ECOLOGY

Defaunation precipitates the extinction of evolutionarily distinct interactions in the Anthropocene

Carine Emer[1]*, Mauro Galetti[1], Marco A. Pizo[2], Pedro Jordano[3], Miguel Verdú[4]

Species on Earth are interconnected with each other through ecological interactions. Defaunation can erode those connections, yet we lack evolutionary predictions about the consequences of losing interactions in human-modified ecosystems. We quantified the fate of the evolutionary history of avian–seed dispersal interactions across tropical forest fragments by combining the evolutionary distinctness of the pairwise-partner species, a proxy to their unique functional features. Both large-seeded plant and large-bodied bird species showed the highest evolutionary distinctness. We estimate a loss of 3.5 to 4.7 × 10^4 million years of cumulative evolutionary history of interactions due to defaunation. Bird-driven local extinctions mainly erode the most evolutionarily distinct interactions. However, the persistence of less evolutionarily distinct bird species in defaunated areas exerts a phylogenetic rescue effect through seed dispersal of evolutionarily distinct plant species.

INTRODUCTION

Biotic interactions form the backbone of biological diversity while delivering the unique ecological functions essential for human and nonhuman well-being (1, 2). Their fate is defined by both the contemporary ecological correlates and the evolutionary trajectories of the interacting species (3, 4). Thus, human activities known to affect species interactions within ecological time frames may likewise affect the evolutionary history of the interaction partners. Among them, defaunation, the worldwide pervasive human-induced extinction of animal populations or entire species, substantially affects large-bodied organisms that often perform interactions whose ecological function cannot be easily replaced by smaller-sized species (5). If these species are highly evolutionarily distinct (e.g., unique lineages in the Tree of Life and those with fewer extant relatives and a longer evolutionary history), then they may harbor greater amounts of evolutionary information than expected by species number alone (6, 7). Aimed at measuring this importance, "evolutionary distinctness" (hereafter ED) estimates the contribution of a given species to the total evolutionary history of its clade while measuring its isolation in the phylogenetic tree (8, 9). We propose to expand this concept by characterizing ecological interactions according to their ED, i.e., how species with different ED values interact with each other (Fig. 1). Thus, we can assess how the contemporary fast-paced defaunation has eroded the evolutionary history embedded in these interactions. Here, we coin the term "evolutionary distinctness of the interaction" (EDi) to refer to the combined ED that both interacting partner species convey to a given interaction, irrespective of how long they have been interacting with one another.

Species interactions entail millions of years of reciprocal effects and a vast amount of the genetic and ecological information that characterize their unique and irreplaceable contribution to support the Earth's biodiversity (10, 11). Mutualism rarely evolves as a process

in which partners have joint, reciprocal evolutionary trajectories involving cospeciation with congruent phylogenetic branching (12, 13). Instead, species with rather different evolutionary trajectories tend to interact in contemporary habitats, showing a marked asymmetry of ED (e.g., the pollination of a basal clade angiosperm species by an insect from a recent clade). For example, the ages of nectar-feeding and fruit-eating bird and mammal families and their core plant families are consistently skewed toward older plant taxa, evidencing that most animal families are younger than their partner plant families (11). In the specific case of tropical forests, avian seed dispersal is mediated by multiple species, with generalized interactions established by the consumption of fruits that do not necessarily require specialized traits (11, 12). Yet, generalist partner species hold distinct evolutionary histories that meet in contemporary time, forming interactions that combine all the evolutionary information that the interacting actors carry.

Because large-bodied animals and large-seeded plants tend to be evolutionarily distinct species owing to both their old age and isolation in the Tree of Life (14, 15), their interactions involve high values of EDi while accounting for the largest amounts of evolutionary history. Therefore, defaunation, by reducing the populations of large-bodied bird species (5) and, consequently, the probability of interactions with large-seeded plant species, would likely extirpate the most evolutionarily distinct interactions. In contrast, lower EDi values are expected for interactions involving small-bodied bird and small-seeded plant species, which conform to be the persisting interactions in fragmented landscapes (16). Thus, both locally extinct and persisting interactions would be characterized by relatively symmetric EDi (i.e., high-ED animal–high-ED plant species for locally extinct and low-ED animal–low-ED plant species for persistent interactions). Otherwise, when the interacting partners have highly divergent ED (e.g., low-ED animal–high-ED plant species), an asymmetric EDi emerges, with unexplored outcomes on the eco-evolutionary functions that support current ecosystems (10). Therefore, defaunation, by selectively pruning species from the Tree of Life (17, 18), is causing the extirpation of interactions with distinct combinations of evolutionary history, with consequences that may go well beyond the current ecological time (19, 20).

We quantify the signature of defaunation in the ED of plant-frugivore interactions in fragmented tropical forests by combining field and
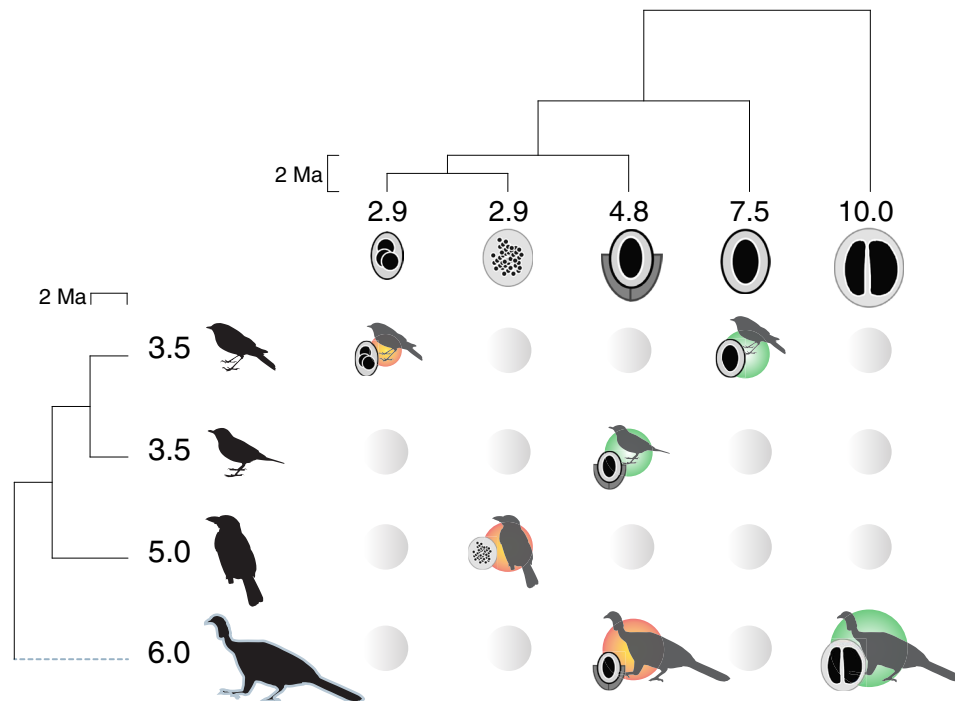
Fig. 1. The EDi is a combination of the ED of the interacting species that can be used to characterize the evolutionary history of the seed dispersal interactions. The ED of each species, calculated by equally dividing the phylogenetic distance of a branch among its daughter branches, is shown at the tips of the phylogenies. The size of the bird and plant fruit silhouettes is proportional to their ED. The ED magnitude of a bird–seed dispersal interaction ranges from very high when distinct plants are dispersed by distinct birds to very low when the opposite is true. The asymmetry can be bird-skewed, when a bird disperses a plant with lower distinctness than its own (orange circles), or plant-skewed otherwise (green circles). Defaunation is expected to have stronger impacts on interactions that involve bird species with a high ED (dashed line, highlighted bird silhouette).

phylogenetic data of the plant and bird species involved in seed dispersal. Here, we take a step forward by considering the effects of defaunation not only on species but also on the current distribution of the EDi of bird–seed dispersal interactions. We compiled 21 studies on seed dispersal by birds in which defaunation was estimated as the difference between the sum of all bird body masses at the regional landscape scale and the summed body masses of the birds that occur at the local, within-fragment scale. As shown in table S1, the studies were carried out in the Atlantic Forest of South America (*21*), a biodiversity hot spot (*22*) that has been drastically reduced to ~12% of its original cover in the past few centuries (*23*). The studied sites vary from small fragments of 0.66 ha to large forest remnants up to 42,000 ha along a disturbance gradient from semipristine-protected areas to secondary forests and restored plantations.

RESULTS

We found that defaunation caused the loss of interactions involving unique lineages of bird and plant species that have faced millions of years of hazards but may not be able to survive human disturbance in the Anthropocene (figs. S1 and S2). The loss of bird clades tends to concentrate on larger-bodied species, which are also the most evolutionarily distinct ($r = 0.21$, $t = 2.78$, $P = 0.007$; fig. S3 and table S2). These include large- and medium-bodied birds, such as guans [e.g., *Pipile jacutinga* (Cracidae): mean weight, 1250 g; mean ED, 28.99 million years (Ma)] and motmots [e.g., *Baryphthengus ruficapillus* (Momotidae): mean weight, 142 g; mean ED, 71.54 Ma] that are

essential to the dispersal of large-seeded plant species with the highest ED, such as palms [e.g., *Euterpe edulis* (Arecaceae): mean seed diameter, 12 mm; mean ED, 98.70 Ma] and nutmegs [e.g., *Virola bicuhyba* (Myristicaceae): mean seed diameter, 16 mm; mean ED, 36.26 Ma] mostly found in less disturbed forests and rarely on disturbed sites. Likewise, the ED of plant species is associated with a larger seed diameter ($r = 0.38$, $t = 5.84$, $P = 0.001$; fig. S3 and table S3). These two effects in combination indicate that interactions involving plant and animal lineages with high ED are selectively lost in more disturbed sites (figs. S1 and S2 and table S4).

Seed dispersal interactions in the Atlantic Forest show significantly asymmetric EDi values, mostly skewed toward plant species although bird-skewed interactions are also present (Fig. 2A and table S4). Bird-plant associations present in a higher number of fragments followed the same trend (Fig. 2B), indicating that most of the persisting interactions involve less evolutionarily distinct bird species dispersing more evolutionarily distinct plants. In contrast, bird-skewed asymmetries, i.e., bird species with a higher ED that disperse plant species with lower ED, often occur in a single or very few fragments (Fig. 2B), revealing their inability to persist in defaunated landscapes.

We observed that the cumulative EDi (i.e., the total EDi per fragment) decreases with increasing defaunation (slope, -5.44 ± 2.09, $t = -2.63$, $P = 0.02$; Fig. 3) even when fragment area (fig. S4) and interaction richness (fig. S5) are controlled for. Seed dispersal interactions vanishing in the Anthropocene represent a loss of evolutionary history that can be estimated by the cumulative EDi lost along the gradient
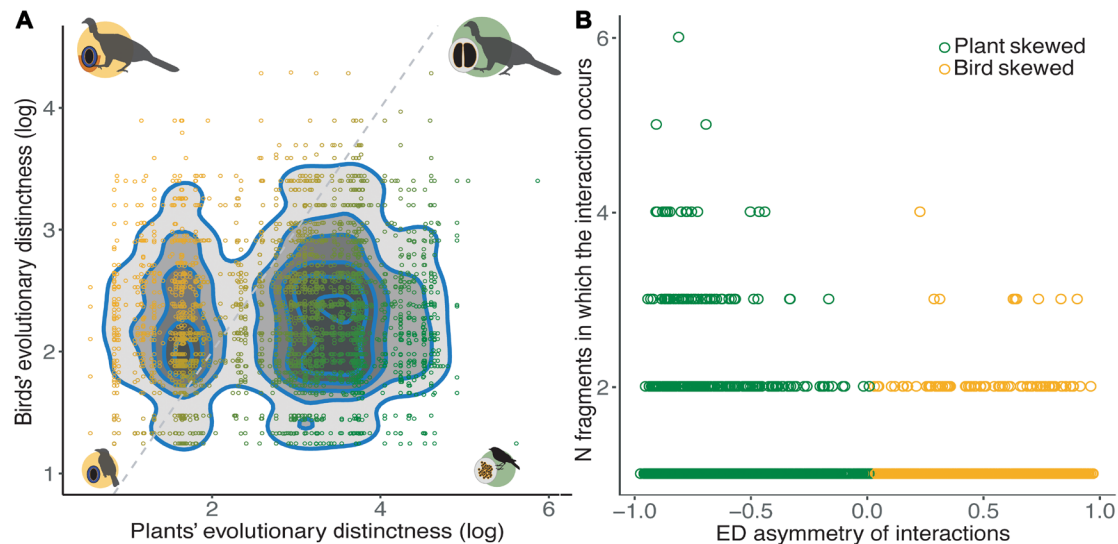
Fig. 2. Asymmetries in the ED of seed dispersal by birds in the Atlantic Forest. (**A**) A density plot showing asymmetries in ED between bird and plant species partners in seed dispersal interactions. Each dot represents a single-interaction event, and the intensity of the gray-shaded areas increases with the concentration of the most common asymmetries. Bird-skewed interactions (orange dots) occur when more evolutionarily distinct bird species disperse less evolutionarily distinct plant species; plant-skewed interactions (green dots) occur when more evolutionarily distinct plant species are dispersed by less evolutionarily distinct bird species. Plant-skewed interactions are twice the number of bird-skewed interactions (bird-skewed, 871; plant-skewed, 1797; $P < 0.001$, binomial test). (**B**) The frequency of the ED asymmetries of seed dispersal interactions in different forest fragments. Results from a generalized linear model indicate that plant-skewed asymmetries occur in a larger number of fragments (slope, -0.09 ± 0.04, $z = -2.46$; $P = 0.01$) and thus are significantly more persistent in the fragmented landscape. The colors of the dots follow the description for plant- and bird-skewed asymmetries, as in (A).

of defaunation, i.e., 3.5 to 4.7×10^4 Ma of cumulative evolutionary time (Fig. 3). The magnitude of EDi lost in the defaunated fragments of the Atlantic Forest is similar to the marked loss of avian and bees' evolutionary history devastated by agricultural practices worldwide (*24*, *25*), and it is intensified in very small fragments. Furthermore, we identified that the most pristine and less defaunated forests, which are located within State Parks, harbor more cumulative EDi than expected from their interaction richness (fig. S5). On the other hand, all other fragments but two are currently supporting less EDi than expected by the local pool of species performing seed dispersal interactions. These findings show that, while the less defaunated sites within protected areas harbor interactions with irreplaceable evolutionary information and unique ecological functions, defaunation pervasively vanishes evolutionary history from forest fragments.

Although overall seed dispersal interactions are drastically lost with small increases in defaunation, the different combinations of bird and plant species' ED respond differently to this scenario (Fig. 4 and fig. S6). Interactions with bird-skewed ED values (i.e., higher ED of the avian partner, yellow lines in Fig. 4) are the first to vanish, resulting in the loss of more than 50% of interactions, with increases as small as 6% in the defaunation index. This reduction of EDi is more severe when both interacting partners are highly evolutionarily distinct (EDi from 32 to 381 Ma).

DISCUSSION

Our findings show that the extirpated bird–seed dispersal interactions tend to include unique species that contain an irreplaceable set of genetic information that may not survive the challenges imposed by contemporary human-driven disturbances. The impoverishment of EDi in the remnants of the Atlantic Forest translates into non-

random local extinctions of ecosystem functions related to seed dispersal by birds, such as the dispersal of large-seeded plant species. The loss of ecological functions due to reduced phylogenetic diversity in mutualistic systems has also been reported recently for agricultural landscapes in which pollination service and crop production are highly affected by the loss of highly evolutionarily distinct bee species (*25*). Furthermore, because the Atlantic Forest biome is mostly composed of highly defaunated small fragments (*23*) and because higher EDi values are restricted to a few relatively pristine and large areas, the restoration of evolutionary history would be extremely difficult with the current rates of local extinction (*26*). However, the reintroduction of species with higher ED can be a way forward to recover the EDi of lost interactions (*27*). Four of our study sites, for example, are composed of restored forests (table S1) that, similar to the highly defaunated fragments, hold low EDi values (Fig. 3), because large-seeded plant species are poorly represented in the pool of species used for restoration (*28*). Thus, including highly evolutionarily distinct plant species in active restoration initiatives would maximize the potential for the restoration of EDi at local and regional levels.

Overall, the loss of bird–seed dispersal interactions with plant-skewed EDi is smaller than that of bird-skewed interactions, which are the first to vanish with defaunation (Fig. 3). The fact that many plant species can be dispersed by bird species with a lower ED, which are often habitat and diet generalists (*16*, *29*), allows them to persist longer in the defaunated areas. In this scenario, plant-skewed interactions involving small-bodied, low-ED bird species dispersing large-seeded, high-ED plant species may occur only occasionally. Thus, rare events of propagule movement are important to maintain viable populations across the fragmented landscape (*30*). Yet, persisting interactions with plant-skewed EDi values such as the common seed dispersal of *Schinus terebinthifolia* (ED, 24.5 Ma) by

Fig. 3. The EDi promoted by bird-mediated seed dispersal decreases sharply along a gradient of defaunation. The cumulative EDi that a fragment carries corresponds to the sum of the EDi values of all interactions recorded in that fragment, here, the sum of the EDi values of all seed dispersal interactions by birds. The most pristine area is the top-left circle (1), which is the largest remnant of the Atlantic Forest and also the least defaunated fragment, used here as the baseline to illustrate the position of a "pristine" forest. The top-shaded facet of the graph represents the amount of cumulative EDi lost from the most pristine area to the second least disturbed fragment (2), while the bottom-shaded facet indicates the amount of cumulative EDi lost from the pristine area to the most disturbed fragment (*16*). Areas (identified by numbers within circles) are presented in a decreasing order of fragment area, according to a detailed description of each site in table S1. Larger fragments tend to be less disturbed, therefore harboring forests closer to the most pristine, best-preserved extreme.
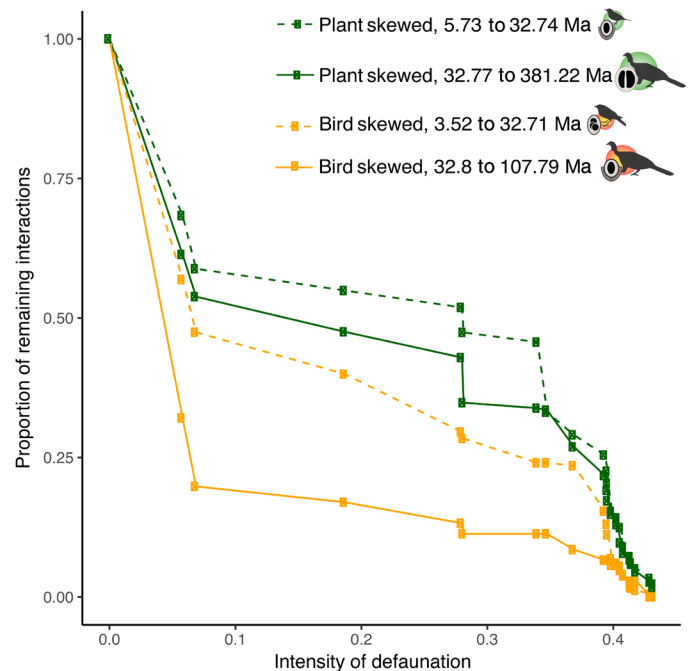

Fig. 4. Defaunation leads to an impoverishment of seed dispersal interactions and their associated asymmetries in the EDi. The proportion of interactions remaining in each fragment significantly decreases with defaunation, and this pattern is maintained when controlling for fragment area (fig. S5). The four types of bird–seed dispersal interaction asymmetries showed a similar trend in losing ED, but the loss was faster for bird-skewed interactions while plant-skewed interactions persisted longer in the gradient of defaunation. The 50th percentile was used as the threshold to define low and high EDi values. The defaunation index is scaled according to the lowest value among all fragments, which corresponds to the largest area and less defaunated remnant of the Atlantic Forest, used here as a baseline value to illustrate the position of a pristine forest. Continuous lines indicate high ED; dashed lines indicate low ED. The four types of asymmetry correspond to different combinations of EDi, as follows: Plant skewed, low ED (minimum EDi, 5.73 Ma; maximum EDi, 32.74 Ma); plant skewed, high ED (32.77 to 381.22 Ma); bird skewed, low ED (3.52 to 32.71 Ma); bird skewed, high ED (32.8 to 107.79 Ma).

Turdus rufiventris (ED, 6.2 Ma) or of *Trema micrantha* (ED, 41.2 Ma) by *Dacnis cayana* (ED, 7.1 Ma) may be more stable in the environmental changes seen in the Anthropocene (*31*).

Our results suggest that the loss of evolutionary history of plant species in the Atlantic Forest is minimized by the rescuing effect performed by bird species with limited ED dispersing unique plant species. The rescuer bird species represent clades of small-bodied, generalist bird species able to thrive in human-modified environments, which functionally "help" some plant species to persist. The functional role of rescuer species includes the dispersal of plant species whose primary seed dispersers have been already lost (*20*) or functionally extinct because of overhunting, for instance (*32*). The large seeds of a keystone, highly evolutionarily distinct tropical palm, *E. edulis*, have rapidly evolved toward smaller sizes in populations in which its main large-bodied, evolutionarily distinct seed disperser, *P. jacutinga*, has been locally extinct (*33*). The response of *E. edulis* to defaunation may increase its probability of being phylogenetically rescued by less distinct, small-bodied bird species.

Yet, rescue effects cannot functionally replace lost interactions. The phenotypic and microevolutionary changes observed in plants that lost their primary large-bodied seed dispersers (*33*, *34*) also indicate that, although small birds can still disperse the smaller

seeds, they do not functionally replace the effectiveness of the seed dispersal service provided by the vanished large-bodied frugivores. Therefore, the rescue effect cannot recover the extinction of the unique evolutionary histories of the interactions affected by defaunation. Moreover, the predominance of plant-skewed asymmetries in the Atlantic Forest may be a reflection of the extinction debt of interactions [sensu (*19*)]. Such a debt means that plants, which have longer life spans than birds, may persist for decades after the interaction has disappeared.

Given the scenario of increasing defaunation in human-altered fragmented landscapes, a marked reshaping of the Tree of Life may be occurring in the Anthropocene. Large-bodied frugivores have been hypothesized to reduce speciation rates of large-fruited plants as a consequence of high gene flow associated with long-distance dispersal ranges, while small-fruited plants tend to speciate more owing to restricted dispersal by small-bodied frugivores (*35*). Therefore, the phylogenetic rescue effect promoted by the persistence of plant-skewed, low-ED interactions would favor higher rates of speciation in small-seeded plant species, which could affect the functioning of tropical forests. Furthermore, local assemblages facing

larger losses of EDi can be expected to be less resilient to disturbance owing to the impoverishment of the functional diversity concomitantly occurring with the loss of phylogenetic history of the partner species (10, 36). This impoverishment is likely to change the niche space occupied by the local assemblage of interacting species (37). New empty niches may create opportunities for the establishment of exotic species (38) and trigger changes in biogeochemical cycles such as CO_2 storage by large-seeded plants dispersed by large-bodied frugivores (39). The resultant Anthropocene landscape will most likely consist of a metacommunity of evolutionarily impoverished fragments, phylogenetically structured by the defaunation of specific clades (40). Our approach can be easily extended to other ecological systems from which similar results are expected on the basis of the loss of specific functional groups, such as the global decline of bee pollinators (6, 25). From a conservation point of view, our results show that we are losing unique evolutionary histories of interactions that cannot be replaced by contemporaneous species. However, these losses may be lessened by a few persisting interactions performed by less evolutionarily distinct bird species rescuing the more evolutionarily distinct plant species from the verge of extinction.

MATERIALS AND METHODS
Study area
The Atlantic Forest is a tropical hot spot of biodiversity (22), highly threatened by human activities (such as logging, habitat conversion to commercial monocultures, and increasing urbanization), that has drastically reduced its original cover to ~12% (23). The remaining landscape constitutes a complex mosaic formed mainly by small fragments (<50 ha, ~80% of the remaining area) and clusters of close neighboring fragments (<200 m apart) (23). These fragments function as a metanetwork of interactions connected by small generalist bird species dispersing small-seeded plant species, while large-bodied bird species able to disperse large-seeded plant species are constrained to a few pristine, large area fragments (16).

Dataset
We used the Atlantic-Frugivory dataset, the largest dataset available for tropical plant-frugivore interactions (21), to test how much evolutionary history of bird–seed dispersal interactions is being lost because of the contemporaneous defaunation. Bird and plant species present in the Atlantic-Frugivory dataset comprise our regional pool of species, which was used to build the correspondent phylogenies and to calculate the defaunation index (see details in the next subsections). From that regional pool, we selected 21 studies of bird–seed dispersal interactions sampled in fragments of the Brazilian Atlantic Forest (table S1). The studied fragments vary from 0.66 to 42,000 ha in a gradient of disturbance from semipristine-protected areas to secondary forests, degraded fragments and restored plantations. The studied fragments were distributed among different vegetation types of the biome, including Ombrophilous and Semidecidous forest, Araucaria Forest, rupestrian, and dry vegetation. Our dataset includes all studies with available information designed to collect fruit-eating bird interactions at the community level in the Atlantic Forest (21); yet, they did not necessarily record effective seed dispersal. We carefully checked the dataset and removed any interaction that would not characterize seed dispersal events. Methods to record interactions varied among studies, including direct bird observations and fecal sampling; only community-level studies with at least

12 months of sampling were included in the analyses. We further added available information to each study site based on field observations and expert knowledge about tropical avian seed dispersal.

Phylogenetic trees
Birds
Given the list of species at the regional pool (21), we obtained 100 phylogenetic trees inferred from the BirdTree.org online database using the "Stage2 MayrParSho Ericson" source tree as birds' master phylogeny (available at http://birdtree.org/methods/). Trees' topology is resolved with a combination of genetic and taxonomic information and dated with a relaxed molecular clock [see (6, 41) for details]. A few species that were identified at genus level in the field (i.e., *Elaenia* sp., *Myiarchus* sp., *Patagioenas* sp., *Penelope* sp., and *Turdus* sp.) therefore could not be found in the master phylogeny. We randomly grafted these species in their correspondent clades using the "add.species.to.genus" function in the phytools package version 0.6-00 in R (42).
Plants
Given the list of plant species at the regional pool (21), we used the megaphylogeny of trees (43) with the "S.PhyloMaker" function (41) to obtain the initial plant tree. The initial tree was based on "scenario 1" in which missing genera and/or species are added as basal polytomies within their higher taxonomic level (44). Then, we simultaneously resolved the polytomies and adjusted the branch lengths using an evolutionary birth-death model with the help of "PolytomyResolver" function (45) and BEAST version 1.5.4 (46). Markov Chain Monte Carlo analyses were run for 10^6 iterations, and trees were sampled every 10^3 iterations. After discarding the 25% first trees, we randomly selected 100 trees for subsequent analyses.

ED of bird–seed dispersal interactions
The ED of a given species quantifies how isolated it is in its own phylogenetic tree and the amount of unique evolutionary history that it embodies (8, 9). Similarly, the amount of evolutionary history that an interaction holds can be estimated by the combination of the ED of the interacting partner species. Therefore, the EDi combines the isolation and unique evolutionary history of the partner species in their correspondent phylogenetic trees. We calculated EDi as follows.

First, we calculated the ED for all plant and bird species based on the correspondent phylogenetic trees that we built for the regional pool of species of the Atlantic Forest (see above). ED was estimated using the equal splits metric available in the "evol.distinct" function in the picante package for R (47). Equal splits metric equally divides the phylogenetic distance represented by a branch by the number of lineages originating from the node directly below it (8). It gives higher values of ED for species placed in clades in which the path length is shared among a lower number of species and is considered a robust metric to capture phylogenetic diversity (9). Then, we obtained the mean ED for each bird (EDb) and plant species (EDp) calculated over 100 solved trees and used it as a proxy for its ED. Last, to quantify the EDi, we summed the ED of the interacting bird (EDb) and plant species (EDp) such as EDi = EDb + EDp.

Statistical analyses
To test whether more evolutionarily distinct bird and plant species were associated with larger body mass and seed diameter, respectively, we used nonparametric Spearman correlation tests (48).

The extremely large sample size caused an overfit of any modeling attempt to assess the form of these relationships, so we resorted to use nonparametric Spearman correlation tests to highlight any non-random associations between traits and ED.

Asymmetries in EDi were calculated as the difference between the ED values of both interacting partners. Bird-skewed asymmetries correspond to interactions in which the bird species has higher ED than the partner plant species, and plant-skewed asymmetries correspond to interactions in which the plant species brings more ED than the partner bird species. We apply a binomial test to estimate which type of asymmetry (bird skewed or plant skewed) is significantly more predominant among the 2668 unique combinations of bird and plant species interactions found in our communities. Then, we used a generalized linear mixed-effects model in the lme4 package (49) to test which type of EDi asymmetry is more persistent in the fragmented landscape. In this model, we fit the number of fragments in which the interaction occurs as a response variable against the asymmetry value of EDi as the independent variable. Bird species and plant species were used as random factors to control for pseudoreplication, given that a single species can perform more than one interaction. We fit the model with a Poisson distribution.

To understand the amount of the cumulative EDi of bird–seed dispersal interactions lost in the gradient of defaunation across tropical forest fragments, we fitted three different linear models. We started by quantifying the cumulative EDi in each fragment by summing up the EDi values of all bird–seed dispersal interactions recorded per fragment. Defaunation was estimated as the difference between the sum of all bird body masses at the regional landscape scale [considering all frugivore bird species present in the Atlantic-Frugivory database (21) as a proxy for the regional pool of species] and the summed body masses of the birds that occur in each fragment. For the first model, we simply used the cumulative EDi as the response variable fitted against the defaunation index to test for the absolute loss of EDi as defaunation increases. For the second model, we used the same approach while controlling for fragment area. We tested for the correlation between fragment area and defaunation using a Pearson correlation test. Then, we used the residuals of a linear regression of defaunation index on fragment area as the independent variable fitted against the cumulative EDi. Last, we used a null model to test whether the cumulative EDi per fragment was significantly different from that expected by the number of bird–seed dispersal interactions recorded in each community. We created an a_{mn} matrix in which m and n correspond to the study site and the bird–seed dispersal interactions, respectively. The a_{mn} element of the matrix is filled according to the presence of an interaction n in site m quantified by the corresponding EDi. Therefore, the marginal total of m corresponds to its observed cumulative EDi. We applied the "shuffle.web" method within the "nullmodel" function in the bipartite package (50), which relocates the a_{mn} element within the matrix while maintaining its dimensionality, i.e., constraining the number of sites and interactions while shuffling the EDi among them. We obtained the mean and SD of the EDi per site over 100 simulations and calculated the corresponding z score based on the observed cumulative EDi. The z scores were fitted against the defaunation index in a linear model. Positive z scores indicate that the site holds more cumulative EDi than expected by the number of bird-plant interactions recorded in that area. On the other hand, negative z scores indicate that the site holds less cumulative EDi than expected by the number of interactions that it encompasses. Statistical analyses were performed in R version 3.4.3 (51).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/5/6/eaav6699/DC1

Fig. S1. Distribution of the ED of the frugivore bird species in the gradient of defaunation across the fragments of the Atlantic Forest.

Fig. S2. Distribution of the ED of the bird-dispersed plant species in the gradient of defaunation across the fragments of the Atlantic Forest.

Fig. S3. Correlation between the ED and the traits of the species involved in seed dispersal interactions in the Atlantic Forest.

Fig. S4. Defaunation leads to a significant impoverishment of the cumulative EDi performed by bird seed dispersal across forest fragments.

Fig. S5. EDi promoted by bird seed dispersal decreases sharply along a gradient of defaunation.

Fig. S6. Defaunation leads to an impoverishment of seed dispersal interactions and their associated asymmetric relationships of EDi.

Table S1. Description of the dataset used in this study.

Table S2. Traits of the bird species recorded in the studied communities of the Atlantic Forest.

Table S3. Traits of the plant species recorded in the studied communities of the Atlantic Forest.

Table S4. The bird–seed dispersal interactions recorded in the studied sites of the Atlantic Forest, followed by their EDi and correspondent asymmetry.

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Carine Emer, Mauro Galetti, Marco A. Pizo, Pedro Jordano and Miguel Verdú

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