBGE, USGS. 1993 Mapa de Vegetacao Do Brasil.

44. Durigan G, Ratter JA. 2006 Successional changes in cerrado and cerrado/forest ecotonal vegetation IN Western São Paulo State, Brazil, 1962–2000. *Edinb. J. Bot.* **63**, 119–130. (doi:10.1017/S0960428606000357)

45. Ruschel AR, Nodari RO, Moerschbacher BM. 2007 Woody plant species richness in the turvo state park, a large remnant of deciduous Atlantic Forest, Brazil. *Biodivers. Conserv.* **16**, 1699–1714. (doi:10.1007/s10531-006-9044-7)

46. Mantovani W. 1993 *Estrutura e dinâmica da floresta atlântica na juréia, iguape-SP*. São Paulo, Brazil: Universidade de São Paulo.

47. Bello C, Galetti M, Pizo MA, Magnago LFS, Rocha MF, Lima RAF, Peres CA, Ovaskainen O, Jordano P. 2015 Defaunation affects carbon storage in tropical forests. *Sci. Adv.* **1**, e1501105. (doi:10.1126/sciadv.1501105)

48. Messeder JVS, Guerra TJ, Dáttilo W, Silveira FAO. 2020 Searching for keystone plant resources in fruit-frugivore interaction networks across the Neotropics. *Biotropica* **52**, 857–870. (doi:10.1111/btp.12804)

49. Handcock MS. 2018 *degreenet: Models for skewed count distributions relevant to networks. R package version 1.3-3*. See https://CRAN.R-project.org/package=degreenet.

50. Bascompte J, Stouffer DB. 2009 The assembly and disassembly of ecological networks. *Phil. Trans. R. Soc. B* **364**, 1781–1787. (doi:10.1098/rstb.2008.0226)

51. Rabinowitz D. 1981 Seven Forms of Rarity. In *Foundations of macroecology: classic papers with commentaries* (eds FA Smith, JL Gittleman, JH Brown), pp. 480–494. Chicago, IL: University of Chicago Press.

52. Baumgartner MT, Almeida-Neto M, Gomes LC. 2020 A novel coextinction model considering compensation and new interactions in ecological networks. *Ecol. Modell* **416**, 108876. (doi:10.1016/j.ecolmodel.2019.108876)

53. Rogers HS, Donoso I, Traveset A, Fricke EC. 2021 Cascading impacts of seed disperser loss on plant communities and ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **52**, 641–666. (doi:10.1146/annurev-ecolsys-012221-111742)

54. Fricke EC, Tewksbury JJ, Rogers HS. 2018 Defaunation leads to interaction deficits, not interaction compensation, in an island seed dispersal network. *Glob. Change Biol.* **24**, e190–e200. (doi:10.1111/gcb.13832)

55. Cao L, Xiao Z, Guo C, Chen J. 2011 Scatter-hoarding rodents as secondary seed dispersers of a frugivore-dispersed tree Scleropyrum wallichianum in a defaunated Xishuangbanna tropical forest, China. *Integr. Zool.* **6**, 227–234. (doi:10.1111/j.1749-4877.2011.00248.x)

56. Sekar N, Sukumar R. 2013 Waiting for Gajah: an elephant mutualist's contingency plan for an endangered megafaunal disperser. *J. Ecol.* **101**, 1379–1388. (doi:10.1111/1365-2745.12157)

57. García D, Martínez D, Stouffer DB, Tylianakis JM. 2014 Exotic birds increase generalization and compensate for native bird decline in plant–frugivore assemblages. *J. Anim. Ecol.* **83**, 1441–1450. (doi:10.1111/1365-2656.12237)

58. Pérez-Méndez N, Jordano P, Valido A. 2018 Persisting in defaunated landscapes: reduced plant population connectivity after seed dispersal collapse. *J. Ecol.* **106**, 936–947. (doi:10.1111/1365-2745.12848)

59. Brodie JF, Helmy OE, Brockelman WY, Maron JL. 2009 Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecol. Appl.* **19**, 854–863. (doi:10.1890/08-0955.1)

60. Brodie JF, Helmy OE, Brockelman WY, Maron JL. 2009 Functional differences within a guild of tropical mammalian frugivores. *Ecology* **90**, 688–698. (doi:10.1890/08-0111.1)

61. Holbrook KM, Loiselle BA. 2009 Dispersal in a Neotropical tree, Virola flexuosa (Myristicaceae): does hunting of large vertebrates limit seed removal? *Ecology* **90**, 1449–1455. (doi:10.1890/08-1332.1)

62. McConkey KR, Drake DR. 2015 Low redundancy in seed dispersal within an island frugivore community. *AoB Plants* **7**, plv088. (doi:10.1093/aobpla/plv088)

63. Boissier O, Feer F, Henry P-Y, Forget P-M. 2020 Modifications of the rain forest frugivore community are associated with reduced seed removal at the community level. *Ecol. Appl.* **30**, e02086. (doi:10.1002/eap.2086)

64. Mello MAR, Marquitti FMD, Guimaraes Jr PR, Kalko EKV, Jordano P, de Aguiar MA. 2011 The missing part of seed dispersal networks: structure and robustness of bat-fruit interactions. *PLoS ONE* **6**, e17395. (doi:10.1371/journal.pone.0017395)

65. Ghanem S, Voigt C. 2013 Defaunation of tropical forests reduces habitat quality for seed-dispersing bats in Western Amazonia: an unexpected connection via mineral licks. *Anim. Conserv.* **17**, 44–51. (doi:10.1111/acv.12055)

66. Hoffmann M et al. 2010 The impact of conservation on the status of the World's vertebrates. *Science* **330**, 1503–1509. (doi:10.1126/science.1194442)

67. Ceballos G, Ehrlich PR, Raven PH. 2020 Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proc. Natl Acad. Sci. USA* **117**, 13 596–13 602. (doi:10.1073/pnas.1922686117)

68. Lamperty T, Brosi BJ. 2022 Data from: Loss of endangered frugivores from seed dispersal networks generates severe mutualism disruption. Figshare. (doi:10.6084/m9.figshare.c.6214775)