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**Estimating Interaction Credit for Trophic Rewilding in  
Tropical Forests**

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3 **1 Estimating Interaction Credit for Trophic Rewilding in Tropical Forests**  
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3     **22 Abstract**

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5     23 Trophic rewilding has been suggested as a restoration tool to reverse defaunation and its  
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7     24 cascading effects on ecosystem functioning. One of the ecological processes that has  
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9     25 been jeopardized by defaunation is animal-mediated seed dispersal. Here, we propose  
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11     26 an approach that combines joint species distribution models with occurrence data and  
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13     27 species interaction records to quantify the potential to restore seed-dispersal interactions  
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15     28 through rewilding and apply it to the Atlantic Forest, a global biodiversity hotspot.  
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17     29 Using this approach, we identify areas that should benefit the most from trophic  
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19     30 rewilding and candidate species that could contribute to cash the credit of seed-dispersal  
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21     31 interactions in a given site. We found that sites within large fragments bearing a great  
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23     32 diversity of trees may have about 20 times as many interactions to be cashed through  
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25     33 rewilding as small fragments in regions where deforestation has been pervasive. We  
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27     34 also ranked mammal and bird species according to their potential to restore seed-  
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29     35 dispersal interactions if reintroduced while considering the biome as a whole and at  
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31     36 finer scales. Our findings can aid future conservation efforts in rewilding projects in  
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33     37 defaunated tropical rainforests.  
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39     39 Keywords: Atlantic Forest, defaunation, seed dispersal, plant-animal interaction,  
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41     40 reintroduction, restoration  
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## 41 **1. Introduction**

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

51 Although rewilding has become an important debate in the last years [8,9], few  
52 projects in the field have applied rewilding for mitigating the loss of species interactions  
53 [10,11]. Because rewilding focuses on restoring ecological processes [4,9], the choice of  
54 the candidate species should be based on the balance between the probability of  
55 population establishment and the benefit of the restored interactions for ecosystem  
56 functions [4,5]. Using an economics analogy, species reintroductions can allow  
57 defaunated areas to gradually “cash” a credit of ecological interactions where their  
58 interaction partners are still extant, which depends on the species-specific traits as well  
59 as on the abundances of the focal species and their partners [12]. The interaction credit  
60 framework is based on the potential to restore interactions (i.e. to reconnect species that  
61 became disconnected) in an area following reintroduction; thus, it can be used to predict  
62 and to evaluate the success of rewilding in reinstating ecological processes.

63 Restoring certain types of interactions, such as seed dispersal, can be particularly  
64 beneficial because it helps natural forest regeneration and may even aid the restoration  
65 of neighbouring areas, creating more suitable habitat and generating a positive feedback

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3 66 for conservation efforts [13]. Most tropical tree species rely on animal-mediated seed  
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5 67 dispersal for recruitment [14]. Yet, many frugivore species that establish non-redundant  
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7 68 seed-dispersal interactions tend to be the same that are overhunted and affected by  
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9 69 fragmentation [15,16]. Therefore, local extinctions can cause the loss of those  
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11 70 ecological interactions, cascading to the loss of functioning in defaunated tropical areas  
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13 71 [17].

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15  
16 72 Tropical forests are highly threatened worldwide but the Atlantic Forest in South  
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18 73 America represents one of the worst-case scenarios for protecting biodiversity: it has  
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20 74 been severely defaunated and is highly fragmented [18,19], with many of the fragments  
21  
22 75 too small to maintain viable populations of certain species. Moreover, the agricultural  
23  
24 76 and urban matrices surrounding forest patches prevent some animals from recolonizing  
25  
26 77 patches where they have been extirpated [20]. Thus, the reestablishment of ecological  
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28 78 interactions even in large fragments is unlikely to occur without more active  
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30 79 approaches, such as trophic rewilding [7,21].

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33 80 Despite the large amount of data available on species distributions and local  
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35 81 interaction patterns, predicting how the reintroduced species will interact with the local  
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37 82 community is still an obstacle [12,22,23]. Devising a comprehensive framework for  
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39 83 trophic rewilding requires integrating information on species distributions and  
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41 84 interaction patterns across their range to allow inferring which interactions are likely or  
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43 85 unlikely to occur [23]. A spatially informed framework is needed to aid decision-  
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45 86 making regarding the prioritization of the areas and the choice of candidate species for  
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47 87 trophic rewilding at broad scales [24].

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50 88 Here we use a probabilistic framework that combines joint species distribution  
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52 89 models [25], the ecological network approach [23] and the credit of ecological  
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54 90 interactions framework [12] to identify priority areas and candidate species for trophic  
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3 91 rewilding, with a focus on restoring seed-dispersal interactions. We use the Atlantic  
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5 92 Forest as a case study and show how the proposed framework can help to unveil  
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7 93 interaction credit hotspots and to detect which species are the best candidates for  
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9 94 rewilding at different spatial scales.  
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## 13 96 **2. Methods**

15 97 The credit of ecological interactions corresponds to the number of animal-plant  
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17 98 interactions expected to be restored if an extirpated species is reintegrated into a given  
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19 99 area [12]. Therefore, quantifying interaction credit requires a toolset for predicting  
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21 100 pairwise species interactions in a locality. The prerequisite for an interaction to take  
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23 101 place is that the focal species co-occur in space and time. Although species occurrences  
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25 102 can be inferred directly from occurrence data, modelling species occurrences, besides  
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27 103 allowing predictions for poorly sampled locations, offers the possibility of  
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29 104 encompassing uncertainty regarding occurrence and co-occurrence patterns. Species  
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31 105 may co-occur because they respond in the same manner to the environment, but co-  
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33 106 occurring does not mean species will necessarily interact. Assuming that two species  
34  
35 107 co-occur in space and time, interactions will still depend on a number of factors, such as  
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37 108 species traits, phenology and abundance [12,26,27]. Because of the inherent challenges  
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39 109 of detecting and predicting interactions in a community, the appropriate way to model  
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41 110 interaction patterns is using a probabilistic approach [23,28]. Pairwise interaction  
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43 111 probabilities can be obtained by the element-wise product between the matrix  $\mathbf{O}$ ,  
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45 112 depicting species co-occurrence probabilities and matrix  $\mathbf{A}$ , depicting the expected  
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47 113 interaction probabilities once the species co-occur [23]. Considering that the aim of  
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49 114 trophic rewilding is to restore processes that have been lost over time, its outcomes in  
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51 115 terms of interaction credit can be predicted and then evaluated by comparing expected  
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3 116 interactions under two different scenarios: (1) a benchmark historical scenario, and (2)  
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5 117 the current scenario where many sites may be defaunated relative to the historical  
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7 118 benchmark. We apply the framework outlined above to estimate the credit of ecological  
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9 119 interactions across the Atlantic Forest in South America.  
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### 13 121 **(a) Data**

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15 122 To infer current distribution patterns of frugivores and plants, we used the most  
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17 123 spatially and taxonomically comprehensive community databases available for the  
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19 124 Brazilian Atlantic Forest (the ATLANTIC series data papers:  
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21 125 [https://github.com/LEEClab/Atlantic\\_series](https://github.com/LEEClab/Atlantic_series); and the Neotropical Tree Communities  
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23 126 database TreeCo version 2.0: <http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start>).

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25 127 We used data on all seed disperser genera with interactions recorded in the Atlantic  
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27 128 Forest [29], excluding species known to behave more as seed predators than dispersers  
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29 129 as well as bats and small mammals due to incomplete data on distribution or interaction  
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31 130 patterns (which could impair the assessment of a spatial credit at broad scale) and to  
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33 131 taxonomic inconsistency in some genera (which could impair the prediction of pairwise  
34  
35 132 interactions). Therefore, we compiled data on 211 vertebrate species (birds and medium  
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37 133 to large-sized mammals) and 1,426 tree and palm species [30–33]. See electronic  
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39 134 supplementary material, appendix A, for the filtered reference list of the plant  
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41 135 occurrence data. We only considered plant species that were identified as zoochoric  
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43 136 [29,34], reported to grow  $\geq 4$  meters high, and having  $\geq 5$  observations in the plant  
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45 137 occurrence dataset. For the full list of included species, see electronic supplementary  
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47 138 material, appendix B. To guarantee a broad coverage across the entire biome, we  
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49 139 created a regular grid of 40,000 prediction sites spanning the Atlantic Forest in ArcGIS  
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51 140 software (version 10.3) and selected for later use those 912 sites that overlapped with  
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3 141 Atlantic Forest fragments. To assess the interaction component, we used interaction  
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5 142 records from the ATLANTIC-FRUGIVORY dataset [29]. From this dataset we built the  
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7 143 final interaction matrix  $\mathbf{P}$ , as described in more detail below.  
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#### 11 145 **(b) Co-occurrence probabilities**

13 146 We inferred co-occurrence probabilities for frugivores and plants across the Atlantic  
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15 147 Forest using joint species distribution models (HMSC [25]). HMSC helps to overcome  
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17 148 the problem of low spatial overlap in the original surveys across taxonomic groups,  
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19 149 generating predicted occurrence probabilities for each frugivore and plant species across  
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21 150 the Atlantic Forest (for more detailed description on the model construction and  
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23 151 included data, see electronic supplementary material, appendix C). The predicted  
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25 152 probabilities of species occurring in a given site are determined not only by the values  
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27 153 of environmental covariates on that site (through the fixed effect part of the HMSC), but  
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29 154 also on the occurrences of the focal and other species in nearby sampling sites (through  
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31 155 spatially structured latent variables included in HMSC, see [35]). We generated 500  
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33 156 predicted communities in each of the 912 prediction sites described above. For each  
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35 157 prediction site, we sampled model parameters from the posterior distribution, and thus  
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37 158 the predictions account for parameter uncertainty.  
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41 159 To generate a historical benchmark distribution of frugivores, we used the  
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43 160 distribution records of frugivores from IUCN [36] complemented by records from  
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45 161 Wikiaves [37] to determine the sub-regions where each species occurs. The Atlantic  
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47 162 Forest comprises seven biogeographical sub-regions that differ in environmental  
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49 163 variables and biodiversity composition: Interior, Araucaria, Serra do Mar, Bahia,  
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51 164 Diamantina, Sao Francisco, and Pernambuco [38]. We assumed in the benchmark  
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53 165 scenario that species would have been present in all prediction sites within all sub-  
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3 166 regions where the species is known to currently occur, and assigned  $p = 1$  for the  
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5 167 probability of species occurrence in those sites. We also performed a sensitivity analysis  
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7 168 by setting the occurrence probabilities of frugivores in the benchmark scenario equal to  
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9 169 the maximum of the mean posterior occurrence probability across all prediction sites.  
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11 170 Because our main interest was in the effects of reintroducing the frugivores, we used the  
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13 171 estimated occurrence probabilities for the plants in both the current and the benchmark  
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15 172 scenario. Even though it is plausible that certain plants had greater occurrence  
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17 173 probabilities in certain sites in the past, this would only increase our credit estimates.  
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19 174 Thus, by setting the benchmark using the current probabilities for plants we adopt a  
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21 175 conservative approach and we can assign differences between the two scenarios to the  
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23 176 differences in frugivore occurrence probabilities.  
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26 177 We constructed predicted co-occurrence matrices for each site as the product of  
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28 178 occurrence probabilities for frugivores (either assuming the benchmark distribution or  
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30 179 the current predicted distribution) and plants (assuming the current predicted  
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32 180 distribution).  
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### 37 182 **(c) Interaction probabilities**

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39 183 We converted records of pairwise interaction data to interaction probabilities using a  
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41 184 semi-quantitative approach. Based on the number of studies where pairwise interactions  
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43 185 were recorded in the ATLANTIC-FRUGIVORY dataset [29] we built an interaction  
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45 186 matrix **A**, where we assigned interactions between any frugivore  $i$  and plant  $j$  to one of  
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47 187 four categories: very likely ( $a_{ij} = 1$ ) when interaction was recorded more than once,  
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49 188 likely ( $a_{ij} = 0.75$ ) when interaction was recorded once, possible ( $a_{ij} = 0.5$ ) when the  
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51 189 frugivore species interacts with another plant species within the focal plant species'  
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53 190 genus, and unlikely ( $a_{ij} = 0.1$ ) when the frugivore species has no observed interactions  
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3 191 with any plant species within the focal plant species' genus. We assign unlikely  
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5 192 interactions a value greater than zero, because differentiating between true and  
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7 193 sampling-induced zeros is challenging [39,40] and it is conceptually wrong to assume  
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9 194 that unobserved interactions are impossible to occur. To test for the sensitivity of the  
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11 195 results to the probabilities assigned to unlikely interactions, we reran all analyses under  
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13 196 two additional scenarios: assuming  $a_{ij} = 0.05$  and  $a_{ij} = 0.001$  for unlikely interactions.  
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#### 18 198 **(d) Calculating the spatial credit of ecological interactions**

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20 199 To estimate the credit of ecological interactions we compared the historical benchmark  
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22 200 and the current scenario of seed-dispersal interactions across the Atlantic Forest. First,  
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24 201 we obtained the probabilistic interaction network (matrix  $\mathbf{P}$ , with elements  $p_{ij}$ ) for each  
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26 202 scenario in each prediction site as the element-wise product of the co-occurrence ( $\mathbf{O}$ )  
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28 203 and interaction matrices ( $\mathbf{A}$ ). We then calculated for each prediction site the expected  
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30 204 number of interactions,  $\hat{L}$ , as the sum of all pairwise interaction probabilities [28]  
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32 205  $\hat{L} = \sum p_{ij}$  and computed the site-specific spatial credit of ecological interactions as the  
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34 206 difference between  $\hat{L}$  for the benchmark and current scenarios.  
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#### 40 208 **(e) Calculating frugivore-specific contributions to the credit of ecological** 41 42 209 **interactions**

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44 210 To understand which species show potential for cashing the highest credit of ecological  
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46 211 interactions through rewilding locally and regionally in the Atlantic Forest, we first  
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48 212 computed for each site the expected number of interactions of each frugivore  $i$  as the  
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50 213 sum of interaction probabilities with all plants in that site [28]:  $\hat{k}_i = \sum_{j=1}^{N_p} p_{ij}$ . The  
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52 214 species-specific local credit of interactions, the local score, was obtained as the  
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54 215 difference between a species  $\hat{k}$  in the current versus the benchmark scenario,  $\Delta\hat{k}$ . We  
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3 216 then built a distribution of  $\Delta\hat{k}$  for each species considering all prediction sites and  
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5 217 ranked the species based on the mean  $\Delta\hat{k}$ . To compute  $\Delta\hat{k}$  we only consider the  
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7 218 prediction sites where a species is expected to occur according to the benchmark  
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9 219 scenario. We selected 12 species with highest regional scores to explore more closely  
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11 220 their potential for restoring seed-dispersal interactions through rewilding. We examined  
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13 221 the distribution of their local scores and discussed the ecology, current threats and  
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15 222 rewilding feasibility considering these species. We also calculated the regional scores  
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17 223 for each biogeographical sub-region separately to illustrate how this approach could  
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19 224 help to guide rewilding at a finer scale.  
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### 24 226 **3. Results**

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27 227 The spatial credit of ecological interactions ranged between 209 and 4,814 interactions  
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29 228 that could be cashed in prediction sites across the Atlantic Forest (figure 1). Sites with  
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31 229 greater credit have about 20 times as many interactions to be cashed through rewilding  
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33 230 as the sites with lower credit. The credit was highest in the Interior sub-region and  
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35 231 lowest in the Pernambuco sub-region (figure 1; electronic supplementary material  
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37 232 appendix D, figure S1). The interaction credit was highest in areas where occurrence  
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39 233 probabilities were high for plant species and low for frugivore species as compared to  
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41 234 their expected distributions in the benchmark scenario (electronic supplementary  
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43 235 material, figures S2; S3). The areas with low interaction credit were either areas having  
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45 236 a high frugivore species richness that matches the expectation in the benchmark  
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47 237 scenario, or areas where plant species richness is currently low and hence there are less  
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49 238 plant species missing frugivore partners.  
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53 239 By estimating the expected number of interactions to be restored by each  
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55 240 frugivore, we observed a large variation in the credit that could be cashed by different  
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3 241 species, both at local and regional scales. Altogether 13 species scored highest in at least  
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5 242 one of the 912 prediction sites, three of which were primates and ten were birds. Species  
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7 243 with high local scores were those that are expected to have a large number of  
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9 244 interactions, but had been extirpated in many prediction sites.

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11 245 We selected 12 species with the highest regional scores in restoring seed  
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13 246 dispersal interactions in the Atlantic Forest to examine their local variation in  
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15 247 interaction credit more carefully (table 1, figure 2). Even though the southern muriqui,  
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17 248 *Brachyteles arachnoides*, scored highest because of the high average in the potential to  
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19 249 contribute with interactions, the credit contribution of the species would be limited due  
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21 250 to its restricted distribution. The rusty-margined guan, *Penelope superciliaris*, had, in  
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23 251 addition to its high score, the lowest variation in local scores, which reflects its broader  
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25 252 range encompassing most of the biome. Sixty-six percent of the species with the highest  
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27 253 regional scores are endemic to the Atlantic Forest.

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31 254 The sub-regions with the largest potential for cashing in the credit of ecological  
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33 255 interactions had similar lists of the highest scoring species; for instance, two thirds of  
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35 256 the highest scoring species were the same for the Interior and Serra do Mar sub-regions  
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37 257 (electronic supplementary material appendix D, table S3). The exceptions are those  
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39 258 species that are endemic to a certain sub-region and thus may be regionally important  
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41 259 but are replaced by other species in the sub-regions where they are not known to occur.  
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44 260 Using the maximum of the mean posterior occurrence probabilities to build the  
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46 261 benchmark scenario (see Methods) yielded similar results, suggesting that our findings  
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48 262 are robust to our choice on how to generate a benchmark for comparison (see electronic  
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50 263 supplementary material, figure S4 and table S4 in appendix D). In addition, the results  
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52 264 showed to be robust to our choice for the probability assigned to unlikely interactions  
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54 265 (see electronic supplementary material, table S5 and figure S5 in appendix D).

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5 267 **4. Discussion**

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7 268 Combining joint distribution modelling and the network approach under a probabilistic  
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9 269 framework allowed us to identify hotspots in the Atlantic Forest where trophic  
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11 270 rewilding could be most beneficial to promote the restoration of seed-dispersal  
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13 271 interactions. We found high variability in the interaction credit throughout the biome.  
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15 272 Hotspots of interaction credit were more pervasive in the Interior sub-region of the  
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17 273 Atlantic Forest. This sub-region is characterized by a highly fragmented landscape  
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19 274 resulting from the expansion of agricultural activities [19]. Although such land use  
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21 275 changes produced a major loss in forest cover and shrinkage of fragments [19], the high  
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23 276 interaction credit revealed by our analyses suggests that animal-dispersed plants are  
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25 277 expected to occur in several of those fragments, whereas their frugivore partners are  
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27 278 likely to be missing. The decline in seed disperser richness implies that regeneration and  
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29 279 the persistence of plant populations in fragments may be impaired in the long term due  
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31 280 to seed dispersal limitation if the fragments are not rewilded [41], which is an additional  
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33 281 threat to the remaining fragments [42,43]. This highlights an insidious feature of  
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35 282 defaunation: defaunation and its ecological consequences are much harder to detect than  
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37 283 deforestation [44].

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41 284 We also identified hotspots for rewilding within some sub-regions known to bear  
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43 285 relatively well-preserved stretches of habitat, such as the Serra do Mar sub-region.  
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45 286 These hotspots are concentrated around the largest urban areas within the biome, which  
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47 287 are known to have low densities of many animal species, especially large-sized  
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49 288 frugivores [45]. However, the high richness of plant species due to preserved forest  
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51 289 patches combined with the low occurrence probability of frugivores due to past or  
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53 290 current threats, promote high potential for interaction restoration through rewilding. The  
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3 291 hotspots detected within sub-regions can be considered promising areas to focus  
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5 292 rewilding strategies on. This reveals that despite the coarse-grained approximations  
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7 293 used here, the proposed framework can help identifying local hotspots for trophic  
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9 294 rewilding.

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11 295         The low credit of ecological interactions in the northern Atlantic Forest, in  
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13 296 particular in the Pernambuco sub-region, may be explained by the long history of  
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15 297 extensive deforestation in the region [46]. Deforestation results in low occurrence  
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17 298 probabilities of many plant species and thus low potential for seed dispersal interactions  
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19 299 to be re-established solely by reintroducing frugivores. The example of the northern  
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21 300 Atlantic Forest shows that a closer examination of our framework's outputs may also  
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23 301 help to inform when trophic rewilding is not the best option due to habitat unsuitability.  
24  
25 302 Low credit may indicate that few interactions remain to be restored in the area.  
26  
27 303 However, studying the patterns of plant species richness and composition within regions  
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29 304 may shed light on the other underlying causes for the low interaction credit. When the  
30  
31 305 spatial credit of ecological interactions is low mainly due to low plant species richness,  
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33 306 rewilding alone will have a minimum impact, and reestablishment the populations of  
34  
35 307 animal-dispersed plants would be required prior to fauna reintroductions [47].  
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37 308 Therefore, our approach may also be helpful in identifying among a set of sites those in  
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39 309 which rewilding alone would not be the most suitable conservation strategy.

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43 310         We found certain frugivores to contribute disproportionately in cashing the  
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45 311 credit of seed dispersal interactions in the Atlantic Forest. These are often species with  
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47 312 high degree of frugivory that interact with multiple plant taxa and have low probability  
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49 313 of occurrence in sites where their plant partners are likely to occur. This list includes  
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51 314 species threatened with local extinction in many areas, such as the primates *Brachyteles*  
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53 315 spp. and the piping guan *Aburria jacutinga*. However, although these species may be  
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3 316 important locally, they have restricted distributions, and their potential as rewilding  
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5 317 candidates does not apply to all sub-regions. On the other hand, some species  
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7 318 considered common, such as small generalist birds, had high scores throughout the  
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9 319 whole biome. These frugivores tend to establish seed-dispersal interactions with many  
10  
11 320 different species, which makes them good candidates despite the fact that they are likely  
12  
13 321 to occur in many sites. Such information is helpful because it signals species that could  
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15 322 have their populations reinforced through management in order to strengthen  
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17 323 interactions at broader scales. In fact, common species may be good candidates for  
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19 324 population reinforcement rather than trophic rewilding *de facto* [48] when the focus is  
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21 325 to restore ecological services [5]. Those species are unlikely to be endangered and are  
22  
23 326 more likely to have sufficient captive stocks or source areas for translocation, which  
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25 327 makes them suitable candidates for such initiatives.

28  
29 328 Although our framework provides a useful tool to identify rewilding candidates  
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31 329 within a region or a given site, the choice on whether a given species is indeed a good  
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33 330 candidate for trophic rewilding is not based solely on interaction patterns. Conservation  
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35 331 planning must encompass a careful assessment to determine if the amount of remaining  
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37 332 habitat is sufficient and if the fragments are suitable for the species to establish a viable  
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39 333 population, especially in severely fragmented landscapes [49]. Habitat suitability can  
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41 334 also be included as an additional layer of information that weights interaction  
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43 335 probabilities, what could alter the outcomes of the models providing more realistic  
44  
45 336 estimates. Evidently, a prerequisite for rewilding is that the underlying threat to the  
46  
47 337 population is under control. Usual threats, such as hunting and predation pressure by  
48  
49 338 invasive species, need to be addressed before the start of any reintroduction, otherwise  
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51 339 the population is not viable in the long term. Finally, reintroductions are only feasible  
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53 340 when there are sufficient captive stocks or wild populations available for translocation,  
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3 341 which is not the case for some of the species that score high in our study, such as  
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5 342 *Brachyteles* spp. The objective of the proposed approach is not to replace any steps of  
6  
7 343 rewilding planning, but to offer one additional tool for conservation. Incorporating  
8  
9 344 predictions on ecological interactions into trophic rewilding planning is crucial and our  
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11 345 framework should be seen as a first step in ranking the ideal candidates for rewilding in  
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13 346 a given region. This list should then be filtered to species that fulfil the basic  
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16 347 requirements of any conservation translocation.

17  
18 348 The lack of source populations was an issue faced by attempts of reintroducing  
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20 349 of the red-billed curassow (*Crax blumenbachii*) in the Atlantic Forest, which was made  
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22 350 possible by efforts of captive breeding [50]. The most successful and widely known  
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24 351 reintroduction program in the Atlantic Forest, which restored the endemic golden lion  
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26 352 tamarin (*Leontopithecus rosalia*) population from around 100 to more than 1600  
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28 353 individuals, only succeeded because it was built on a partnership between researchers,  
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30 354 conservation initiatives and zoos around the world. They committed to protect the  
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32 355 remaining habitat while reintroducing individuals [51]. Proportional efforts in terms of  
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35 356 resources are not always required when the focal species is a relatively common one, as  
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37 357 in the case of rewilding projects that aim to restore ecological processes and not to  
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39 358 protect a given endangered species [52].

40  
41 359 By identifying the areas with the highest credit, the framework presented here  
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43 360 may help to determine areas where trophic rewilding efforts should be targeted in order  
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45 361 to maximize functional gains. Despite taking a number of simplifying steps, such as  
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47 362 generating a naïve historical benchmark, we show in this first attempt that the proposed  
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49  
50 363 approach is a robust framework that helps producing testable predictions about the  
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52 364 community responses to species reintroductions, besides aiding decision-making in  
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54 365 conservation planning. We worked at a broad spatial scale encompassing the Atlantic  
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3 366 Forest as a whole, but the same approach can also be useful when analysing the local  
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5 367 interaction credit, aiding in selecting candidate species and then evaluating success.  
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7 368 Although this framework has never been used before to prioritize areas and species for  
8  
9 369 rewilding, the concept of interaction credit has already been effectively used to predict  
10  
11 370 and evaluate reintroduction success. In a protected area within the Serra do Mar sub-  
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13 371 region, reintroduction of agoutis (*Dasyprocta leporina*) and howler monkeys (*Alouatta*  
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15 372 *guariba*), both important seed dispersers which had been locally extirpated, were  
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17 373 assessed in terms of interaction restoration, and a large proportion of the interaction  
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19 374 credit identified for the area was cashed in the first years after the release [12,53].  
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22 375 We focused here on seed dispersal interactions in a tropical biodiversity hotspot,  
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24 376 but the proposed framework can be applied to different biomes or types of interaction.  
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26 377 Even when considering other types of interactions, prioritizing the reintroduction of  
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28 378 species that are able to cash a high credit of ecological interactions may be important to  
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30 379 restore ecosystem functioning. Providing conservation practitioners with sufficient  
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32 380 information on how to prioritize species and areas in terms of ecological interaction  
33  
34 381 restoration is crucial for reversing the consequences of defaunation.  
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37 382

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### 389 **Data accessibility**

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3 390 All data used in this manuscript is published as data papers from the ATLANTIC series  
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5 391 data papers: [https://github.com/LEEClab/Atlantic\\_series](https://github.com/LEEClab/Atlantic_series); and the Neotropical Tree  
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7 392 Communities database TreeCo version 2.0:  
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9 393 <http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start>. The packages and codes for  
10  
11 394 joint distribution models are available at  
12  
13 395 <https://www.helsinki.fi/en/researchgroups/statistical-ecology/hmsc>  
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### 397 **Author's contributions**

398 MG, LG, ASP and FASF conceived the idea; EM, LG, MMP and MG designed the  
399 study; RAFL, AAO and PIP compiled the tree data; EM conducted analyses; EM, LG  
400 and MMP wrote the first draft of the manuscript, and all authors contributed  
401 substantially to the final manuscript.

402

### 403 **Competing interests**

404 We have no competing interests.

405

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27 **Figure and table captions**

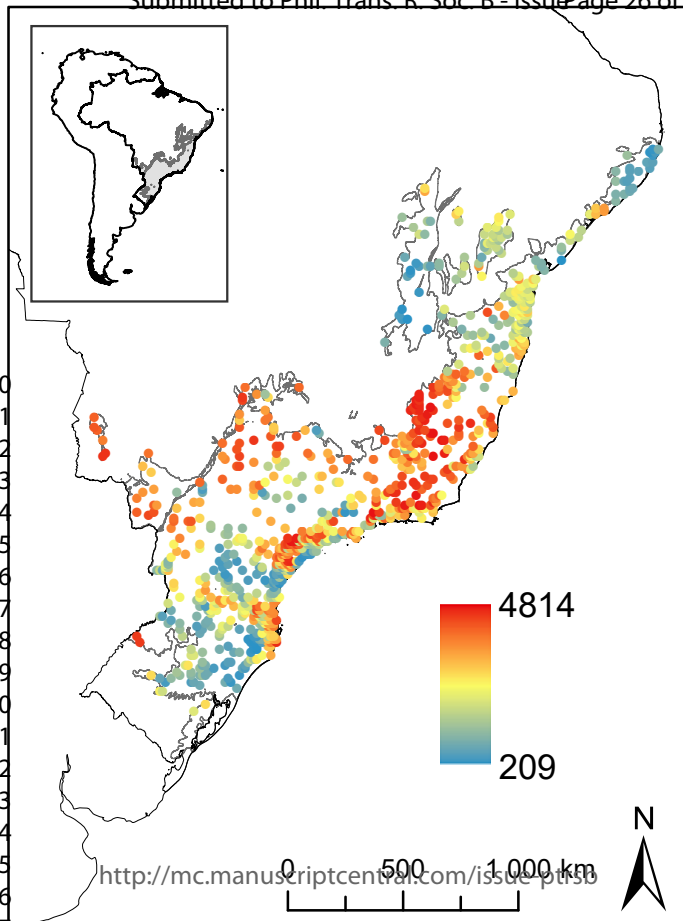
28  
29 577 **Figure 1.** Spatial credit of ecological interactions to be cashed through rewilding across  
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31 578 prediction sites in the Atlantic Forest. We calculated the interaction credit as the  
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33 579 difference between a historical benchmark of species occurrences and their current  
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35 580 predicted occurrences. The number of interactions expected to be restored by rewilding  
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37 581 is depicted by a colour gradient. The warmest colours represent credit hotspots, whereas  
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39 582 the coldest colours represent sites where there are fewer seed dispersal interactions to be  
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41 583 restored through reintroductions.  
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45 584 **Table 1.** Interaction credit of the 12 highest scoring frugivore species across the  
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47 585 Atlantic Forest. We measured the interaction credit contribution as the mean expected  
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49 586 number of interactions across prediction sites where the frugivore is predicted to occur  
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51 587 according to the benchmark scenario. The total credit is the sum of credit contribution  
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53 588 for all sites. We ranked species according to the mean contribution and present the  
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55 589 minimum and maximum of local ranks across all prediction sites and the standard  
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3 590 deviation of the ranks. The last column represents the IUCN threat categories each  
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5 591 species is assigned to: LC = Least concern, NT = Near threatened, VU = vulnerable, EN  
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7 592 = Endangered, CR = Critically endangered [36].  
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10 593 **Figure 2.** Distribution of the frugivore contributions to the credit of seed-dispersal  
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12 594 interactions across prediction sites in the Atlantic Forest. The large histogram in the  
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14 595 centre shows the distribution of the average credit contribution of each species  
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16 596 considering all sites. Smaller histograms show the distributions of credit contribution  
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18 597 for the 12 highest scoring species across prediction sites.  
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Family	Species	Mean credit	Total credit	Rank range	Rank SD	IUCN class
Atelidae	<i>Brachyteles arachnoides</i>	47.99	11132.69	1-160	62.66	EN
Cracidae	<i>Penelope superciliaris</i>	34.04	31048.42	1-105	6.85	LC
Cracidae	<i>Aburria jacutinga</i>	30.45	24424.16	1-101	28.93	EN
Cotingidae	<i>Carpornis cucullata</i>	28.68	6652.67	2-160	59.91	NT
Ramphastidae	<i>Selenidera maculirostris</i>	28.33	24282.49	1-133	28.97	LC
Cotingidae	<i>Lipaugus lanioides</i>	27.76	17324.89	3-131	50.57	NT
Ramphastidae	<i>Pteroglossus bailloni</i>	26.55	21907.07	2-116	25.5	NT
Thraupidae	<i>Tangara sayaca</i>	26.26	23946.78	1-120	10.78	LC
Atelidae	<i>Brachyteles hypoxanthus</i>	25.95	8354.46	3-155	59.99	CR
Thraupidae	<i>Tangara cyanoptera</i>	25.33	10434.38	3-160	65.47	NT
Tyrannidae	<i>Elaenia flavogaster</i>	24.89	22702.16	1-106	14.19	LC
Ramphastidae	<i>Ramphastos dicolorus</i>	24.77	16768.37	3-138	47.69	LC

For Review Only

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