

Predicting the consequences of disperser extinction: richness matters the most when abundance is low

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Summary

1. The ongoing biodiversity crisis entails the concomitant loss of species and the ecological services they provide. Global defaunation, and particularly the loss of frugivores, may negatively affect the seed dispersal of fleshy-fruited plant species, with predictable stronger impacts in simplified communities such as those on oceanic islands. However, logistical difficulties have hindered the experimental and theoretical need to disentangle the roles of species identity, richness (i.e. number of species) and abundance. Consequently, studies to date have focused exclusively on the loss of species richness leaving us largely ignorant regarding how species identity and abundance affect the loss of ecosystem functions.

2. Here, we applied a network approach to disentangle the effects of disperser abundance, richness and identity on the seed dispersal service provided by frugivores to the Galapagos plant community.

3. We found that both abundance and richness of the dispersers significantly affect the function of seed dispersal and that richness becomes increasingly important as disperser abundance declines. Extinction simulations revealed that the order of species loss has profound implications to the plant community. On the one hand, abundant generalist dispersers like the Galapagos lizards, can mitigate the loss of specialized dispersers. On the other hand, specific threats affecting key dispersers can lead to the rapid collapse of the community-level dispersal services.

4. Our results suggest that the identity of the disperser species lost can have a large effect on the number of plant species dispersed, and generalist species are essential to the persistence of the community dispersal service. Both abundance and species richness of seed dispersers are key and synergistic drivers of the number of plant species dispersed. Consequently, the coupled negative effect of population declines and species extinctions in frugivore assemblages may lead to an accelerated loss of the seed dispersal function.

Key-words: biodiversity loss, biotic homogenization, defaunation, dispersal failure, ecological networks, ecosystem function, Galapagos Islands, mutualism disruption, oceanic islands, seed dispersal service

Introduction

The accelerated loss of biodiversity worldwide (Ceballos *et al.* 2015) has caused a growing concern about its consequences for the resilience of key ecosystem

functions and the services that humans derive from biodiversity (Thébaud & Loreau 2003; Díaz *et al.* 2006). Nowadays, there is a broad consensus that biodiversity *per se* is critical for maintaining high ecosystem service rates due to the importance of facilitative interactions among species and functional complementarity (Hooper *et al.* 2005).

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Species are not equally vulnerable to anthropogenic disturbances. Rare and specialist species face a disproportionately high risk of extinction (Kunin & Gaston 1997; Davies, Margules & Lawrence 2004), while some abundant and generalist species might even benefit from certain perturbations such as land-use change or the extinction of co-occurring species (Siriwardena *et al.* 1998; La Sorte 2006; Devictor *et al.* 2008). The success of disturbance-tolerant species can, to a certain degree, offset the loss of the most vulnerable species, leading to a simplification of the community (i.e. biotic homogenization) (McKinney & Lockwood 1999) without necessarily implying an overall loss of ecosystem service providers. Several studies have reported such “density compensation” following local extinctions. For example, while the relative abundances of several native bee species have decreased in the northeastern United States over the last century, other species known to be more tolerant to human disturbances have increased their populations (Bartomeus *et al.* 2013). Neotropical primates (Peres & Dolman 2000) and ranid frog communities in Canada (Hecnar & Robert 1997) show similar responses. The replacement of local specialist species, many of which are endemic and highly threatened, by a few widespread generalists (including invasive species) is thus leading to a homogenization of ecosystems (McKinney & Lockwood 1999). However, the functional consequences of such replacement have seldom been addressed (see Olden *et al.* 2004 and references therein).

Species can differ strongly in their contributions to specific ecological services and in their vulnerability to anthropogenic disturbances (Elmqvist *et al.* 2003). It is therefore crucial to consider both the richness of the mutualist community and the overall abundance of mutualists when predicting the effects of the ongoing biodiversity crisis on ecosystem functions (see Larsen, Williams & Kremen 2005). Until now, such predictions have focused almost exclusively on the consequences of pollinator loss on plant reproduction (e.g. Cox & Elmqvist 2000; Klein, Steffan-Dewenter & Tscharnke 2003; Blüthgen & Klein 2011; Bartomeus & Winfree 2013). Thus, the consequences of diversity loss on other key services such as seed dispersal (Şekercioğlu, Wenny & Whelan 2016) remain largely unexplored.

Fleshy-fruited species depend on frugivorous vertebrates to disperse their seeds; frugivores increase their chances of finding suitable germination sites, occupying available niches, and expanding their distribution area (Howe & Smallwood 1982; Traveset, Heleno & Nogales 2014). Consequently, the local extinction of all potential dispersers of a given plant species will reduce its fitness, potentially causing an interaction-based extinction debt (Guimarães, Galetti & Jordano 2008; Valiente-Banuet *et al.* 2015; but see also Jansen *et al.* 2012). The disruptive effects of disperser loss are expected to be particularly severe on oceanic islands, where simplified and naïve communities are particularly vulnerable to external threats like invasive

species (Traveset & Richardson 2006; Kaiser-Bunbury, Traveset & Hansen 2010).

Even in relatively simplified systems, such as oceanic islands, seed dispersal is a complex process, involving interactions between diverse animal and plant communities (Jordano *et al.* 2007; Heleno *et al.* 2013). A network approach, encompassing all species and their interactions, is therefore particularly useful to identify keystone species (Mello *et al.* 2015), and to capture the mechanisms underlying biodiversity and ecosystem function relationships in natural assemblages (Reiss *et al.* 2009; Hines *et al.* 2015; Schleuning, Fründ & García 2015).

Here, we took advantage of available data on a well-resolved, year-round quantitative ecological network to test whether the loss of vertebrate seed dispersers in the Galapagos Islands is accompanied by a sharp decline in the service provided to plants – as expected in simplified insular communities – or alternatively if the dispersal service is highly robust to defaunation due to a high level of trophic generalism. Specifically, we predict the functional consequences of disperser decline in terms of both species abundance and community richness. To do that, we simulated how the quantity of the seed dispersal service in terms of number of seeds and number of species dispersed (Schupp, Jordano & Gómez 2010) would be affected by five future extinction scenarios based on current threats to the archipelago biota: (i) homogeneous decline in the overall abundance of dispersers; then four scenarios involving loss of disperser richness while keeping their abundance constant, but assuming, respectively, that: (ii) all species have a similar extinction risk, (iii) rare dispersers face a greater extinction risk than abundant species, (iv) a species-poor disperser guild (giant tortoise and lava lizards) faces a greater extinction risk, and (v) a species-rich disperser guild (birds) faces a greater extinction risk. See electronic supplementary material for dispersers’ conservation status and specific threats supporting each extinction scenario (Tables S1 and S2, Supporting Information). By examining *scenarios 2 to 5*, we evaluated the importance of disperser identity and level of generalism, and whether the spread of disturbance-tolerant disperser species could offset the consequences of the extinction of the most vulnerable ones.

Materials and methods

STUDY SYSTEM AND SEED DISPERSAL INTERACTIONS

The Galapagos Islands are well known for the uniqueness of their biota, which has evolved in isolation c. 1000 km from South America, under severe physical conditions. The archipelago harbours three main guilds of frugivorous seed dispersers: terrestrial birds (including the 14 species of Darwin finches), lava lizards (nine species of the genus *Microlophus*, Benavides *et al.* 2009) and the giant tortoise (*Chelonoidis nigra*) (Blake *et al.* 2012; Heleno *et al.* 2013). These three groups face different but equally serious threats from anthropogenic disturbance. For centuries, sailors hunted giant tortoises, decimating their populations and even

leading to local extinctions (Hendrickson 1966; MacFarland, Villa & Toro 1974). Nowadays, the major threat to them is the introduced little fire ant *Wasmannia auropunctata*, which has a negative impact on young tortoises and birds (Wetterer & Porter 2003). Galapagos birds, in addition to the fire ant attacks, are being heavily affected by the parasitic nest fly *Philornis downsi* (Kleindorfer *et al.* 2014; Koop *et al.* 2016). Finally, the endemic lava lizards are preyed upon by feral dogs and cats (Barnett & Rudd 1983; Konecny 1987). Compared to other oceanic archipelagos, the Galapagos fauna has hardly been affected by extinction; however, 35% of the vertebrates are endangered to some degree (Jiménez-Uzcátegui *et al.* 2007), and it is therefore important to understand the potential consequences that probable future changes in the structure of the seed disperser community might have on the overall richness of the fleshy-fruited plants they disperse.

The Galapagos seed dispersal network was studied by Heleno *et al.* (2013), based on the identification of 9157 intact seeds (i.e. those that were not mechanically destroyed in the gut of the frugivores and that showed no signs of predation) retrieved from 2879 droppings belonging to birds and non-avian sauropsids (a giant tortoise and two lava lizard species). Droppings were collected regularly at eight sites on the two main Galapagos Islands: Santa Cruz and San Cristóbal. These sites supported the two most representative vegetation types in the Galapagos (dry lowland and humid highland), and were sampled across an entire year (from March 2010 to February 2011). During the main fruiting period (February–July) corresponding to the hot/wet season, each site was visited twice per month, and in the remaining months (cold/dry season) they were visited once per month. Bird droppings were collected during ringing sessions with mist-nests by individually capturing and releasing c. 2265 birds, allowing us to unequivocally assign the droppings to their corresponding bird species. This sampling method also captured regurgitated seeds, as these can be found inside the bird holding bags where captured birds defecate; nevertheless, they cannot be distinguished consistently from defecated seeds. Sauropsid droppings (giant tortoise and lava lizards) were collected along fixed linear transects parallel to the nets on the same days of ringing sessions. The divergent distribution of the tortoise (only present on San Cristóbal) and the two lava lizard species (each of them restricted to one of the islands) also allowed us to unequivocally assign the droppings to their corresponding species. The seeds identified belonged to 58 plant species and the droppings to 18 disperser species.

Almost half of the plant species ($n = 24$) have fleshy fruits that are particularly adapted for internal dispersal by animals (endozoochory), thus these species would very likely have a reduced reproductive output if all their dispersers became extinct. Contrarily, dry-fruited species usually have adaptations to abiotic means of dispersal and their reproductive fitness might not be affected by the extinction of dispersers, so these species were excluded from the dataset, leaving a final matrix composed of 2841 droppings that quantified the dispersal of 24 fleshy-fruited species by 17 frugivores: one giant tortoise, two lava lizards and 14 birds, including nine Galapagos finches (Tables S3 and S4, Data S1). This matrix is comprehensive and includes interactions between all potential bird, lizard and tortoise frugivores present on both islands, as well as the vast majority of fleshy-fruited species with substantial representation in both the dry and humid zones (see Heleno *et al.* 2013). Thus, our extensive sampling, together with the simplified community of the Galapagos Islands, allowed us to assemble highly comprehensive knowledge of seed dispersal interactions. To assess the achieved sampling completeness, species accumulation curves were estimated using the package *VEGAN* (Oksanen *et al.* 2016) for the statistical software *R* (R Development Core Team 2015). We calculated the Chao index (Chao 1987) to predict the expected number of plant species in the system and evaluate the

proportion of detected species. In the final matrix, the interaction frequency between animal species i and plant species j was estimated as the number of droppings of i containing at least one seed from j (Table S4). Hereafter, we use the terms dispersers and frugivores as equivalents to refer to the animal species dispersing seeds in our study.

EXTINCTION SIMULATIONS AND DATA ANALYSIS

We performed modelling of the interaction matrix and evaluated plant dispersal failure following the decline of seed dispersers under five different scenarios. All simulations were performed in *R* (R Development Core Team 2015) (Data S2), and the number of interacting species (i.e. degree) was calculated with the package *bipartite* for *R* (Dormann, Gruber & Fründ 2008). We also calculated seeds dispersed in the case of *extinction scenario 1*. We focused in these two descriptors and ruled out exploring other network parameters because both the number of interacting species and number of seeds dispersed directly reflect the consequences of defaunation on the degradation of the community-level dispersal service. Moreover, at least some topological descriptors can be affected by network size (Dormann *et al.* 2009; Costa *et al.* 2016; Vizin-Bugoni *et al.* 2016), which means that as seed dispersers are progressively lost in the simulations, it would be difficult to tell apart which topological consequences are exclusively due to defaunation and which are a mathematical consequence of considering increasingly smaller networks. We assumed that seed dispersers remaining after an extinction event in the community increase their abundances because of reduced competition from other disperser species. However, we also assumed that the remaining dispersers do not expand their trophic niche to include fruits from plants not previously consumed (Kondoh 2003; Kaiser-Bunbury *et al.* 2010). Although a certain level of trophic niche expansion could be expected, our exhaustive sampling suggests that the margin for such rewiring should be small. Furthermore, modelling potential trophic niche expansions would require extremely detailed data on morphological trait matching, behavioural preferences, and phenological and spatial coupling between species. Allowing trophic rewiring under broader assumptions could severely underestimate the effects of disperser extinctions. Therefore, our approach examines the quantitative consequences for seed dispersal assuming that after the extinction of a particular disperser species, plants left without interacting partners are no longer dispersed and their populations might eventually collapse as a consequence of a reduced reproductive fitness (Traveset, González-Varo & Valido 2012).

The overall number of droppings from each seed disperser species was used as a proxy of its relative abundance (see Fig. S1). The systematic collection of bird and lizard droppings can be used as a reliable indirect estimate of relative abundances, as the number of droppings produced per unit of time and area will be directly associated with animal density (Schwarz & Seber 1999; Correia *et al.* 2017). The unpredictability of the five extinction scenarios assessed precludes either of them being considered more likely than the rest. We briefly explain here the biological arguments behind each of these realistic scenarios, but see electronic supplementary material (Tables S1 and S2) for additional information:

Scenario 1 – simulates the homogeneous decrease in abundance of all dispersers. This was achieved by performing rarefactions of the whole dataset of disperser droppings according to variable sampling intensities (2000, 1500, 1000, 500, 300, 200 and 100 droppings). One thousand randomly generated networks were constructed at each sampling level to evaluate the disperser richness (i.e. number of species), the richness of plant species served by those dispersers, and the number of seeds dispersed. Within each level of disperser abundance, the effect of disperser species richness on the number of plant species dispersed was explored with linear

regressions. We then performed an overall generalized linear model (GLM) to disentangle the effect of sampling intensity (factor), disperser richness (continuous variable), and their interaction, on the number of plant species dispersed (response variable with Poisson distribution error). An additional linear regression was fitted to evaluate if the relationship between disperser richness and the number of plant species that lost all dispersers was constant across all levels of disperser abundance.

Scenario 2 – simulates a loss in frugivore richness assuming the same extinction risk for all seed dispersers. In this and the following scenarios, disperser abundance was kept constant in order to focus exclusively on the effect of the loss of frugivore species, assuming that disturbance-tolerant species can spread and thereby density compensate. Thus, seed dispersers were randomly and progressively eliminated from the community. At each extinction step, the number of plant species dispersed was calculated from 100 networks that were resampled using a constant sampling intensity of 300 droppings randomly selected from the pooled droppings produced by the remaining dispersers. This constant sampling level of 300 droppings was optimized after confirming the consistency of the results when selecting other sampling levels. It is a sufficiently large sample to provide a wide variation in the richness of dispersers but small enough to allow extinction simulations even when only a few disperser species remain extant. For this scenario of random loss of frugivores, the sequence of lost dispersers was repeated 100 times to reduce the effects of species identity in the sequence of extinction. In contrast, for *Scenarios 3, 4* and *5*, the extinction sequence was experimentally determined.

Scenario 3 – simulates a loss in frugivore richness by assuming that the rarest species (the one represented in our dataset by less droppings) face increased extinction risk, i.e. dispersers were lost according to their abundance.

Scenario 4 – simulates the higher extinction risk of the species-poor disperser guild, i.e. the giant tortoise and the two species of lava lizards are lost prior to birds. The order of extinction within the non-avian saurospids and birds followed their rarity level.

Scenario 5 – Simulates a higher extinction risk of the species-rich disperser guild, i.e. birds are more prone to extinction than the giant tortoise and lizards. Again, the order of extinction within the two guilds of dispersers followed their rarity level.

One important advantage of simulating dispersal failure by bootstrapping a large dataset is that seed dispersal failure (i.e. the “extinction of the interaction”) can be detected before the “formal extinction” of the species providing the service. This phenomenon, coined functional extinction, has been empirically observed in several systems, when the abundance of the service providers is so low that they cease to perform effective ecosystem functions, despite being still extant (McConkey & Drake 2006; Anderson *et al.* 2011b; Santamaría *et al.* 2016). In our simulations, the bootstrap protocol ensures that all droppings are given an equal probability of being sampled at each run, thus interactions dependent on rare dispersers will more often be absent from virtually assembled networks, thereby appropriately incorporating the effect of functional extinction.

In order to evaluate the importance of each frugivore for the overall seed dispersal services, we calculated the strength and proportional similarity at the frugivore-species level, using the *bipartite* package (Dormann, Gruber & Fründ 2008). Species strength measures the relevance of each frugivore across all its partners in the fleshy-fruited plant community, whereas proportional similarity measures the overlap between the services provided by each frugivore and the services provided by the whole frugivore assemblage (Feinsinger, Spears & Poole 1981). Besides this species-level similarity (i.e. overall functional redundancy), we also assessed similarity among pairs of frugivore species according to the plant species they dispersed (i.e. functional redundancy among pairs of frugivores). We used the Jaccard’s index to assess pairwise similarity in qualitative terms, and a proportional similarity index to

assess pairwise similarity when accounting for the frequency of interactions. Jaccard’s index was calculated as $J = c/(a + b - c)$; where a and b are the number of plant species dispersed by the frugivore species A and B , respectively, while c is the number of plant species dispersed by both species. We calculated the proportional similarity index (PS; Hurlbert 1978) as

$$PS = \sum_{i=1}^n \min(p_{ia}, p_{ib});$$

where, for n plant species, p_{ia} is the frequency of seed dispersal (proportion) of the plant species i by the frugivore A , and p_{ib} is the frequency of seed dispersal of the plant species i by the frugivore B . Both indices range from 0 (no overlap) to 1 (complete overlap).

Results

COMBINED EFFECTS OF DISPERSER ABUNDANCE AND SPECIES RICHNESS ON SEED DISPERSAL

The total number of seeds and plant species dispersed were both severely affected by a reduced overall frugivore abundance (*scenario 1*) (Fig. 1a,b). However, this effect was not independent of the parallel decline in disperser species richness (Fig. 1c). The GLM allowed us to disentangle these effects, showing that while both abundance and richness of frugivores in the community were significantly and positively related to the number of plant species dispersed, frugivore richness alone accounted for 89% of the deviance explained by the model, while frugivore abundance explained 11% (Table 1, Fig. 2). Interestingly, there was a significant interaction between these two variables (Table 1), since the magnitude of the effect of disperser species richness varied across the whole range of disperser abundance (Table 2). This effect became increasingly important at lower frugivore abundances, as shown by the significant negative relationship between sampling intensity and the slope of the regression lines ($R^2 = 0.90$, $P < 0.001$) (Table 2). Indeed, the relationship between richness of disperser species and plants became weak to non-significant at higher disperser abundances (i.e., ≥ 300 droppings, Table 2, Fig. 2). Although plant richness was positively associated with sampling intensity, the number of plant species dispersed reached its asymptotic maximum when we used 1500 droppings in the simulation. That means considering 2000 droppings no longer increased the number of plants dispersed, confirming an appropriate sampling completeness of the original dataset (Fig. 2). The result of the accumulation curve and Chao estimate of total fleshy-fruited species (24.67 ± 1.3) also indicated a high robustness of the sampling, in which 97.3% of the expected richness was detected in the droppings (see, Fig. S2).

SCENARIOS OF DISPERSER RICHNESS LOSS

For all scenarios except when the tortoise and lizards were extinct prior to birds (*scenario 4*), the decline in the seed dispersal service was less sharp than expected for a hypothetical linear decline in which plant species cease to be dispersed at a rate similar to the extinction rate of

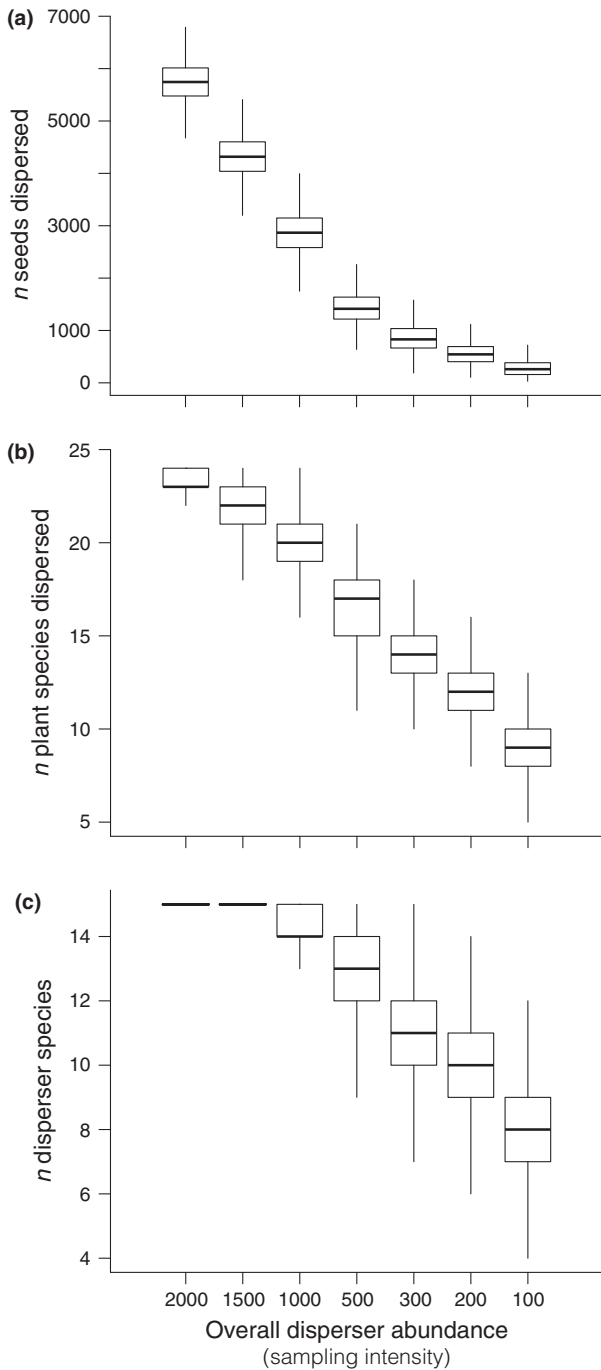


Fig. 1. Boxplots showing median, range and interquartile range of the expected decline in (a) the total number of seeds dispersed, (b) the number of fleshy-fruited species dispersed, and (c) the number of seed disperser species, following a reduction in overall frugivore abundance (*scenario 1*, simulated here by decreasing sampling intensities of disperser droppings and assuming that density compensation does not occur).

dispersers (dashed line, Fig. 3e). *Scenario 5* in which birds are lost prior to the giant tortoise and the lizards was the most favorable, because it predicted a much later entire loss of the dispersal service. Here, the declining role of birds was largely compensated by an increased dispersal service by the two lizard and a tortoise species (Fig. 3d,e).

Table 1. Results of the generalized linear model (GLM) evaluating the effect of disperser richness (continuous variable), sampling level (factor), and their interaction, on the number of dispersed plant species (Poisson distribution)

Predictor variables	d.f.	Deviance	Relative deviance explained (%)	P-value
Disperser richness	1, 6998	9578.2	88.5	<0.001
Disperser abundance (sampling intensity)	6, 6992	1234.2	11.4	<0.001
Disperser richness × Disperser abundance	6, 6986	14.9	0.1	0.021

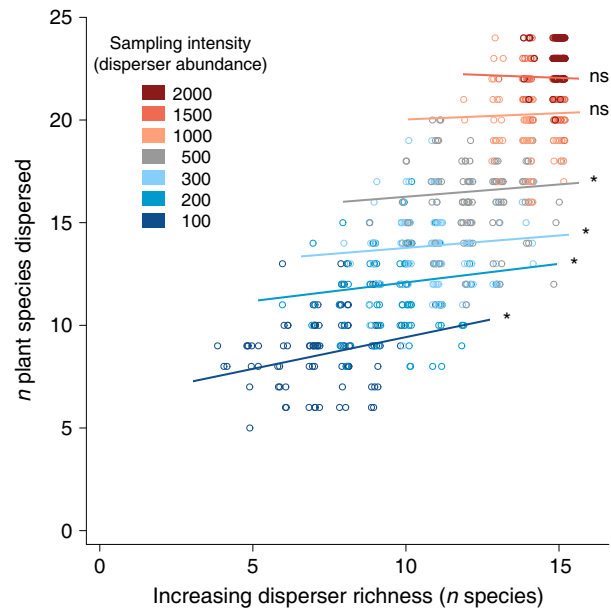


Fig. 2. Number of fleshy-fruited plant species served by seed dispersers along a gradient of frugivore richness (i.e. number of species, X-axis) and abundance (colour temperature rank; simulated by increasing sampling intensities of disperser droppings). A linear regression has been fitted to each group of 1000 bootstrapped networks constructed at each level of disperser abundance, and their significance is indicated as: ns = not significant; * $P < 0.05$ after sequential Bonferroni adjustment (see Table 2). To facilitate visualization and avoid a large overlap of points, only the values for 100 networks are shown at each sampling level. The number of plant species dispersed is reduced both by the decline in disperser abundance and by the loss of disperser richness at each level, with steeper slopes at lower sampling intensities (Table 2).

That increment in the number of plant species dispersed is caused by an eventual expansion of the non-avian sauropods populations benefiting from niches released after the extinction of birds. Finally, a sharp decline occurred when the tortoise and the two lizards also went extinct (Fig. 3d, e). *Scenarios 2* and *3* where dispersers are lost randomly irrespective of their abundance or when the rarest species are lost first, respectively, had a very similar effect on the community-level dispersal service (Fig. 3a,b,e). Both induced a later decline in it, and most plants went extinct

Table 2. Results of the linear regression models fitted to the different sampling levels (a proxy of disperser abundance), exploring the effect of frugivore richness on the number of plant species dispersed (see Fig. 2). Above sampling level 1500, we did not fit a linear regression model due to the poor dispersal of the data (not normally distributed). At each sampling level, 1000 seed dispersal networks were built by bootstrapping

Sampling intensity (disperser abundance)	Regression slope	Residual SE	d.f.	R^2	F -statistic	P -value
100	0.332	1.850	998	0.063	67.90	<0.001*
200	0.220	1.940	998	0.023	24.97	<0.001*
300	0.132	1.846	998	0.009	8.81	0.003*
500	0.152	1.801	998	0.009	10.33	0.001*
1000	0.113	1.483	998	0.003	3.70	0.055 ns
1500	-0.104	1.150	998	0.001	1.71	0.192 ns

Significance levels are indicated as: ns = not significant; * $P < 0.05$ after sequential Bonferroni adjustment.

at the end of the simulations. The decline in the random extinction *scenario 2*, with fewer sharp drops, resulted from the average effect of 100 simulated extinction sequences (Fig. 3a), while *scenario 3* represents a single extinction sequence where the largest drop was caused by the extinction of the Santa Cruz lava lizard (*Microlophus indefatigabilis*) at step 15 (Fig. 3b). In contrast, when the giant tortoise and the two lava lizards were lost prior to birds (Fig. 3c, *scenario 4*), the number of dispersed plant species declined rapidly, triggering an accelerated loss of dispersal service that approximately followed a linear decline (Fig. 3e, dashed line).

FUNCTIONAL RELEVANCE AND REDUNDANCY OF FRUGIVORES

We found a positive correlation between the degree and strength of the disperser species (Spearman's rank correlation: $r_s = 0.84$, $P < 0.001$), indicating that generalist species (i.e. high degree) were those on which most of the fleshy-fruited plant species rely for their dispersal (Fig. 4a). The most important generalists were the tortoise (*C. nigra*), the two lava lizards (*Microlophus* spp.), the two mockingbirds (*Mimus* spp.) and the flycatcher (*Myiarchus magnirostris*). The mean value of the species-level proportional similarity of these few species was higher than the mean of the non-generalists species (0.43 vs. 0.34), denoting a more redundant dispersal role among generalists (Fig. 4b).

Those simulations in which seed dispersers were lost in a deterministic order (*scenarios 3, 4 and 5*) allowed us to identify the impact of losing each animal species on the overall dispersal service (see Fig. 3b–d, where the identity of the disperser lost at each step is indicated). In most scenarios, the steepest decline in the number of plant species being dispersed occurred after the extinction of the Santa Cruz lava lizard (*M. indefatigabilis*) (Fig. 3e, thick lines), which dispersed 13 out of the 24 fleshy-fruited species (Fig. 4a; Tables S3 and S4). This lizard, besides of being an abundant species, showed the highest value (57%; shared with *Crotophaga ani*) of species-level proportional similarity with regard to the whole seed disperser community (see Fig. 4b, diagonal). Consequently, our results showed *M. indefatigabilis* to be the most functionally

important species. Interestingly, pairwise similarity between the two lizard species was relatively low (28 and 16% according to Jaccard and PS indices, respectively; Fig. 4b), indicating low redundancy among these congeneric species. On the other hand, despite being a generalist, the tortoise had a unique seed dispersal role, showing the lowest values of species-level proportional similarity (0.09) and pairwise similarity indices (both Jaccard and PS values were zero in 10 out of 14 comparisons; Fig. 4b).

Scenario 4, in which the tortoise and the lizards are lost prior to birds, revealed a functional complementarity among seed dispersers that was masked by the presence of a few abundant and generalist dispersers remaining in *scenarios 2, 3 and 5*. After losing the key services offered by *M. indefatigabilis* (Fig. 3c, step 3), the role of other generalist birds (*Mimus* spp. and *M. magnirostris*) became more visible.

Discussion

Our results suggest that a decrease in either abundance or richness of seed dispersers in the Galapagos would lead to a reduced reproductive fitness of fleshy-fruited species due to dispersal failure. However, we found that while disperser diversity is always intrinsically important for seed dispersal function, it became increasingly important when frugivore abundance declined. Together, these results suggest that while a few disturbance-tolerant generalist dispersers can, to some extent, maintain the seed dispersal service for most fleshy-fruited species (see Palacio, Valderama-Ardila & Kattan 2016), such compensation is no longer effective when defaunation simultaneously reduces the richness of the vertebrate community and their overall abundance. Additionally, we show that the extinction order of disperser species can have a critical effect on the degradation rate of community-level dispersal services. The simulations confirmed that as certain frugivore species are lost, the identity of the remaining species might lead to notable differences in the number of plant species still served by dispersers. These effects are determined by the redundancy and complementary of seed dispersers (see also Donatti *et al.* 2011; Mello *et al.* 2011; Sarmiento *et al.* 2014). Particularly, we show that generalist dispersers are essential to maintain the seed dispersal function.

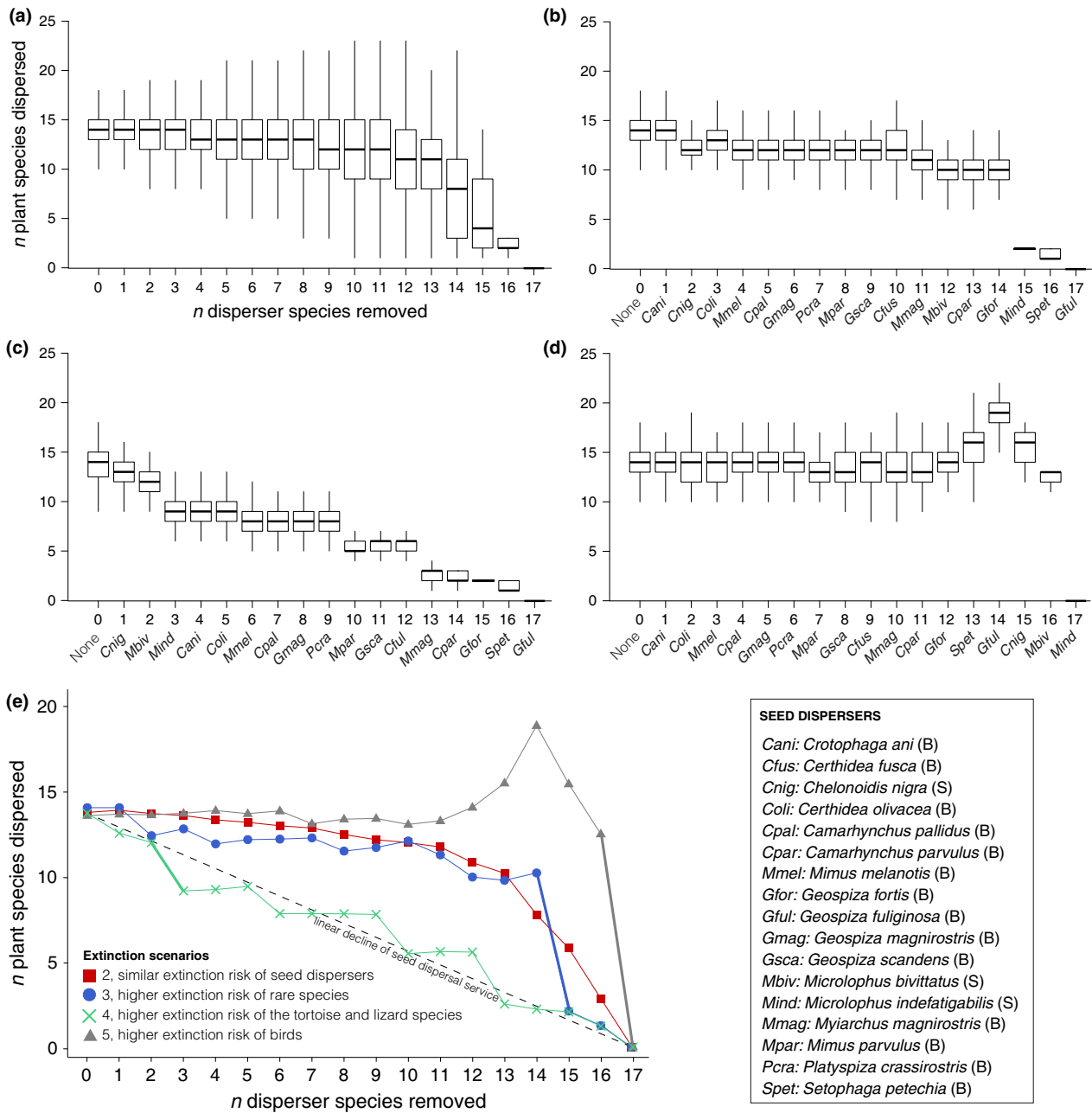


Fig. 3. Predicted decline in the number of fleshy-fruited species provided with seed dispersal under four likely extinction scenarios of frugivore richness in the Galapagos Islands (a–d): Boxplots showing median, range and interquartile range of plant species dispersed. At each step of the extinction simulation, the number of plant species dispersed resulted from 100 replicated networks based on a constant sampling intensity of 300 droppings, thus assuming that a phenomenon of density compensation can occur and disentangling the effect of disperser richness from that of disperser abundance (which is kept constant). (a) *scenario 2*, disperser species are randomly extinct; (b) *scenario 3*, rare species are more prone to extinction than common abundant ones, so frugivores are lost according to their abundance (from the least to the most abundant species, see Fig. S1); (c) *scenario 4*, the giant tortoise and the two lizards show a higher extinction risk than birds; (d) *scenario 5*, birds become extinct prior to the giant tortoise and the two lizards. In *scenarios 4* and *5*, the order of disperser loss within each guild (non-avian sauropsids and birds) follows the abundance level of the species. The identity of the seed dispersers lost at each step is indicated in the legend: (S) non-avian sauropsids; (B) bird. (e) Comparison of the average effect of each of the four extinction scenarios described above. The dashed line indicates a hypothetical linear decline in the seed dispersal service, i.e. plant species are no longer dispersed at the same rate that frugivore species are lost.

SYNERGISTIC EFFECTS OF ABUNDANCE DECREASE AND LOSS OF DISPERSER RICHNESS

The decline in species abundance due to anthropogenic disturbances can have important consequences in

ecosystems long before species actually become extinct (Chapin *et al.* 2000; McConkey & O’Farrill 2015). This is because the efficiency of most services depends on the frequency of specific biological interactions that occur at the level of individuals (Ings *et al.* 2009; Tur *et al.* 2014;

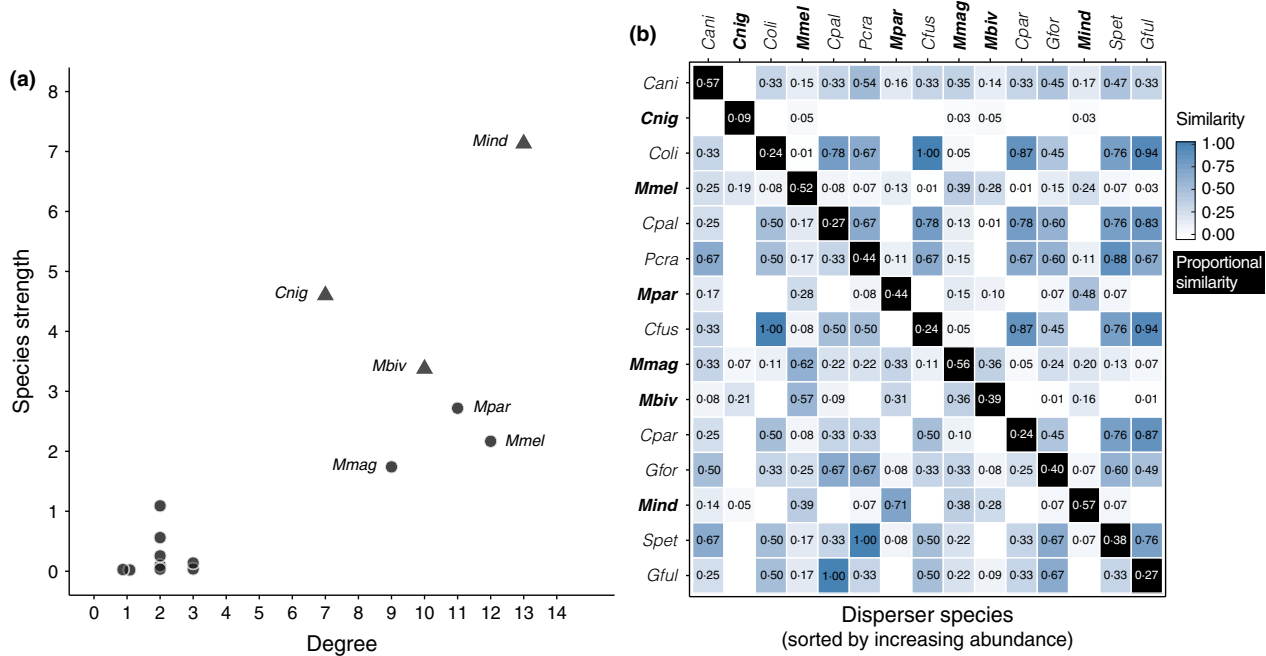


Fig. 4. (a) Positive correlation between dispersers' degree (i.e. number of plant species dispersed) and their species strength (i.e. cumulative importance for the whole plant community) (Spearman's rank correlation: $r_s = 0.84$, $P < 0.001$). Frugivores with higher degree (generalists) are labelled with acronyms. Triangles indicate the tortoise and two lizard species, whereas dots indicate birds; (b) Pairwise similarity between frugivore species in the qualitative (Jaccard's index; below diagonal) and the proportional (PS index; above diagonal) composition of the plant species they disperse. Values in the diagonal denote proportional similarity between plant dispersal by each frugivore species and the overall plant dispersal by the whole frugivore assemblage. All acronyms are as in Fig. 3; acronyms of generalist frugivores are shown in bold. *Geospiza magnirostris* and *G. scandens* were not included in these analyses because they were not found to disperse intact seeds in this study.

Vázquez *et al.* 2015). Nevertheless, most studies on biodiversity and ecosystem function still tend to focus on species richness alone, and the potential effects of reducing animal population densities remain much less understood (but see Chapin *et al.* 2000; Şekercioğlu, Daily & Ehrlich 2004; Larsen, Williams & Kremen 2005; McConkey & Drake 2006). The probability that individuals of two species will interact is reduced if one or both species becomes rare (Vázquez *et al.* 2007), so frugivores may stop to be functionally relevant if their populations fall below certain abundance thresholds (McConkey & Drake 2006). Therefore, low disperser abundance is likely to result in a decline in seed dispersal.

Our results show that a decrease in the overall abundance of Galapagos frugivores would result in a rapid decline in both the total number of seeds and plant species dispersed (Fig. 1a,b). However, this effect is mostly a consequence of the parallel loss of frugivore richness in the community (Fig. 1c, Table 1). High levels of seed disperser abundance tend to dampen the relationship between species richness and seed dispersal function. But when the overall abundance of dispersers decreases, the richness of the remaining species becomes a powerful predictor of the number of plant species still covered by the dispersal service (Table 2, Fig. 2). Therefore, species richness matters, but it matters even more when disperser abundance is very low. This may be a common scenario in most

anthropogenic landscapes, since human activities influence the relative abundances of species more frequently and rapidly than the actual presence of species (Chapin *et al.* 2000). Furthermore, the effect of abundance loss can be even greater when taking into account qualitative aspects of the seed dispersal (Schupp, Jordano & Gómez 2010), such as particular changes in animal behaviour or the loss of certain individuals bearing particular traits (e.g. larger individuals within a given species) (Anderson *et al.* 2011a; Galetti *et al.* 2013; McConkey & O'Farrill 2015).

THE IMPORTANCE OF EXTINCTION ORDER

During the last century, the extinction rate of vertebrates has increased 50 times in relation to the background rate of natural extinctions (Ceballos *et al.* 2015). However, not all species are equally vulnerable to anthropogenic disturbance and indeed many species increase their populations and expand their distributions in disturbed habitats (Siriwardena *et al.* 1998; La Sorte 2006; Devictor *et al.* 2008). Therefore, although disturbance might not always imply a loss of overall animal abundance, it will almost inevitably result in a simplification of the community due to a loss of species (McKinney & Lockwood 1999; Larsen, Williams & Kremen 2005). The different extinction orders of the scenarios tested here are based on this rationale and focus solely on the effect of richness loss, while allowing for a

density compensation of disturbance-tolerant species. We show that frugivore richness is important for maintaining the integrity of the dispersal service at the community level, which is degraded by biotic homogenization. In addition, the functional consequences of disperser species loss largely depend on the actual extinction sequence, particularly because some disperser species play a more important role than others by providing redundancy to the seed dispersal services, thus mitigating the consequences of previous extinctions.

Our simulation models revealed that, in most situations, the dispersal function is lost at a considerably lower rate than disperser species (Fig. 3e). This pattern is shaped by (i) the functional redundancy of dispersers, and (ii) the lower susceptibility of the functionally most important dispersers (Schwartz *et al.* 2000; Schleuning, Fründ & García 2015; but see Correa *et al.* 2016). This finding corroborates the predictions of Larsen, Williams & Kremen (2005) that density compensation in response to local species extinctions can, to a certain degree, buffer against functional loss. However, it is important to notice that our measure of disperser redundancy is likely overestimated by focusing exclusively on the identity and frequency of the interactions. Including specific estimates of the qualitative contribution of each disperser species (e.g. in terms of deposition sites or the gut treatment conferred to the seeds), could further improve our estimates of dispersal failure (Bronstein 1994; Schupp, Jordano & Gómez 2010; Aizen *et al.* 2014; Schleuning, Fründ & García 2015).

Lava lizards (*Microlophus* spp.), and especially the Santa Cruz lava lizard (*M. indefatigabilis*), are among the most abundant frugivores in the Galapagos and disperse the seeds of most fleshy-fruited species, conferring a high redundancy on the community-level dispersal service against loss of dispersers (*scenario 3*). The functional value of common species has also been detected in pollination systems where a few very common insect species can maintain high levels of crop pollination (Bartomeus & Winfree 2013; Kleijn *et al.* 2015). Our results reveal that, at least in simple communities like those of the Galapagos and many islands, a small proportion of the dispersers can indeed be responsible for the bulk of this service, and that these disproportionately important species tend to be regionally common. Nevertheless, even common species can be struck by important conservation threats (Gaston 2010). In this regard, our results also raise concerns since the loss of any of these abundant and key functional species, particularly lizards, can lead to a rapid collapse of seed dispersal (see *scenario 4*).

These results, however, should not be interpreted as an argument against the conservation of rare species. Less common species have been demonstrated to be keystone species with functional impacts disproportional to their abundance (Lyons *et al.* 2005). In the Galapagos seed dispersal community, the extinction of the giant tortoise alone involved the dispersal failure of four plant species (Tables S3, S4), two of them (*Hippomane mancinella* and

Psidium galapageium) being unable to undergo dispersal by any other frugivore, due to their large fruit size. This highlights that the loss of any frugivore can be critical for the dispersal and long-term survival of certain plant species, and is in this sense an important conservation concern, even without a dramatic decline in the overall number of plants served by dispersers.

The particular sequences of disperser loss also revealed that non-avian sauropsids and birds are largely complementary in the dispersal service provided to plants as birds cannot cover the functional loss of the lizard and tortoise extinctions (Fig. 4, *scenario 4*). Furthermore, the key role of some bird dispersers was also evidenced when the lizards and the tortoise became extinct prior to birds. In this case, generalist species, namely *Mimus* spp. and *M. magnirostris* triggered the most important declines in the seed dispersal service. We showed that generalist species are disproportionately important for maintaining high levels of seed dispersal, and therefore that the identity of the frugivore species extinct and extant at each moment is central in predicting how many plant species are still served by dispersers.

Conclusions

All species are embedded within an intricate web of interactions upon which they directly and indirectly depend for long-term survival (Thompson 2009). Here we show that the richness of the seed disperser assemblage is a key driver of the dispersal services provided to Galapagos fleshy-fruited plants and that the overall abundance of seed dispersers is also an important, yet often neglected driver of seed dispersal services. Importantly, we also show that while disperser richness is intrinsically important, it becomes increasingly relevant when the abundance of dispersers can no longer mitigate the effects of species loss. At the same time, as the generalist dispersers are disproportionately important to secure high levels of seed dispersal by providing functional redundancy, the identity of the species lost is also critical to understand the consequences for the number of plants served by dispersers.

Here we used the natural laboratory furnished by the simplified community of the Galapagos Islands to highlight that the coupled loss of animal abundance and richness can result in positive feedbacks, further accelerating the loss of essential functions in degraded ecosystems.

Authors' contributions

R.H., A.T. and B.R. conceived the general idea. M.D. and B.R. designed the simulation models. B.R. performed the analyses. B.R. and R.H. led the writing of the manuscript, and all authors contributed substantially to revisions.

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Data accessibility

All data for this study can be found in the main article and supporting information.

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Conservation status of the seed dispersers focused on this study.

Table S2. Biological basis for the assumptions of the five extinction scenarios.

Table S3. Seed dispersal interaction matrix showing the number of seeds dispersed as a result of each interaction.

Table S4. Seed dispersal interaction matrix in which matrix elements show the interaction frequency (number of droppings from the dispersers containing seeds from the plant species).

Fig. S1. Percentage of droppings analysed from each seed disperser species.

Fig. S2. Accumulation curve assessing the overall sampling robustness of the dataset.

Data S1. Number and identity of the seeds retrieved in each dropping analysed.

Data S2. R script for the simulation of the extinction scenarios.