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Research

Global patterns of the double mutualism phenomenon

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A double mutualism (DM) occurs when two interacting species benefit each other in two different functions, e.g. when an animal species acts both as pollinator and seed disperser of the same plant. Besides the double benefit, a DM also imposes a larger risk to both functions if the performance of one partner declines. We conducted the first global review of DMs involving pollinators and seed dispersers, aiming to: 1) assess their prevalence across ecosystems and biogeographical regions; 2) identify the main plant and animal taxa, and their traits, implicated in DMs; and 3) evaluate the conservation status of double mutualist species. We compiled published and unpublished DM records using specific search terms, noting the species involved, their conservation status and geographic location, as well as the type of study (species vs community-level) in which the DM was detected. We identified 302 DM cases involving 207 plant and 92 animal species from 16 mainland and 17 island areas. Most records come from tropical regions and islands. Animals included birds (62%), mammals (22%), and reptiles (16%), mostly opportunist species; only 18% were nectarivores. Plants were mainly fleshy-fruited shrub or tree species (59%) with actinomorphic flowers that were visited by several or many pollinator species (87%). Most (56%) DMs were detected in community-level studies. DMs are mostly prevalent in ecosystems with limited food resources and mutualist partners, and with high generalization levels. Nearly 30% of the species involved in DMs are threatened according to IUCN criteria, 68% of which are found on islands. The high prevalence of DM on islands paired with the threat status of island species suggest that the loss of a double mutualists and its cascading consequences may have a severe impact on community composition and functioning of fragile island ecosystems.

Keywords: mutualistic disruptions, oceanic islands, pollination and seed dispersal

Introduction

Pollination and seed dispersal are vital processes in the life cycle of plants, and consequently, contribute substantially to ecosystem functioning (Neuschulz et al. 2016). Pollination has a strong influence on the quality and quantity of plant reproduction, whereas seed dispersal is responsible for propagule transport away from the



mother plant and for colonization of new areas. Both processes are most often mediated by animals (Jordano 2000, Ollerton et al. 2011) which benefit primarily from floral and fruit resources.

Animals that serve as pollinators and/or seed dispersers belong to a wide variety of taxa of many families of invertebrates (mainly insects), birds, fishes, mammals, and reptiles (Proctor et al. 1996, Farwig and Berens 2012). In some cases, the same animal species ‘reuses’ the same food plant, first harvesting its floral resources and, later on in the season, feeding upon its fruits. By doing so, the animal may act both as pollinator and seed disperser of the same plant species. This type of dual dependency between two mutualists was coined ‘double mutualism’ (hereafter DM; Hansen and Müller 2009a) and it has since been reported from different ecosystems. Much information is scattered across primary and grey literature, and the fact that most studies focus on either pollination or seed dispersal makes it difficult to detect double mutualisms. In this work, we present an extensive compilation and review of pollination and seed dispersal data to assess the importance of DMs globally.

A DM may generate a double positive feedback loop (Olesen et al. 2018) whereby an animal species that obtains nectar and pollen as reward when pollinating a plant generates a viable fruit crop, which in turn will attract the same animal species to feed on the fruit of the same plant species and thereby disperse its seeds. In other words, the more flowers pollinated by the animal species the more fruits it will have available for feeding and dispersal, which will translate into elevated plant recruitment and safeguard food supplies in subsequent seasons. Theoretical models predict a low likelihood of highly-dependent mutualistic relationships in a community, due to their destabilizing effects (Allesina and Tang 2012) i.e. reducing the resilience of the system, being the community more sensible to perturbations. One intriguing question is therefore why DMs occur in the first place and how they are maintained in an ecosystem, given that the strong double benefit for both partners come into conflict with the potential drawbacks that DMs imply. There are cases, however, which may also involve a selection for and strong benefit to a double interaction with a particular partner, e.g. the interaction between the yucca plant and its specialized yucca moth (Godsoe et al. 2008) (nevertheless, this interaction does not constitute a DM because, although both partners interact in two processes, they are not doubly benefited).

Scarcity of interaction partners may be one contributing factor resulting in the engagement of plants and animals in DM relationships. Geographically isolated ecosystems are those harboring the lowest number of species (MacArthur and Wilson 1967), which constrains the species pool of potential mutualistic partners. Examples include islands (Kaiser-Bunbury et al. 2010), deserts (Gomes et al. 2014) and mountain tops (García et al. 2012). In such ecosystems, species may evolve generalized and opportunistic behaviors, establishing interactions with a large proportion of the local biota. Alternatively, a DM can emerge when there is a shortage

of interaction partners due to natural and anthropogenic disturbances. The latter is expected to become more common as ecosystems are increasingly disturbed and biodiversity is lost. In the decimated native bird fauna of Hawaii, for instance, the introduced Japanese white-eye *Zosterops japonica* feeds on floral and fruit resources of the same plant species, acting both as a pollinator and disperser (Aslan et al. 2014). In some cases, non-natives species can act as double mutualists and, by doing so, they can act as functional surrogates for lost native interactions in the community. Nevertheless, an increased frequency of DMs involving at least one non-native partner, coupled with a decline in pollination and dispersal quality, might be an early warning signal of community deterioration. Also, the presence of specialized mutualistic relationships might render ecological communities more vulnerable to secondary extinctions and loss of functions (Traveset et al. 2017).

Little is known about the frequency, distribution, and drivers of DMs in native plant–animal communities. Here, we conducted a systematic review of all published and unpublished data to provide geographical, taxonomical and ecological baseline information for future research on the mechanisms and consequences of DMs for ecosystem functioning. We aimed to explore several hypotheses. We predict that DMs occur more frequently in areas with a scarcity of interaction partners and in communities with a greater proportion of generalized species, i.e. species with broad trophic niches that interact with a high number of the available partners. Thus, we expect a higher occurrence of DMs on islands than on mainland areas. Further, we expect the tropics to have a higher prevalence of DMs because of the higher frequency of mutualisms in the species-rich tropics (Jordano 2000) and higher levels of species generalization found towards the equator (Schleuning et al. 2012). Generalized species are anticipated to be more likely involved in DMs than specialized species as they are able to expand their trophic niche when resources are scarce. Plants with actinomorphic flowers (i.e. with radial symmetry), which are considered to be generalized, should also be more frequently involved in DMs than those with specialized zygomorphic flowers (i.e. bilateral symmetry) (Fenster et al. 2004). Finally, we predict that fleshy-fruited plants are more likely to be partners in DMs than dry-fruited ones, given their greater dependence on animals for seed dispersal (Jordano 2000). Owing to the potential importance of double mutualists for community stability and their high interdependence, we further assessed their conservation status.

Material and methods

Literature search

We searched for records on confirmed and potential DMs in primary and grey literature using the search engines SCOPUS, ISI Web of Knowledge and Google Scholar (last search 28 February 2017), and further extracted information

on potential DMs from photos and videos available on the internet. Online searches included the following terms: 'double mutualism' OR 'poll*' OR 'flower visit' OR 'mutualism' OR 'nectar*' AND 'animal group'. The specific words for 'animal group' were in each case: 'vertebrate', 'lizard', 'gecko', 'reptile', 'bird', 'mammal', 'bat', 'primate', 'ape', 'monkey', 'lemur', 'rodent', 'mice' or 'ant'. Moreover, for every taxon participating in a plant–pollinator interaction, we scanned the literature for information on specific frugivory and seed dispersal interactions involving these taxa. Terms used for the second set of searches included: 'plant species name' AND 'dispers*' OR seed dispersal' OR 'fruit consum*' OR 'fruit use' OR 'fruit removal' and 'animal species name' AND 'diet'. Note that by referring to 'flower visitors' and 'fruit/seed eaters' we are not considering how effective the species are as pollinators or seed dispersers, respectively, as this information is rarely available in the literature.

For each recorded DM, we noted class, order, and family of both the plant and animal partners. In addition, plants were characterized by life form, flower color and symmetry (actinomorphic vs zygomorphic), and fruit type (dry vs fleshy), whereas animals were categorized as nectar-specialists (commonly consuming nectar) or opportunistic nectar feeders (with a wide diet breadth, according to available literature). The conservation status of every double mutualist species, either plant or animal, was determined using the IUCN Red List of Threatened Species (IUCN 2018). We further noted the geographic location of all interactions, distinguishing between islands and mainland areas, and the biogeographic region and biome (following the categorization by Olson et al. 2001). Finally, we recorded the type of study in which the DMs were detected: community-level, animal-focused or plant-focused study; a fourth category ('others') included anecdotal observations, as well as photos and videos found in internet.

Data analysis

To test the relationship between the frequency of DM occurrence and the area (island vs mainland), we used a generalized linear mixed model (GLMMs) and fitted a negative binomial error structure to account for over-dispersion (Zuur et al. 2009). We included area as fixed effect and biogeographic region (seven levels: Afrotropical, Australasia, Indomalaya, Nearctic, Neotropical, Oceania, Palearctic) as a random effect. Each location where the DM was reported was the sampling unit. All other relationships between the response variables number of DMs and species involved in DMs and the explanatory variables biogeographical region, taxonomical group, and several plant and animal traits (plant life form, flower color and symmetry and fruit type, and the animal diet breadth – i.e. nectar-specialist or -opportunistic) were tested by using Chi-square statistics. Studies that report DMs differ in scope and scale. Here, we distinguish between detailed studies on one or a few species pairs (mutualists) and those that describe mutualistic interaction from a community. To test whether study type has an influence on the

detection frequency of DMs we run a GLMM with study type as explanatory variable and controlled by biogeographic region and area, entered as random factors. All analyses were performed in R (ver. 3.3.3; R Development Core Team), and the GLMM models were run with the 'glmer.nb' function from the lme4 package (Bates et al. 2015).

Data deposition

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.r8s0s8q>> (Fuster et al. 2018).

Results

Distribution of DMs

We compiled a total of 302 records of DMs between 207 plant and 92 animal species, from a total of 82 sources (Supplementary material Appendix 1; 79 publications, of which 62 were in primary and 17 in grey literature, two unpublished observations, and one video available on internet). DMs appear to be widely distributed (between 52°N and 54°S, and 171°E and 172°W) and have been documented from 16 mainland areas and 17 islands (Fig. 1), spanning most biogeographic regions (Table 1). The distribution of DMs, however, is highly heterogeneous across regions ($\chi^2=308.44$, $df=6$, $p < 0.001$), most having been recorded in the Neotropics and Australasia (43.4 and 28.5%, respectively). More than half (65.5%) of the DMs actually are from tropical areas. The Palearctic and Nearctic regions contribute only 3.6 and 2.3% to all DMs, respectively (Table 1). DMs appear also to be more frequent on islands than on mainland areas ($\chi^2=7.14$, $p=0.008$, $n=32$; Supplementary material Appendix 2 Fig. A1).

We detected most DM cases in community-level studies compared to any other study type ($\chi^2=24.04$, $df=3$, $p < 0.001$; Supplementary material Appendix 2 Fig. A2), whereas no differences existed between single plant-focused and animal-focused studies ($Z=-1.63$, $p=0.324$; Supplementary material Appendix 2 Fig. A2).

Plant double mutualists

Plant species involved in DMs belonged to 31 orders and 75 families (Supplementary material Appendix 2 Table A1 and Fig. A3). A total of 44 species (21.3%) attracted more than one animal species as double mutualist, and most of such plants (ca 82%) were island species ($\chi^2=17.82$, $df=1$, $p < 0.001$). Moreover, of the 163 plant species with only one DM partner, a significantly higher proportion (ca 67.5%; 110 sp.) were island species ($\chi^2=19.93$, $df=1$, $p < 0.001$). Two plant families (Cactaceae and Fabaceae) were the most represented in the dataset, each with ≥ 15 species involved in DMs. Within the Cactaceae, DMs have been recorded both from tropical and arid zones, and from island and mainland sites in the Americas, where the family originated and is

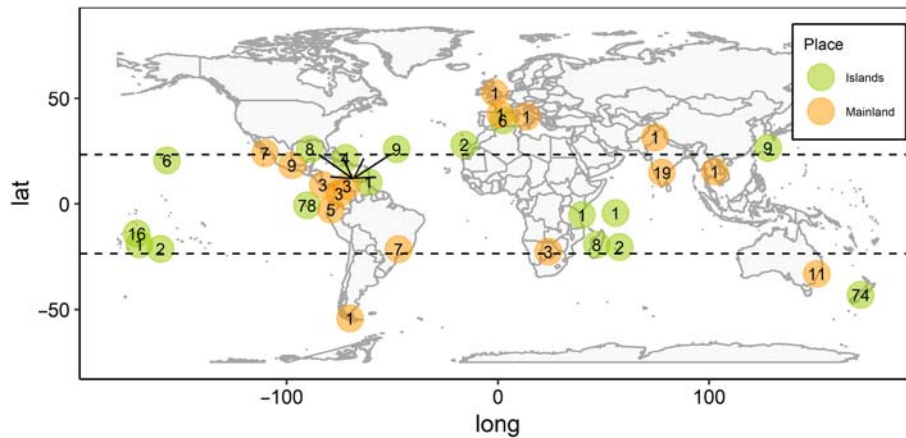


Figure 1. World map of the locations from which double interactions are reported. Dashed lines delimit intertropical zone. Island localities are indicated in green whereas mainland ones in orange. The numbers inside each circle indicate the number of DMs interactions detected in each location.

widely distributed. The Fabaceae, on the other hand, is the most common family in the dry forests of tropical America and tropical Africa (Burnham and Johnson 2004), and all DM cases in this family were reported from such forests. A species in the Euphorbiaceae, *Bursera graveolens*, native to South America and very common in Galápagos, was also found to be involved in up to eight DMs.

Most plant double mutualists (85%) were woody (175 sp. involved in 263 DMs), including trees and shrubs, whereas 25 (12.1%) were herbaceous (involved in 31 DMs) ($\chi^2 = 112.5$, $df = 1$, $p < 0.001$). Moreover, the flowers of most (41.1%) of such plants were white, although another good fraction (19.3%) were either reddish (including pink, purple and red flowers) or yellow. The rest produced green, orange, or brown flowers or flowers with contrasted colours. Actinomorphic flowers were more prevalent than zygomorphic flowers (87 vs 11.6%; $\chi^2 = 123.58$, $df = 1$, $p < 0.001$). We also found most plant species in the dataset to be fleshy-fruited (142 sp.; 69%) compared to 61 species (30%) that produce dry fruits ($\chi^2 = 32.32$, $df = 1$, $p < 0.001$). More than twice as many plant species (including some dry-fruited ones) were dependent on the same animal mutualist than vice versa.

The conservation status of plant double mutualists was evaluated for 49 species listed in the IUCN database (Supplementary material Appendix 1). Of these three were

critically endangered, one endangered, four vulnerable, and two near threatened, whereas the rest (~80%) were listed as least concern or data deficient.

Animal double mutualists

Except for one case, all animal double mutualists were birds, mammals or reptiles (Fig. 2). Half of them (50%) were engaged in more than one DM, and a high proportion of these species (30; 65.2%) occurred on islands (compared to mainland; $\chi^2 = 4.26$, $df = 1$, $p = 0.039$). The exception is a species of ant in the *Lasius* genus which has been recorded to pollinate the flowers and disperse the seeds of the herb *Borderea chouardii* (Supplementary material Appendix 1). Birds made up a total of 187 cases (62.1%), whereas mammals and reptiles were involved in 65 (21.6%) and 49 (16.3%) cases, respectively; thus, the distribution across taxa was not evenly distributed ($\chi^2 = 248.94$, $df = 3$, $p < 0.001$). Bird and reptile double mutualists were more frequently reported from islands than from mainland sites (birds: $\chi^2 = 65.89$; reptiles: $\chi^2 = 17.16$, both $p < 0.001$; Fig. 3), in contrast to mammals (most of them bats), which were similarly frequent in the two areas ($\chi^2 = 1.86$, $p = 0.17$; Fig. 3). On islands, mammals and reptiles were comparably common double mutualists ($\chi^2 = 0.01$, $df = 1$, $p = 0.91$), yet mammals were more and reptiles less common in mainland areas ($\chi^2 = 7.81$, $df = 1$, $p = 0.005$). Although the number of DM cases involving birds was about fourfold on islands than on mainland areas (Fig. 3), the actual number of bird species participating in DMs was similar between areas (30 and 25, respectively; $\chi^2 = 0.46$, $df = 1$, $p = 0.5$).

Most animal double mutualists were generalized and opportunistic nectar feeders (247 DMs; 81.8%), and were largely represented by the order Passeriformes (28 sp. in 98 DMs), although parrots (14 sp.), bats (10 sp.), and lizards (15 sp.) were also frequent double mutualists (Table 2). On the contrary, specialized nectar consumers were involved in fewer DMs (55; 18.2%; $\chi^2 = 122.07$, $df = 1$, $p < 0.001$),

Table 1. Number of cases of double mutualisms in the different biogeographic regions reported from insular and mainland areas. In parentheses is the percentage (%) of the total of each column.

Biogeographic region	Islands	Mainland	Total
Afrotropical	12 (5.3)	3 (4.0)	15 (5.0)
Australasia	75 (33.2)	11 (14.5)	86 (28.5)
Indomalaya	9 (4.0)	21 (27.6)	30 (9.9)
Nearctic	0 (0)	7 (9.2)	7 (2.3)
Neotropical	100 (44.3)	31 (40.8)	131 (43.4)
Oceania	22 (9.7)	0 (0)	22 (7.3)
Palaearctic	8 (3.5)	3 (4.0)	11 (3.6)
Total	226	76	302



Figure 2. Examples of double mutualisms involving different taxonomic groups: reptiles, birds and mammals. *Podarcis lilfordi* (Lacertidae) taking nectar (a) and fruit (b) of *Ephedra fragilis* (Ephedraceae) in Dragonera (Balearic Islands). *Mimus parvulus* (Mimidae) feeding upon the flowers (c) and fruits (d) of *Opuntia galapageia* (Cactaceae) in Pinta, Galápagos Islands. *Cynopterus sphinx* (Pteropodidae) feeds on the flowers (e) and fruits (f) of *Musa paradisiaca* (Musaceae) in India. Note that the bat species in (f), however, is *Rousettus leschenaultii* (Pteropodidae) as no pictures of *Cynopterus sphinx* feeding upon fruits of the plant were available. Photo credits: (a) F. Fuster; (b) J. Rodríguez-Pérez; (c) and (d) R. Heleno; (e) Merlin Tuttle's Bat Conservation in Science photo library: <www.sciencephoto.com/>; (f) N. Baker.

including 11 bird species and three bat species (Table 2). At the family level, the most DM cases were recorded in the Thraupidae, which includes the Galapagos finches, followed by the Meliphagidae (honeyeaters) and the Psittacidae (true parrots). Among mammals and reptiles, the Pteropodidae (flying foxes) and Iguanidae were most commonly engaged in DMs, whereas the Tropicuridae (Neotropical ground lizards) was the most species-rich reptile family.

More than three-quarter (41; 75.9%) of double mutualist bird species are categorized as 'least concern' (LC), three species (5.6%) as 'near threatened' (NT), and 10 (18.5%)

species as one of the three threatened categories: 'vulnerable' (VU), 'endangered' (EN) or 'critically endangered' (CR). The Hawaiian crow *Corvus hawaiiensis*, reported to have fed on *Freycinetia arborea* is now extinct in the wild (EW) (Supplementary material Appendix 1 and Fig. 4). Mammal double mutualists appear to be particularly vulnerable: 22 species (50%) are threatened and three (13.6%) are near threatened. Concerning reptiles, three species (20%) are threatened, five species (33.3%) are of least concern, and seven species (46.7%) are not yet evaluated (NE) or data deficient (DD). Overall, more than one quarter (27%) of

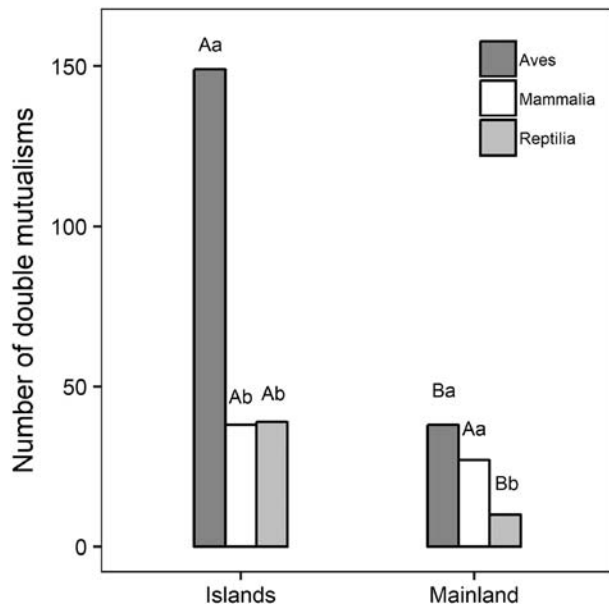


Figure 3. Frequency of double mutualistic interactions involving different vertebrate groups for both island and mainland locations. Capital letters refer to the Chi-square test comparisons of the same animal group between islands and mainland, whereas lowercase letters refer to the comparisons between the three animal groups within the same biota (either islands or mainland). Different letters indicate significant differences ($p < 0.005$).

the double mutualist species in our dataset are threatened, 68% of them being island species. Moreover, the same proportion (26%) of both generalist and nectar-specialist species are threatened.

Table 2. The number of double mutualism interactions (Int.) and species (Sp.) in specialized and non-specialized nectar-feeder guilds belonging to different classes, orders and families. *Phyllostomidae in the Glossophaginae subfamily, and **Phyllostomidae not in the Glossophaginae subfamily.

Specialized nectarivores			Non-specialized nectarivores					
	Int.	Sp.		Int.	Sp.		Int.	Sp.
Birds	44	11	Insecta	1	1	Mammalia	54	18
Passeriformes	44	11	Hymenoptera	1	1	Chiroptera	41	10
Coerebidae	1	1	Formicidae	1	1	Mystacinidae	1	1
Dicaeidae	2	2	Birds	143	43	Phyllostomidae**	2	1
Meliphagidae	36	3	Columbiformes	3	2	Pteropodidae	38	8
Mohoidae	2	2	Columbidae	3	2	Diprotodontia	1	1
Nectariniidae	2	2	Passeriformes	98	27	Phalangeridae	1	1
Notiomystidae	1	1	Corvidae	1	1	Primates	10	6
Mammalia	11	4	Emberizidae	1	1	Aotidae	1	1
Chiroptera	11	4	Fringillidae	3	2	Callitrichidae	1	1
Phyllostomidae*	11	4	Mimidae	10	3	Lemuridae	8	4
			Pycnonotidae	2	2	Rodentia	2	1
			Rhipiduridae	1	1	Sciuridae	2	1
			Sturnidae	2	2	Reptilia	49	15
			Sylviidae	1	1	Squamata	49	15
			Thraupidae	57	8	Gekkonidae	1	1
			Turdidae	1	1	Iguanidae	21	4
			Tyrannidae	4	2	Lacertidae	8	2
			Zosteropidae	15	3	Scincidae	1	1
			Psittaciformes	42	14	Teiidae	9	1
			Psittacidae	42	14	Tropiduridae	9	6

Discussion

Factors determining the distribution of double mutualisms

Our global review indicates that DMs occur in most biogeographic regions, yet they appear to be most common in the tropics and on islands. Whether this is primarily a true reflection of a biological pattern or due to reporting bias is difficult to determine at this point. There is evidence for a combination of both factors. For instance, despite the widespread distribution of the Thraupidae finches across the tropics, all interactions but one were reported from the Galápagos. This may be due to intensively studied plant–animal interactions on the archipelago (Heleno et al. 2013, Traveset et al. 2015) compared to large parts of the Neotropics where tanagers are common. Similarly occurs with the plant *Bursera graveolens*, common in Galápagos and involved in up to eight DMs, although this number of cases may be also due to the intensive research investment in this archipelago. Despite these uncertainties in the geographical distribution of DMs, some strong patterns emerged. Islands hold a relatively small proportion of the land area but DMs are similarly reported from islands and mainland, suggesting that island ecosystems are particularly suitable to create and maintain DMs.

Regardless of the geographical bias of the studies, the regional differences observed in the prevalence of DMs might be driven by the geographical variation in species richness and generalization levels. The tropics contain the highest species richness (Hillebrand 2004), and most locations with reported

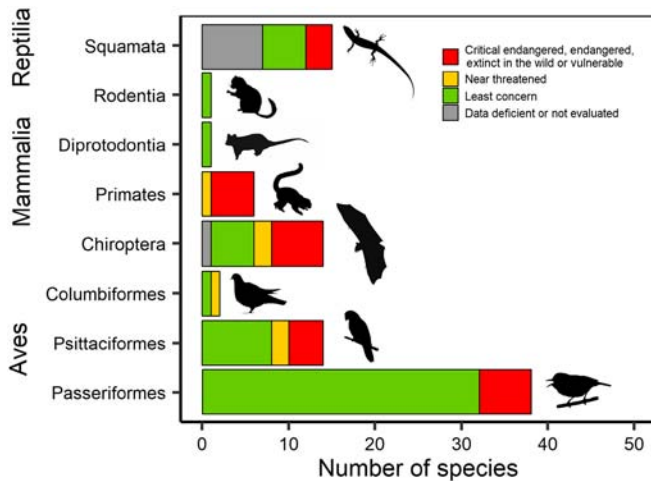


Figure 4. Number of animal species involved in double mutualisms within the different orders categorized by IUCN threat levels.

DMs overlap with areas of high vertebrate species richness (Ceballos et al. 2017). Moreover, plant–animal mutualism (Jordano 2000, Schemske et al. 2009) and the level of generalization in pollination and seed dispersal interactions (Schleuning et al. 2012) become more common towards the equator, which may further explain the higher prevalence of DMs in the tropics.

Less pronounced or absent seasonality in the tropics may also contribute to the distribution of DMs. Continuous flowering and fruiting may render certain species more attractive to the same pollinator and seed disperser species (Blázquez and Rodríguez-Estrella 2007, Hansen and Müller 2009a, Olesen et al. 2018). A direct consequence of seasonality is the absence of migrants during both the flowering and the fruiting season. Of the 55 bird species in the dataset, only one (*Elaenia albiceps*) is a migrant, suggesting that DMs evolve more readily in areas with many sedentary species. In fact, the scarce prevalence of DMs in North America and Eurasia might be associated to the high diversity of migrant bird species (Somville et al. 2013).

On islands, where species richness is generally low, the higher frequency of DMs may be explained by the special conditions inherent to these ecosystems. Interaction release and niche expansion are common in island species; thus, island frugivores and insectivores, for instance, may often also consume other resources such as pollen or nectar (Traveset et al. 2015), whereas presumed nectarivores have also been reported to feed on fruits (Spurr et al. 2011). Pollination and seed dispersal by lizards have been described as insular phenomena (Olesen and Valido 2003), and we showed that lizards are common double mutualists on islands. Interaction release in opportunistic flower-visitor bird taxa has been documented from oceanic islands (Traveset et al. 2015) although, to a lesser degree, it also occurs in mainland ecosystems (da Silva et al. 2017). Another, non-exclusive, explanation for the higher frequency of DMs on islands may be lower chemical defense loads in island plants due to enemy release,

which results in more palatable flowers and/or fruits to a wider array of animals than in mainland areas (Bowen and Van Vuren 1997). Besides island systems, other geographically isolated ecosystems as deserts and mountains also harbor few potential interaction partners. We would therefore expect a high proportion of species being involved in DMs in these habitats, but few have been described to date (but see iguana *Ctenosaura hemilopha* and different cactus in Mexico or the parrot *Nestor notabilis* in New Zealand; Supplementary material Appendix 1).

Traits of the double mutualists

Most plant double mutualists are generalized species, interacting with a wide number of partners. The plant family with most double mutualisms is the Cactaceae, which occurs primarily in arid ecosystems, such as mainland deserts and dry oceanic islands. These ecosystems often lack animals that are reliable pollinators elsewhere (e.g. bees, butterflies), and cacti often depend on a few vertebrate species for both pollination and seed dispersal (Dar et al. 2006). Many cacti rely on bats for pollination (Fleming et al. 2009), and the importance of nectarivorous Neotropical Glossophaginae bats as double mutualists in this family actually suggests that bats and cacti have co-evolved DMs. By contrast, all birds and reptiles involved in DMs with the Cactaceae appear to be generalized species, suggesting an ecological rather than an evolutionary driver of the interactions. Most (87%) plant double mutualists had easily accessible actinomorphic flowers and are thus considered to be more generalized. This fraction, however, does not differ from the proportion of actinomorphic, specialized flowers, found in nature (Neal et al. 1998; reported it in 83% of dicotyledons) and it is likely that pollinators visit these flowers more often because of their abundance (Vázquez 2005, Kaiser-Bunbury et al. 2014). Generalized pollinators may also visit these species more frequently than specialized plants, evolved to attract particular sets of pollinators (e.g. long-proboscis insects). Regarding seed dispersal, the large majority of vertebrate-dispersed plants produce fleshy fruits (Jordano 2000) and the fraction of animal-dispersed plants increases towards low latitudes (Moles et al. 2007). This is probably the reason why fleshy-fruited species were also more frequent double mutualists than dry-fruited ones.

Although most animal double mutualists are generalized species, nectarivorous birds were also involved in DMs; in fact, ca 20% of the bird species in the dataset are considered typical nectarivores, and also consume fruits. The Meliphagidae (honeyeaters), in particular, showed a high frequency of DMs. One example is the New Zealand honeyeater *Anthornis melanura*, which was the species involved in most DMs; this species is an important pollinator and seed disperser of several New Zealand plants (Anderson et al. 2006), and its loss has been predicted to be detrimental to plant reproductive success (Iles and Kelly 2014). In the Palearctic, with no nectarivorous species (da Silva et al. 2017), DMs involving birds are scarce. In Europe, specifically, some birds visit flowers opportunistically (da Silva et al.

2014) depending upon the season (Cecere et al. 2011). Given the importance of birds as seed dispersers for a great variety of plants in Europe (Herrera 1995), we would expect a higher frequency of DMs here. Recent studies on bird nectarivory and pollination have sparked a wave of received attention (reviewed by da Silva et al. 2014, 2017), which may reveal more DMs in the near future. There could be additional factors, however, determining the establishment of DMs. For example, there are often morphological constraints regarding animal size. Individuals of generalized animal species must be or have foraging tools (i.e. gape size, beak length, etc.) large enough to swallow and move seeds, but small enough to interact effectively with flowers. This combination may not be possible for some species and ‘forbidden links’ are pervasive, even within a species given strong variability among individuals (González-Varo and Traveset 2016).

The only non-vertebrate double mutualist documented so far is an ant species. Flower visitation by ants is frequently reported, although their functional relevance in pollination remains controversial (de Vega and Gómez 2014). Ants are also known to effectively disperse many plant species, both in mainland and island areas (Lengyel et al. 2010). Ants involved in DMs are mainly expected in semiarid or desert ecosystems (e.g. South African fynbos, Australian deserts), where other pollinators or seed dispersers are scarce and where there is a high diversity of ant species (see antmaps.org; Janicki et al. 2016).

Both native and alien animal and plant species can develop DMs. Among animals, the silvereye *Zosterops lateralis* (Zosteropidae), is a bird of the southwestern Pacific that arrived to New Zealand from Australia in 1856, becoming an important flower visitor and seed disperser of many plants (Spurr et al. 2011). Another *Zosterops* species, *Z. japonicus* from east Asia, was introduced to Hawaii (Simberloff and Boecklen 1991) where it has replaced extinct native mutualists (Aslan et al. 2014) but also has contributed to the invasion of plant species (Woodward et al. 1990). Among plants, the introduced *Psidium guajava* and *Rubus niveus* engage in several DMs in Galápagos (Heleno et al. 2013, Traveset et al. 2015). Non-native species can play both positives or negative roles, replacing functions which have been lost (Aslan et al. 2014), or displacing native species and breaking mutualistic relationships that will be lost in the community (Hansen and Müller 2009b). DMs are most likely to establish between generalist non-native species and they are expected to become more common given the ongoing spread of non-native species.

Functional role of double mutualisms in ecosystems and conservation implications

Species-poor ecosystems, such as islands, mountains tops, and deserts are particularly sensitive to alterations by non-native, invasive species and to species extinctions (Bellard et al. 2017). When an animal double mutualist declines in abundance or disappears locally, the associated plant may suffer from the loss of two functions, pollination and seed dispersal.

An illustrative example of a disruption of a tight DM is the endangered Mauritian *Roussea simplex*, which is pollinated and dispersed by the blue day gecko *Phelsuma cepedianana*. Both reproductive processes are interrupted by the invasive white-footed ant *Technomyrmex albipes*, resulting in a marked decline in abundance of the species (Hansen and Müller 2009b, Bissessur et al. 2017). Ecosystems with many DMs and low functional redundancy are probably more vulnerable to the decline or local extinction of some species compared to more diverse communities (Traveset et al. 2017). A recent study using data from the Galápagos Islands (Olesen et al. 2018) showed that double mutualists by no means generate marginal interactions in the community but form part of the central core of pollination and seed dispersal networks.

Depending on the stability of the community, the double potential benefits of DMs might outweigh the potential risks. Nevertheless, the increasing vulnerability of the ecosystems, in which DMs seem to occur most frequently (i.e. tropical areas and islands) suggests that they impose a greater risk than a benefit for the ecosystems with many DMs. A relatively high number of animal double mutualists are currently threatened (27%) and their proportion is higher than the proportion of global threatened vertebrate pollinators and seed dispersers found in Aslan et al. (2013). Mammal double mutualists are disproportionately vulnerable (50%) than mammal pollinators or seed dispersers alone (26 and 23%, respectively). Birds and reptiles show a similar trend, yet to a slightly lesser extent. We might have expected that given that most double mutualists are generalist species, they should exhibit lower threat levels than specialists; however, the proportion (26%) of threatened species was similar between the two groups. The loss of threatened animal double mutualists is imminent, especially for primates, bats and Psittaciformes birds. The resulting mutualistic disruptions may cause a cascade of coextinctions, especially for those plants highly dependent on DM animals. Bats, for example, are the only pollinators and important seed dispersers for some cactus species, (Valiente-Banuet et al. 1997), and their decline would impose a double risk on the plants. Aslan et al. (2013) actually estimated that ca 17% of vertebrate pollinators and 26% of dispersers are threatened with extinction, and these levels are likely to be higher for island species. High prevalence of DMs on islands and the vulnerability of these ecosystems suggest that many DMs in these environments are also threatened with still unknown consequences for the maintenance of community composition and ecosystem functioning. The consequences are likely to be substantial, however, as double mutualists form part of the core of mutualistic interactions in the community (Olesen et al. 2018). Identifying DMs is therefore a useful strategy to assess the vulnerability of the ecosystem and establish conservation priorities. From this review, we foresee that community-level studies are the most effective in detecting double mutualists, yet focusing on one or a few species may also be highly valuable to identify DMs if more than one ecological process is investigated. This is particularly important when considering the efficiency of a double mutualist. To assess the role double mutualists plays in pollination and

seed dispersal effectiveness, both in their quantity and quality components, more in-depth studies are required.

In summary, this work sheds light on an important facet of mutualistic systems that has been mostly overlooked in both community and single-species studies, but that seems to be relatively common and critical to the functioning of ecosystems (Olesen et al. 2018). We show that DMs are more likely developed between generalist vertebrate animal and plant species, and are prevalent in tropical ecosystems, where the generalization in pollination and seed dispersal is higher, as well as the proportion of animal mutualisms. Moreover, DMs are also prevalent in species-poor communities, which makes them vulnerable to disturbance and species extinctions. We anticipate that the patterns described here will serve as a starting point for future research on ecological and evolutionary drivers of DMs and their consequences for ecosystem robustness.

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References

- Allesina, S. and Tang, S. 2012. Stability criteria for complex ecosystems. – *Nature* 483: 205–208.
- Anderson, S. H. et al. 2006. Birds as pollinators and dispersers: a case study from New Zealand. – *Acta Zool. Sinica* 52 (Suppl.): 112–115.
- Aslan, C. E. et al. 2013. Mutualism disruption threatens global plant biodiversity: a systematic review. – *PLoS One* 8: e66993.
- Aslan, C. E. et al. 2014. Imperfect replacement of native species by non-native species as pollinators of endemic Hawaiian plants. – *Conserv. Biol.* 28: 478–488.
- Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Bellard, C. et al. 2017. A global picture of biological invasion threat on islands. – *Nat. Ecol. Evol.* 1: 1862–1869.
- Bissessur, P. et al. 2017. Rapid population decline of an endemic oceanic island plant despite resilience to extensive habitat destruction and occurrence within protected areas. – *Plant Ecol. Divers.* 10: 293–302.
- Blázquez, M. C. and Rodríguez-Estrella, R. 2007. Microhabitat selection in diet and trophic ecology of a spiny-tailed iguana *Ctenosaura hemilopha*. – *Biotropica* 39: 496–501.
- Bowen, L. and Van Vuren, D. 1997. Insular endemic plants lack defenses against herbivores. – *Conserv. Biol.* 11: 1249–1254.
- Burnham, R. J. and Johnson, K. R. 2004. South American palaeobotany and the origins of neotropical rainforests. – *Phil. Trans. R. Soc. B* 359: 1595–1610.
- Ceballos, G. et al. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. – *Proc. Natl Acad. Sci. USA* 114: e6089–e6096.
- Cecere, J. G. et al. 2011. Nectar: an energy drink used by European songbirds during spring migration. – *J. Ornithol.* 152: 923–931.
- da Silva, L. P. et al. 2014. Flower visitation by birds in Europe. – *Oikos* 123: 1377–1383.
- da Silva, L. P. et al. 2017. Flower visitation by European birds offers the first evidences of interactions release in continents. – *J. Biogeogr.* 44: 687–695.
- Dar, S. et al. 2006. Diurnal and nocturnal pollination of *Marginatocereus marginatus* (Pachycereeae: Cactaceae) in central Mexico. – *Ann. Bot.* 97: 423–427.
- de Vega, C. and Gómez, J. M. 2014. Polinización por hormigas: conceptos, evidencias y futuras direcciones. – *Ecosistemas* 23: 48–57.
- Farwig, N. and Berens, D. G. 2012. Imagine a world without seed dispersers: a review of threats, consequences and future directions. – *Basic Appl. Ecol.* 13: 109–115.
- Fenster, C. B. et al. 2004. Pollination syndromes and floral specialization. – *Annu. Rev. Ecol. Evol. Syst.* 35: 375–403.
- Fleming, T. H. et al. 2009. The evolution of bat pollination: a phylogenetic perspective. – *Ann. Bot.* 104: 1017–1043.
- Fuster, F. et al. 2018. Data from: Global patterns of the double mutualism phenomenon. – Dryad Digital Repository, <<https://doi.org/10.5061/dryad.r8s0s8q>>.
- García, M. B. et al. 2012. Extreme reproduction and survival of a true cliffhanger: the endangered plant *Borderea chouardii* (Dioscoreaceae). – *PLoS One* 7: e44657.
- Godsoe, W. et al. 2008. Coevolution and divergence in the Joshua tree/yucca moth mutualism. – *Am. Nat.* 171: 816–823.
- Gomes, V. G. N. et al. 2014. Pollination and seed dispersal of *Melocactus ernestii* Vaupel subsp. *ernestii* (Cactaceae) by lizards: an example of double mutualism. – *Plant Biol.* 16: 315–322.
- González-Varo, J. P. and Traveset, A. 2016. The labile limits of forbidden interactions. – *Trends Ecol. Evol.* 31: 700–710.
- Hansen, D. M. and Müller, C. B. 2009a. Reproductive ecology of the endangered enigmatic Mauritian endemic *Roussea simplex* (Rousseaceae). – *Int. J. Plant Sci.* 170: 42–52.
- Hansen, D. M. and Müller, C. B. 2009b. Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant *Roussea simplex* in Mauritius. – *Biotropica* 41: 202–208.
- Heleno, R. H. et al. 2013. Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. – *Proc. R. Soc. B* 280: 20122112.
- Herrera, C. M. 1995. Plant–vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary and historical determinants. – *Annu. Rev. Ecol. Evol. Syst.* 26: 705–727.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. – *Am. Nat.* 163: 192–211.
- Iles, J. M. and Kelly, D. 2014. Restoring bird pollination of *Fuchsia excorticata* by mammalian predator control. – *N. Z. J. Ecol.* 38: 297–306.
- IUCN 2018. The IUCN Red List of threatened species, version 2017.3. – International Union of Conservation of Nature, <www.iucnredlist.org> accessed 10 January 2018.
- Janicki, J. et al. 2016. Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: the design and implementation of antmaps.org. – *Ecol. Inform.* 32: 185–193.
- Jordano, P. 2000. Fruits and frugivory. – In: Fenner, M. (ed.), *Seeds: the ecology of regeneration in plant communities*, 2nd ed. CABI Publ., pp. 125–165.
- Kaiser-Bunbury, C. N. et al. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. – *Ecol. Lett.* 13: 442–452.

- Kaiser-Bunbury, C. N. et al. 2014. Determinants of the microstructure of plant–pollinator networks. – *Ecology* 95: 3314–3324.
- Lengyel, S. et al. 2010. Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. – *Perspect. Plant. Ecol.* 12: 43–55.
- MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.
- Moles, A. T. et al. 2007. Global patterns in seed size. – *Global Ecol. Biogeogr.* 16: 109–116.
- Neal, P. R. et al. 1998. Floral symmetry and its role in plant–pollinator systems: terminology, distribution and hypothesis. – *Annu. Rev. Ecol. Syst.* 29: 345–373.
- Neuschulz, E. L. et al. 2016. Pollination and seed dispersal are the most threatened processes of plant regeneration. – *Sci. Rep.* 6: 29839.
- Olesen, J. M. and Valido, A. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. – *Trends Ecol. Evol.* 18: 177–181.
- Olesen, J. M. et al. 2018. Disclosing the double mutualist role of birds on Galápagos. – *Sci. Rep.* 8: doi:10.1038/s41598-017-17592-8
- Ollerton, J. et al. 2011. How many flowering plants are pollinated by animals? – *Oikos* 120: 321–326.
- Olson, D. M. et al. 2001. Terrestrial ecoregions of the world: a new map of life on earth. – *Bioscience* 51: 933–938.
- Proctor, M. et al. 1996. The natural history of pollination. – Harper Collins.
- Schemske, D. W. et al. 2009. Is there a latitudinal gradient in the importance of biotic interactions? – *Annu. Rev. Ecol. Evol. Syst.* 40: 245–269.
- Schleuning, M. et al. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. – *Curr. Biol.* 22: 1925–1931.
- Simberloff, D. and Boecklen, W. 1991. Patterns of extinction in the introduced Hawaiian avifauna: a reexamination of the role of competition. – *Am. Nat.* 138: 300–327.
- Somveille, M. et al. 2013. Mapping global diversity patterns for migratory birds. – *PLoS One* 8: e70907.
- Spurr, E. B. et al. 2011. Food preferences of the bellbird (*Anthornis melanura*) in native forest remnants on the Port Hills, Banks Peninsula, New Zealand. – *Notornis* 58: 139–157.
- Traveset, A. et al. 2015. Bird–flower visitation networks in the Galapagos unveil a widespread interaction release. – *Nat. Commun.* 10: 6376.
- Traveset, A. et al. 2017. Plant survival and keystone pollinator species in stochastic coextinction models: role of intrinsic dependence on animal–pollination. – *Sci. Rep.* 7: doi:10.1038/s41598-017-07037-7
- Valiente-Banuet, A. et al. 1997. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, central Mexico. – *Am. J. Bot.* 84: 452–455.
- Vázquez, D. P. 2005. Degree distribution in plant–animal mutualistic networks: forbidden links or random interactions? – *Oikos* 108: 421–426.
- Woodward, S. A. et al. 1990. Use of the exotic tree *Myrica faya* by native and exotic birds in Hawai'i Volcanoes National Park. – *Pac. Sci.* 44: 88–93.
- Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.

Supplementary material (Appendix ECOG-04008 at <www.ecography.org/appendix/ecog-04008>). Appendix 1–2.