Authors for correspondence:
Emma-Liina Marjakangas
e-mail: emma-liina.marjakangas@ntnu.no
Mauro Galetti
e-mail: mgaletti@rc.unesp.br

THE ROYAL SOCIETY PUBLISHING

Estimating interaction credit for trophic rewilding in tropical forests

Emma-Liina Marjakangas[1,†], Luísa Genes[2,†], Mathias M. Pires[3,†], Fernando A. S. Fernandez[2], Renato A. F. de Lima[4], Alexandre A. de Oliveira[4], Otso Ovaskainen[1,5], Alexandra S. Pires[6], Paulo I. Prado[4] and Mauro Galetti[7]

[1]Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, N-7491 Trondheim, Norway
[2]Departamento de Ecologia, Universidade Federal do Rio de Janeiro, CP 68020, Rio de Janeiro, RJ 21941-590, Brazil
[3]Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP CEP 13.083-862, Brazil
[4]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP CEP 05508-090, Brazil
[5]Faculty of Biological and Environmental Sciences, University of Helsinki, PO Box 65, Helsinki FI-00014, Finland
[6]Departamento de Ciências Ambientais, Universidade Federal Rural do Rio de Janeiro, Seropédica, RJ 23890-000, Brazil
[7]Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), CP 199, Rio Claro, SP 13506-900, Brazil

EM, 0000-0002-5245-3779; LG, 0000-0001-7556-4562; MMP, 0000-0003-2500-4748; OO, 0000-0001-9750-4421; MG, 0000-0002-8187-8696

Trophic rewilding has been suggested as a restoration tool to restore ecological interactions and reverse defaunation and its cascading effects on ecosystem functioning. One of the ecological processes that has been jeopardized by defaunation is animal-mediated seed dispersal. Here, we propose an approach that combines joint species distribution models with occurrence data and species interaction records to quantify the potential to restore seed-dispersal interactions through rewilding and apply it to the Atlantic Forest, a global biodiversity hotspot. Using this approach, we identify areas that should benefit the most from trophic rewilding and candidate species that could contribute to cash the credit of seed-dispersal interactions in a given site. We found that sites within large fragments bearing a great diversity of trees may have about 20 times as many interactions to be cashed through rewilding as small fragments in regions where deforestation has been pervasive. We also ranked mammal and bird species according to their potential to restore seed-dispersal interactions if reintroduced while considering the biome as a whole and at finer scales. The suggested approach can aid future conservation efforts in rewilding projects in defaunated tropical rainforests.

This article is part of the theme issue 'Trophic rewilding: consequences for ecosystems under global change'.

1. Introduction

The pervasive biodiversity crisis we live in has prompted active conservation approaches to reverse the effects of defaunation [1,2]. As animal populations and species decline in natural environments, the ecological interactions involving them are also lost, threatening the functioning of ecological systems [3]. Trophic rewilding, defined as species reintroductions and surrogate introductions to restore ecological interactions [4,5], is increasingly considered as one of the few viable options to reinstate ecosystem functions [6]. However, species introductions entail intensive planning, integrating detailed natural history and ecological knowledge to ensure the desired results while reducing the potential risks [4,7].

Although rewilding has become an important debate in recent years [8,9], few projects in the field have applied rewilding for mitigating the loss of species interactions [10,11]. Because rewilding focuses on restoring ecological processes

[4,9], the choice of the candidate species should be based on the balance between the probability of population establishment and the benefit of the restored interactions for ecosystem functions [4,5]. Using an economics analogy, species reintroductions could allow defaunated areas to gradually 'cash' a credit of ecological interactions where their interaction partners are still extant, which depends on the species-specific traits as well as on the abundances of the focal species and their partners [12]. The interaction credit framework is based on the potential to restore interactions (i.e. to reconnect species that became disconnected) in an area following reintroduction; thus, it can be used to predict and to evaluate the success of rewilding in reinstating ecological processes.

Restoring certain types of interactions, such as seed dispersal, can be particularly beneficial. Seed dispersal helps natural forest regeneration and may even aid the restoration of neighbouring areas, creating more suitable habitat and generating a positive feedback for conservation efforts [13]. Most tropical tree species rely on animal-mediated seed dispersal for recruitment [14]. Yet, many frugivore species that establish non-redundant seed-dispersal interactions tend to be the same that are overhunted and affected by fragmentation [15,16]. Therefore, local extinctions can cause the loss of those ecological interactions, cascading to the loss of functioning in defaunated tropical areas [17].

Tropical forests are highly threatened worldwide but the Atlantic Forest in South America represents one of the worst-case scenarios for protecting biodiversity: it has been severely defaunated and is highly fragmented [18,19], with many of the fragments too small to maintain viable populations of certain species. Moreover, the agricultural and urban matrices surrounding forest patches prevent some animals from recolonizing patches where they have been extirpated [20]. Thus, the re-establishment of ecological interactions even in large fragments is unlikely to occur without more active approaches, such as trophic rewilding [7,21].

Despite a large amount of data available on species distributions and local interaction patterns, predicting how the reintroduced species will interact with the local community is still an obstacle [12,22,23]. Devising a comprehensive framework for trophic rewilding requires integrating information on species distributions and interaction patterns across their range to allow inferring which interactions are likely or unlikely to occur [23]. Thus, a spatially informed framework that takes interactions into account is needed to aid decision-making regarding the prioritization of the areas and the choice of candidate species for trophic rewilding at broad scales [24].

Here we use a probabilistic framework that combines joint species distribution models [25], the ecological network approach [23] and the credit of ecological interactions framework [12] to identify priority areas and candidate species for trophic rewilding, with a focus on restoring seed-dispersal interactions. We use the Atlantic Forest as a case study and show how the proposed framework can help to unveil interaction credit hotspots and to detect which species are the best candidates for rewilding at different spatial scales.

2. Material and methods

The credit of ecological interactions corresponds to the number of animal–plant interactions expected to be restored if an extirpated species is reintegrated into a given area [12]. Therefore, quantifying interaction credit requires a toolset for predicting pairwise species interactions in a locality. The prerequisite for an interaction to take place is that the focal species co-occur in space and time. Although species occurrences can be inferred directly from occurrence data, modelling species occurrences, besides allowing predictions for poorly sampled locations, offers the possibility of encompassing uncertainty regarding occurrence and co-occurrence patterns. Species may co-occur because they respond in the same manner to the environment, but co-occurring does not mean species will necessarily interact. Assuming that two species co-occur in space and time, interactions will still depend on a number of factors, such as species traits, phenology and abundance [12,26,27]. Because of the inherent challenges of detecting and predicting interactions in a community, the appropriate way to model interaction patterns is using a probabilistic approach [23,28]. Pairwise interaction probabilities can be obtained by the element-wise product between the matrix O, depicting species co-occurrence probabilities, and matrix A, depicting the expected interaction probabilities once the species co-occur [23]. Considering that the aim of trophic rewilding is to restore processes that have been lost over time, its outcomes in terms of interaction credit can be predicted and then evaluated by comparing expected interactions under two different scenarios: (i) a benchmark historical scenario, and (ii) the current scenario, where many sites may be defaunated relative to the historical benchmark. We apply the framework outlined above to estimate the credit of seed-dispersal interactions across the Atlantic Forest in South America.

(a) Data

To infer current distribution patterns of frugivores and plants, we used the most spatially and taxonomically comprehensive community databases available for the Brazilian Atlantic Forest (the ATLANTIC series data papers: https://github.com/LEE-Clab/Atlantic_series; and the Neotropical Tree Communities database TreeCo version 2.0: http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start). We used data on all seed disperser genera with interactions recorded in the Atlantic Forest [29], excluding species known to behave more as seed predators than dispersers, as well as bats and small mammals owing to incomplete data on distribution or interaction patterns (which could impair the assessment of a spatial credit at broad scale) and to taxonomic inconsistency in some genera (which could impair the prediction of pairwise interactions). Therefore, we compiled data on 211 vertebrate species (birds and medium- to large-sized mammals) and 1426 tree and palm species [30–33]. See electronic supplementary material, appendix A, for the filtered reference list of the plant occurrence data. We only considered plant species that were identified as zoochoric [29,34], reported to grow greater than or equal to 4 m high, and having greater than or equal to five observations in the plant occurrence dataset. For the full list of included species, see electronic supplementary material, appendix B. To guarantee a broad coverage across the entire biome, we created a regular grid of 40 000 prediction sites spanning the Atlantic Forest in ArcGIS software (version 10.3) and selected for later use those 912 sites that overlapped with Atlantic Forest fragments. To assess the interaction component, we used interaction records from the ATLANTIC-FRUGIVORY dataset [29]. From this dataset, we built the final interaction matrix P, as described in more detail below.

(b) Co-occurrence probabilities

We inferred co-occurrence probabilities for frugivores and plants across the Atlantic Forest using joint species distribution models (HMSC [25]). HMSC helps to overcome the problem of low spatial overlap in the original surveys across taxonomic groups, generating predicted occurrence probabilities for each frugivore and plant species across the Atlantic Forest (for more detailed

description on the model construction and included data, see electronic supplementary material, appendix C). The predicted probabilities of species occurring in a given site are determined not only by the values of environmental covariates on that site (through the fixed effect part of the HMSC), but also on the occurrences of the focal and other species in nearby sampling sites (through spatially structured latent variables included in HMSC, see [35]). We generated 500 predicted communities in each of the 912 prediction sites described above. For each prediction site, we sampled model parameters from the posterior distribution, and thus the predictions account for parameter uncertainty.

To generate a historical benchmark distribution of frugivores, we used the distribution records of frugivores from IUCN [36] complemented by records from Wikiaves [37] to determine the sub-regions where each species occurs. The Atlantic Forest comprises seven biogeographical sub-regions that differ in environmental variables and biodiversity composition: Interior, Araucaria, Serra do Mar, Bahia, Diamantina, Sao Francisco and Pernambuco [38]. We assumed in the benchmark scenario that species could have been present in all prediction sites within all sub-regions where the species is known to currently occur, and assigned $p = 1$ for the probability of species occurrence in those sites. We also performed a sensitivity analysis by setting the occurrence probabilities of frugivores in the benchmark scenario equal to the maximum of the mean posterior occurrence probability across all prediction sites. Because our main interest was in the effects of reintroducing the frugivores, we used the estimated occurrence probabilities for the plants in both the current and the benchmark scenario. Even though it is plausible that certain plants had greater occurrence probabilities in certain sites in the past, this would only increase our credit estimates. Thus, by setting the benchmark using the current probabilities for plants, we adopt a conservative approach and we can assign differences between the two scenarios to the differences in frugivore occurrence probabilities.

We constructed predicted co-occurrence matrices for each site as the product of occurrence probabilities for frugivores (either assuming the benchmark distribution or the current predicted distribution) and plants (assuming the current predicted distribution).

(c) Interaction probabilities

We converted records of pairwise interaction data to interaction probabilities using a semi-quantitative approach. Based on the number of studies where pairwise interactions were recorded in the ATLANTIC-FRUGIVORY dataset [29], we built an interaction matrix **A**, where we assigned interactions between any frugivore i and plant j to one of four categories: very likely ($a_{ij} = 1$), when interaction was recorded more than once; likely ($a_{ij} = 0.75$), when interaction was recorded once; possible ($a_{ij} = 0.5$), when the frugivore species interacts with another plant species within the focal plant species' genus; and unlikely ($a_{ij} = 0.1$), when the frugivore species has no observed interactions with any plant species within the focal plant species' genus. We assign unlikely interactions a value greater than zero, because differentiating between true and sampling-induced zeros is challenging [39,40] and it is conceptually wrong to assume that unobserved interactions are impossible to occur. To test for the sensitivity of the results to the probabilities assigned to unlikely interactions, we re-ran all analyses under two additional scenarios: assuming $a_{ij} = 0.05$ and $a_{ij} = 0.001$ for unlikely interactions.

(d) Calculating the spatial credit of ecological interactions

To estimate the credit of ecological interactions, we compared the historical benchmark and the current scenario of seed-dispersal interactions across the Atlantic Forest. First, we obtained the probabilistic interaction network (matrix **P**, with elements p_{ij}) for each scenario in each prediction site as the element-wise product of the co-occurrence (**O**) and interaction matrices (**A**). We then calculated for each prediction site the expected number of interactions, $\hat{L}$, as the sum of all pairwise interaction probabilities [28] $\hat{L} = \sum p_{ij}$ and computed the site-specific spatial credit of ecological interactions as the difference between $\hat{L}$ for the benchmark and current scenarios.

(e) Calculating frugivore-specific contributions to the credit of ecological interactions

To understand which species show potential for cashing the highest credit of ecological interactions through rewilding locally and regionally in the Atlantic Forest, we first computed for each site the expected number of interactions of each frugivore i as the sum of interaction probabilities with all plants in that site [28]: $\hat{k}_i = \sum_{j=1}^{N_p} p_{ij}$. The species-specific local credit of interactions, the local score, was obtained as the difference between a species $\hat{k}$ in the current versus the benchmark scenario, $\Delta\hat{k}$. We then built a distribution of $\Delta\hat{k}$ for each species considering all prediction sites and ranked the species based on the mean $\Delta\hat{k}$. To compute $\Delta\hat{k}$ we only consider the prediction sites where a species is expected to occur according to the benchmark scenario. We selected 12 species with the highest regional scores to explore more closely their potential for restoring seed-dispersal interactions through rewilding. We examined the distribution of their local scores and discussed the ecology, current threats and rewilding feasibility considering these species. We also calculated the regional scores for each biogeographical sub-region separately to illustrate how this approach could help to guide rewilding at a finer scale.

3. Results

The spatial credit of ecological interactions ranged between 209 and 4814 interactions that could be cashed in prediction sites across the Atlantic Forest (figure 1). Sites with greater credit have about 20 times as many interactions to be cashed through rewilding as the sites with lower credit. The credit was highest in the Interior sub-region and lowest in the Pernambuco sub-region (figure 1; electronic supplementary material, appendix D, figure S1). The interaction credit was highest in areas where occurrence probabilities were high for plant species but low for frugivore species as compared to their expected distributions in the benchmark scenario (electronic supplementary material, appendix D, figures S2 and S3). The areas with low interaction credit were either areas having a high frugivore species richness that matches the expectation in the benchmark scenario, or areas where plant species richness is currently low and hence there are fewer plant species missing frugivore partners.

By estimating the expected number of interactions to be restored by each frugivore, we observed a large variation in the credit that could be cashed by different species, both at local and regional scales. Altogether 13 species scored highest in at least one of the 912 prediction sites, 3 of which were primates and 10 were birds. Species with high local scores were those that were expected to have a large number of interactions, but had been extirpated in many prediction sites.

We selected 12 species with the highest regional scores in restoring seed-dispersal interactions in the Atlantic Forest to examine their local variation in interaction credit more
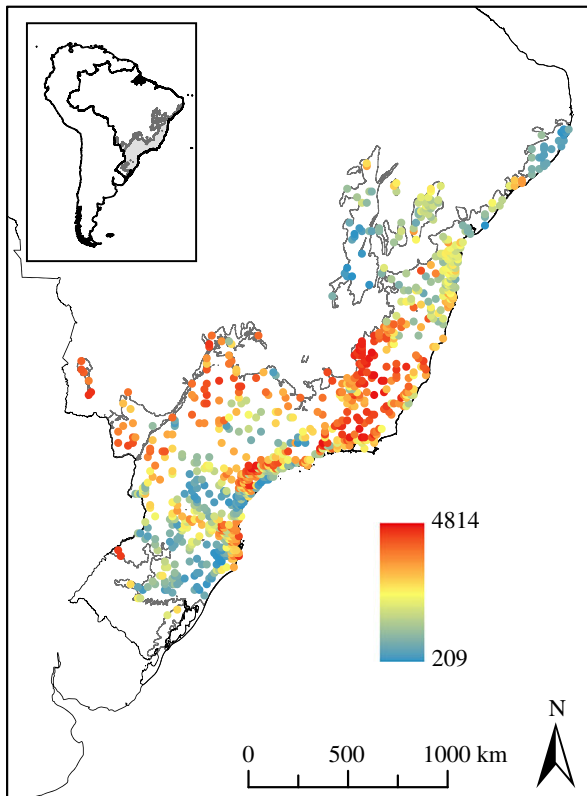
4

Figure 1. Spatial credit of ecological interactions to be cashed through rewilding across prediction sites in the Atlantic Forest. We calculated the interaction credit as the difference between a historical benchmark of species occurrences and their current predicted occurrences. The number of interactions expected to be restored by rewilding is depicted by a colour gradient. The warmest colours represent credit hotspots, whereas the coldest colours represent sites where there are fewer seed-dispersal interactions to be restored through reintroductions.

carefully (table 1, figure 2). Even though the southern muriqui, *Brachyteles arachnoides*, scored highest because of the high average in the potential to contribute with interactions, the credit contribution of the species would be limited owing to its restricted distribution. The rusty-margined guan, *Penelope superciliaris*, had, in addition to its high score, the lowest variation in local scores, which reflects its broader range encompassing most of the biome. Sixty-six per cent of the species with the highest regional scores are endemic to the Atlantic Forest.

The sub-regions with the largest potential for cashing in the credit of ecological interactions had similar lists of the highest scoring species; for instance, two-thirds of the highest scoring species were the same for the Interior and Serra do Mar sub-regions (electronic supplementary material, appendix D, table S3). The exceptions are those species that are endemic to a certain sub-region and thus may be regionally important but are replaced by other species in the sub-regions where they are not known to occur. Using the maximum of the mean posterior occurrence probabilities to build the benchmark scenario (see Material and methods) yielded similar results, suggesting that our findings are robust to our choice on how to generate a benchmark for comparison (see electronic supplementary materials, figure S4 and table S4 in appendix D). In addition, the results were robust to our choice of the probability assigned to unlikely interactions (see electronic supplementary material, table S5 and figure S5 in appendix D).

4. Discussion

Combining joint distribution modelling and the network approach under a probabilistic framework allowed us to identify hotspots in the Atlantic Forest where trophic rewilding could be most beneficial to promote the restoration of seed-dispersal interactions. We found high variability in the interaction credit throughout the biome. Hotspots of interaction credit were more pervasive in the Interior sub-region of the Atlantic Forest. This sub-region is characterized by a highly fragmented landscape resulting from the expansion of agricultural activities [19]. Although such land-use changes produced a major loss in forest cover and shrinkage of fragments [19], the high interaction credit revealed by our analyses suggests that animal-dispersed plants are expected to occur in several of those fragments, whereas their frugivore partners are likely to be missing. The decline in seed disperser richness implies that regeneration and the persistence of plant populations in fragments may be impaired in the long term due to seed-dispersal limitation if the fragments are not rewilded [41], which is an additional threat to the remaining fragments [42,43]. This highlights an insidious feature of defaunation: defaunation and its ecological consequences are much harder to detect than deforestation [44].

We also identified hotspots for rewilding within some sub-regions known to bear relatively well-preserved stretches of habitat, such as the Serra do Mar sub-region. These hotspots are concentrated around the largest urban areas within the biome, which are known to have low densities of many animal species, especially large-sized frugivores [45]. However, the high richness of plant species due to preserved forest patches combined with the low occurrence probability of frugivores due to past or current threats promote the high potential for interaction restoration through rewilding. The hotspots detected within sub-regions can be considered promising areas on which to focus rewilding strategies. This reveals that, despite the coarse-grained approximations used here, the proposed framework can help identify local hotspots for trophic rewilding.

The low credit of ecological interactions in the northern Atlantic Forest, in particular in the Pernambuco sub-region, may be explained by the long history of extensive deforestation in the region [46]. Deforestation results in low occurrence probabilities of many plant species and thus the low potential for seed-dispersal interactions to be re-established solely by reintroducing frugivores. The example of the northern Atlantic Forest shows that a closer examination of our framework's outputs may also help to inform when trophic rewilding is not the best option because of habitat unsuitability. Low credit may indicate that few interactions remain to be restored in the area. However, studying the patterns of plant species richness and composition within regions may shed light on the other underlying causes for the low interaction credit. When the spatial credit of ecological interactions is low, mainly due to low plant species richness, rewilding alone will have a minimum impact, and re-establishment of the populations of animal-dispersed plants will be required before fauna reintroductions [47]. Therefore, our approach may also be helpful in identifying, among a set of sites, those in which rewilding alone would not be the most suitable conservation strategy.
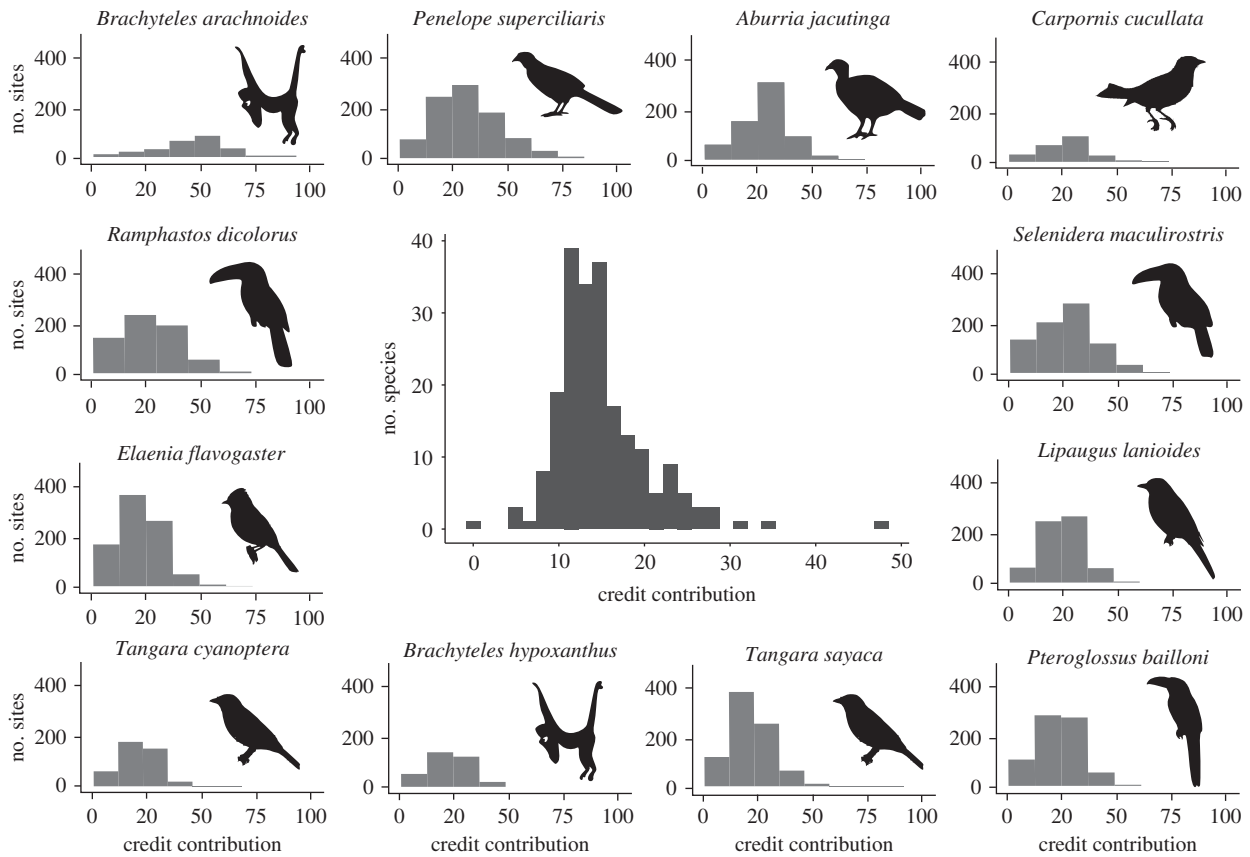
Figure 2. Distribution of the frugivore contributions to the credit of seed-dispersal interactions across prediction sites in the Atlantic Forest. The large histogram in the centre shows the distribution of the average credit contribution of each species considering all sites. Smaller histograms show the distributions of credit contribution for the 12 highest scoring species across prediction sites.

Table 1. Interaction credit of the 12 highest scoring frugivore species across the Atlantic Forest. We measured the interaction credit contribution as the mean expected number of interactions across prediction sites where the frugivore is predicted to occur according to the benchmark scenario. The total credit is the sum of credit contribution for all sites. We ranked species according to the mean contribution and present the minimum and maximum of local ranks across all prediction sites and the standard deviation of the ranks. The last column represents the IUCN threat categories each species is assigned to: LC = Least concern, NT = Near threatened, EN = Endangered, CR = Critically endangered [36].

family	species	mean credit	total credit	rank range	rank s.d.	IUCN class
Atelidae	Brachyteles arachnoides	47.99	11132.69	1 – 160	62.66	EN
Cracidade	Penelope superciliaris	34.04	31048.42	1 – 105	6.85	LC
Cracidade	Aburria jacutinga	30.45	24424.16	1 – 101	28.93	EN
Cotingidae	Carpornis cucullata	28.68	6652.67	2 – 160	59.91	NT
Ramphastidae	Selenidera maculirostris	28.33	24282.49	1 – 133	28.97	LC
Cotingidae	Lipaugus lanioides	27.76	17324.89	3 – 131	50.57	NT
Ramphastidae	Pteroglassus bailloni	26.55	21907.07	2 – 116	25.5	NT
Thraupidae	Tangara sayaca	26.26	23946.78	1 – 120	10.78	LC
Atelidae	Brachyteles hypoxanthus	25.95	8354.46	3 – 155	59.99	CR
Thraupidae	Tangara cyanoptera	25.33	10434.38	3 – 160	65.47	NT
Tyrannidae	Elaenia flavogaster	24.89	22702.16	1 – 106	14.19	LC
Ramphastidae	Ramphastos dicolorus	24.77	16768.37	3 – 138	47.69	LC

We found certain frugivores to contribute disproportionately in cashing the credit of seed-dispersal interactions in the Atlantic Forest. These are often species with a high degree of frugivory that interact with multiple plant taxa and have a low probability of occurrence in sites where their plant partners are likely to occur. This list includes species threatened with local extinction in many areas, such as the primates *Brachyteles* spp. and the piping guan, *Aburria jacutinga*. However, although these species may be important locally, they have restricted distributions, and their potential

as rewilding candidates does not apply to all sub-regions. On the other hand, some species considered common, such as small generalist birds, had high scores throughout the whole biome. These frugivores tend to establish seed-dispersal interactions with many different plant species, which makes them good candidates despite the fact that they are likely to occur in many sites. Such information is helpful because it signals species that could have their populations reinforced through management in order to strengthen interactions at broader scales. In fact, common species may be good candidates for population reinforcement rather than trophic rewilding de facto [48] when the focus is to restore ecological services [5]. Those species are unlikely to be endangered and are more likely to have sufficient captive stocks or source areas for translocation, which makes them suitable candidates for such initiatives.

Although our framework provides a useful tool to identify rewilding candidates within a region or a given site, the choice on whether a given species is indeed a good candidate for trophic rewilding is not based solely on interaction patterns. Conservation planning must encompass a careful assessment to determine whether the amount of remaining habitat is sufficient and whether the fragments are suitable for the species to establish a viable population, especially in severely fragmented landscapes [49]. Habitat suitability can also be included as an additional layer of information that weights interaction probabilities, which could alter the outcomes of the models providing more realistic estimates. A prerequisite for rewilding is that the underlying threat to the population is under control. Usual threats, such as hunting and predation pressure by invasive species, need to be addressed before the start of any reintroduction, otherwise the population is not viable in the long term. Finally, reintroductions are only feasible when there are sufficient captive stocks or wild populations available for translocation, which is not the case for some of the species that score high in our study, such as Brachyteles spp. The objective of the proposed approach is not to replace any steps of rewilding planning, but to offer one additional tool for conservation. Incorporating predictions on ecological interactions into trophic rewilding planning is crucial and our framework should be seen as a first step in ranking the ideal candidates for rewilding in a given region. This list should then be filtered to species that fulfil the basic requirements of any reintroduction.

The lack of source populations was an issue faced by attempts at reintroducing of the red-billed curassow (Crax blumenbachii) in the Atlantic Forest, which was made possible by efforts of captive breeding [50]. The most successful and widely known reintroduction programme in the Atlantic Forest, which restored the endemic golden lion tamarin (Leontopithecus rosalia) population from around 100 to more than 1600 individuals, only succeeded because it was built on a partnership between researchers, conservation initiatives and zoos around the world. They committed to protect the remaining habitat while reintroducing individuals [51]. Proportional efforts in terms of resources are not always required when the focal species is a relatively common one, as in the case of rewilding projects that aim to restore ecological processes and not to protect a given endangered species [52].

By identifying the areas with the highest credit, the framework presented here may help to determine areas where trophic rewilding efforts should be targeted in order to maximize functional gains. Despite taking a number of simplifying steps, such as generating a naive historical benchmark, we show in this first attempt that the proposed approach is a robust framework that helps produce testable predictions about the community responses to species reintroductions, besides aiding decision-making in conservation planning. We worked at a broad spatial scale encompassing the Atlantic Forest as a whole, but the same approach can also be useful when analysing the local interaction credit, aiding in selecting candidate species and then evaluating success. Although this framework has never been used before to prioritize areas and species for rewilding, the concept of interaction credit has already been effectively used to predict and evaluate reintroduction success. In a protected area within the Serra do Mar sub-region, reintroduction of agoutis (Dasyprocta leporina) and howler monkeys (Alouatta guariba), both important seed dispersers which had been locally extirpated, were assessed in terms of interaction restoration, and a large proportion of the interaction credit identified for the area was cashed in the first years after the release [12,53].

We focused here on seed-dispersal interactions in a tropical biodiversity hotspot, but the proposed framework can be applied to different biomes or types of interaction. Even when considering other types of interaction, prioritizing the reintroduction of species that are able to cash a high credit of ecological interactions may be important to restore ecosystem functioning. Providing conservation practitioners with sufficient information on how to prioritize species and areas in terms of ecological interaction restoration is crucial for reversing the consequences of defaunation.

References

1. 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)

2. Johnson CN, Balmford A, Brook BW, Buettel JC, Galetti M, Guangchun L, Wilmshurst JM. 2017 Biodiversity losses and conservation responses in the Anthropocene. *Science* **356**, 270–275. (doi:10.1126/science.aam9317)

3. Tylianakis JM, Laliberté E, Nielsen A, Bascompte J. 2010 Conservation of species interaction networks. *Biol. Conserv.* **143**, 2270–2279. (doi:10.1016/j.biocon.2009.12.004)

4. Svenning J-C et al. 2016 Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proc. Natl Acad. Sci. USA* **113**, 898–906. (doi:10.1073/pnas.1502556112)

5. Galetti M, Pires AS, Brancalion PHS, Fernandez FAS. 2017 Reversing defaunation by trophic rewilding in empty forests. *Biotropica* **49**, 5–8. (doi:10.1111/btp.12407)

6. Jepson P. 2016 A rewilding agenda for Europe: creating a network of experimental reserves. *Ecography (Cop.)* **39**, 117–124. (doi:10.1111/ecog.01602)

7. Oliveira Santos LGR, Fernandez FAS. 2010 Pleistocene rewilding, Frankenstein ecosystems, and an alternative conservation agenda. *Conserv. Biol.* **24**, 4–5. (doi:10.1111/j.1523-1739.2009.01379.x)

8. Donlan J. 2005 Re-wilding North America. *Nature* **436**, 913–914. (doi:10.1038/436913a)

9. Sandom C, Donlan CJ, Svenning J-C, Hansen D. 2013 Rewilding. In *Key topics in conservation biology 2* (eds DW Macdonald, KJ Willis), pp. 430–451. Oxford, UK: John Wiley & Sons.

10. Griffiths CJ, Jones CG, Hansen DM, Puttoo M, Tatayah R V., Muller CB, Harris S. 2010 The use of extant non-indigenous tortoises as a restoration tool to replace extinct ecosystem engineers. *Restor. Ecol.* **18**, 1–7. (doi:10.1111/j.1526-100X.2009.00612.x)

11. Griffiths CJ, Hansen DM, Jones CG, Zuël N, Harris S. 2011 Resurrecting extinct interactions with extant substitutes. *Curr. Biol.* **21**, 762–765. (doi:10.1016/j.cub.2011.03.042)

12. Genes L, Cid B, Fernandez FAS, Pires AS. 2017 Credit of ecological interactions: a new conceptual framework to support conservation in a defaunated world. *Ecol. Evol.* **7**, 1892–1897. (doi:10.1002/ece3.2746)

13. Ribeiro da Silva F, Montoya D, Furtado R, Memmott J, Pizo MA, Rodrigues RR. 2015 The restoration of tropical seed dispersal networks. *Restor. Ecol.* **23**, 852–860. (doi:10.1111/rec.12244)

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

15. Bueno RS, Guevara R, Ribeiro MC, Culot L, Bufalo FS, Galetti M. 2013 Functional redundancy and complementarities of seed dispersal by the last neotropical megafrugivores. *PLoS ONE* **8**, e56252. (doi:10.1371/journal.pone.0056252)

16. 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)

17. Valiente-Banuet A et al. 2015 Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* **29**, 299–307. (doi:10.1111/1365-2435.12356)

18. Jorge MLSP, Galetti M, Ribeiro MC, Ferraz KMPMB. 2013 Mammal defaunation as surrogate of trophic cascades in a biodiversity hotspot. *Biol. Conserv.* **163**, 49–57. (doi:10.1016/j.biocon.2013.04.018)

19. 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)

20. Banks-Leite C et al. 2014 Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science* **345**, 1041–1045. (doi:10.1126/science.1255768)

21. Hobbs RJ, Valentine LE, Standish RJ, Jackson ST. 2018 Movers and stayers: novel assemblages in changing environments. *Trends Ecol. Evol.* **33**, 116–128. (doi:10.1016/j.tree.2017.11.001)

22. Seddon PJ, Armstrong DP, Maloney RF. 2007 Developing the science of reintroduction biology. *Conserv. Biol.* **21**, 303–312. (doi:10.1111/j.1523-1739.2006.00627.x)

23. Pires MM. 2017 Rewilding ecological communities and rewiring ecological networks. *Perspect. Ecol. Conserv.* **15**, 257–265. (doi:10.1016/j.pecon.2017.09.003)

24. Root-Bernstein M, Galetti M, Ladle RJ. 2017 Rewilding South America: ten key questions. *Perspect. Ecol. Conserv.* **15**, 271–281. (doi:10.1016/j.pecon.2017.09.007)

25. Ovaskainen O, Tikhonov G, Norberg A, Guillaume Blanchet F, Duan L, Dunson D, Roslin T, Abrego N. 2017 How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecol. Lett.* **20**, 561–576. (doi:10.1111/ele.12757)

26. Gravel D, Poisot T, Albouy C, Velez L, Mouillot D. 2013 Inferring food web structure from predator-prey body size relationships. *Methods Ecol. Evol.* **4**, 1083–1090. (doi:10.1111/2041-210X.12103)

27. Morales-Castilla I, Matias MG, Gravel D, Araújo MB. 2015 Inferring biotic interactions from proxies. *Trends Ecol. Evol.* **30**, 347–356. (doi:10.1016/j.tree.2015.03.014)

28. Poisot T, Cirtwill AR, Cazelles K, Gravel D, Fortin M-J, Stouffer DB. 2016 The structure of probabilistic networks. *Methods Ecol. Evol.* **7**, 303–312. (doi:10.1111/2041-210X.12468)

29. 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)

30. Culot L, Pereira LA, Agostini I, Almeida MAB, Alves RSC, Aximoff I, Bager A, Baldovino MC, Bella TB, Bicca-Marques JC et al. 2018 ATLANTIC-PRIMATES: A dataset of communities and occurrences of primates in the Atlantic Forests of South America. *Ecology.* In Press.

31. Lima RAF et al. 2015 How much do we know about the endangered Atlantic Forest? Reviewing nearly 70 years of information on tree community surveys. *Biodivers. Conserv.* **24**, 2135–2148. (doi:10.1007/s10531-015-0953-1)

32. Hasui É et al. 2018 ATLANTIC BIRDS: a data set of bird species from the Brazilian Atlantic Forest. *Ecology* **99**, 497. (doi:10.1002/ecy.2119)

33. Lima F et al. 2017 ATLANTIC-CAMTRAPS: a dataset of medium and large terrestrial mammal communities in the Atlantic Forest of South America. *Ecology* **98**, 2979. (doi:10.1002/ecy.1998)

34. Almeida-Neto M, Campassi F, Galetti M, Jordano P, Oliveira-Filho A. 2008 Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. *Glob. Ecol. Biogeogr.* **17**, 503–513. (doi:10.1111/j.1466-8238.2008.00386.x)

35. Ovaskainen O, Abrego N, Halme P, Dunson D. 2016 Using latent variable models to identify large networks of species-to-species associations at different spatial scales. *Methods Ecol. Evol.* **7**, 549–555. (doi:10.1111/2041-210X.12501)

36. IUCN. 2017 *The IUCN red list of threatened species*. Version 2017-3. See www.iucnredlist.org (accessed on 16 March 2018).

37. WikiAves. 2008 WikiAves, a Enciclopédia das Aves do Brasil: http://www.wikiaves.com.br/ (accessed on 16 March 2018).

38. da Silva J, Casteleti C. 2003 Status of the biodiversity of the Atlantic Forest of Brazil. In *The Atlantic Forest of South America: biodiversity status, threats, and outlook* (eds C Gallindo-Leal, I Câmara), pp. 43–59. Washington, DC: CABS and Island Press.

39. Olesen JM, Bascompte J, Dupont YL, Elberling H, Rasmussen C, Jordano P. 2011 Missing and forbidden links in mutualistic networks. *Proc. R. Soc. B* **278**, 725–732. (doi:10.1098/rspb.2010.1371)

40. Jordano P, Stouffer D. 2016 Sampling networks of ecological interactions. *Funct. Ecol.* **30**, 1883–1893.

41. Harrison RD, Tan S, Plotkin JB, Slik F, Detto M, Brenes T, Itoh A, Davies SJ. 2013 Consequences of defaunation for a tropical tree community. *Ecol. Lett.* **16**, 687–694. (doi:10.1111/ele.12102)

42. Cordeiro NJ, Howe HF. 2003 Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proc. Natl Acad. Sci. USA* **100**, 14 052–14 056. (doi:10.1073/pnas.2331023100)

43. Galetti M, Alves-Costa CP, Cazetta E. 2003 Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. *Biol. Conserv.* **111**, 269–273. (doi:10.1016/S0006-3207(02)00299-9)

8

rstb.royalsocietypublishing.org   Phil. Trans. R. Soc. B 373: 20170435

44. Galetti M, Dirzo R. 2013 Ecological and evolutionary consequences of living in a defaunated world. *Biol. Conserv.* **163**, 1–6. (doi:10.1016/j.biocon.2013.04.020)

45. Galetti M *et al.* 2017 Defaunation and biomass collapse of mammals in the largest Atlantic Forest remnant. *Anim. Conserv.* **20**, 270–281. (doi:10.1111/acv.12311)

46. Silva J, Tabarelli M. 2000 Tree species improverishment and the future flora of the Atlantic Forest of northeast Brazil. *Nature* **404**, 72–74.

47. Brancalion PHS, Bello C, Chazdon RL, Galetti M, Jordano P, Lima RAF, Medina A, Pizo MA, Reid JL. 2018 Maximizing biodiversity conservation and carbon stocking in restored tropical forests. *Conserv. Lett.* **11**, e12454. (doi:10.1111/conl.12454)

48. Seddon PJ, Griffiths CJ, Soorae PS, Armstrong DP. 2014 Reversing defaunation: restoring species in a changing world. *Science* **345**, 406–412. (doi:10.1126/science.1251818)

49. IUCN/SSC. 2013 *Guidelines for reintroductions and other conservation translocations.* Version 1.0.

50. Bernardo CSS. 2012 Reintroduction as a conservation tool for threatened Galliformes: the red-billed curassow *Crax blumenbachii* case study from Rio de Janeiro state, Brazil. *J. Ornithol.* **153**, 135–140. (doi:10.1007/s10336-011-0805-z)

51. Kierulff MCM, Ruiz-Miranda CR, Oliveira PP, Beck BB, Martins A, Dietz JM, Rambaldi DM, Baker AJ. 2012 The golden lion tamarin *Leontopithecus rosalia*: a conservation success story. *Int. Zoo Yearb.* **46**, 36–45. (doi:10.1111/j.1748-1090.2012.00170.x)

52. Kenup CF, Sepulvida R, Kreischer C, Fernandez FAS. 2017 Walking on their own legs: unassisted population growth of the agouti *Dasyprocta leporina*, reintroduced to restore seed dispersal in an Atlantic Forest reserve. *Oryx* **52**, 571–578. (doi:10.1017/S0030605316001149)

53. Genes L, Fernandez FAS, Vaz-de-Mello FZ, da Rosa P, Fernandez E, Pires AS. 2018 Effects of howler monkey reintroduction on ecological interactions and processes. *Conserv. Biol.* (doi:10.1111/cobi.13188)