

# Global importance of vertebrate pollinators for plant reproductive success: a meta-analysis

Fabrizia Ratto<sup>1</sup>, Benno I Simmons<sup>2</sup>, Rebecca Spake<sup>3</sup>, Veronica Zamora-Gutierrez<sup>1,4</sup>, Michael A MacDonald<sup>5</sup>, Jennifer C Merriman<sup>6</sup>, Constance J Tremlett<sup>1</sup>, Guy M Poppy<sup>1</sup>, Kelvin S-H Peh<sup>1,2\*†</sup>, and Lynn V Dicks<sup>7†</sup>

Vertebrate pollinators are increasingly threatened worldwide, but little is known about the potential consequences of declining pollinator populations on plants and ecosystems. Here, we present the first global assessment of the importance of vertebrate pollinators in the reproductive success of selected flowering plants. Our meta-analysis of 126 experiments on animal-pollinated plants revealed that excluding vertebrate pollinators – but not insect pollinators – reduced fruit and/or seed production by 63% on average. We found bat-pollinated plants to be more dependent on their respective vertebrate pollinators than bird-pollinated plants (an average 83% reduction in fruit/seed production when bats were excluded, as compared to a 46% reduction when birds were excluded). Plant dependence on vertebrate pollinators for fruit/seed production was greater in the tropics than at higher latitudes. Given the potential for substantial negative impacts associated with the loss of vertebrate pollinators, there is a clear need for prompt, effective conservation action for threatened flower-visiting vertebrate species. Additional research on how such changes might affect wider ecosystems is also required.

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Animal pollination is necessary in the life cycle of many plant species. An estimated 87.5% of the world's flowering plant species are animal pollinated (Ollerton *et al.* 2011), with 75% of the world's major crop species benefitting to some degree from animal

pollination (Klein *et al.* 2007). Animal-pollinated plants are also used for medicines, forage, and construction materials (Potts *et al.* 2010, 2016; Ollerton *et al.* 2011), and play a crucial role in the long-term maintenance of biodiversity and natural ecosystems. While much scholarly and media attention has been focused on insect pollinators, the role of vertebrate pollinators is not as widely recognized. A global study revealed that, in recent decades, both mammal and bird pollinators are becoming increasingly threatened with extinction over time, with an average of 2.5 species per year moving one category closer to extinction on the IUCN Red List of Threatened Species (Regan *et al.* 2015). These declines in the populations of mammal and bird pollinators are thought to be driven by agricultural expansion, the spread of invasive alien species, hunting, and fire (Regan *et al.* 2015).

Over 920 species of birds are known to pollinate plants (Whelan *et al.* 2008) including those belonging to the Nectarinidae (sunbirds), Trochilidae (hummingbirds), Meliphagidae (honeyeaters), and Loridae (lories) (Figure 1a). Birds pollinate about 5.4% of the 960 cultivated plant species for which pollinators are known (Nabhan 1997) and typically pollinate 5% of a region's flora or 10% of flora if that region is an island (Anderson 2003; Kato and Kawakita 2004; Bernardello *et al.* 2006). Among mammals, bats are the major pollinators, with flower-visiting bats mostly found in two families: Pteropodidae (fruit bats), occurring mainly in Asia and Australia, and Phyllostomidae (leaf-nosed bats), distributed throughout the Neotropics (Fleming and Muchhala 2008) (Figure 1b). Approximately 528 plant species in 67

## In a nutshell:

- We assess the importance of vertebrate pollinators for the reproductive success of the plants they pollinate
- In our meta-analysis, we found that excluding vertebrate pollinators from plants visited by both insects and vertebrate pollinators reduced fruit and seed production by 63%, indicating a strong dependence on these pollinators
- Tropical plants are more reliant on vertebrate pollination than temperate plants and bat-pollinated plants are more reliant on vertebrate pollination than plants pollinated by other vertebrates
- We emphasize the importance of conserving vertebrate pollinators and stress the need for more empirical data on the pollination systems of plants and their vertebrate pollinator communities

<sup>1</sup>Biological Sciences, University of Southampton, Southampton, UK \*(kelvin.peh@gmail.com); <sup>2</sup>Department of Zoology, University of Cambridge, Cambridge, UK; <sup>3</sup>Geography and Environment, University of Southampton, Southampton, UK; <sup>4</sup>CONACYT-Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR) Unidad Durango, Instituto Politécnico Nacional, Durango, Mexico; <sup>5</sup>Centre for Conservation Science, Royal Society for the Protection of Birds (RSPB), Sandy, UK; <sup>6</sup>BirdLife International, Cambridge, UK; <sup>7</sup>School of Biological Sciences, University of East Anglia, Norwich, UK; †these authors contributed equally to this work



**Figure 1.** Example taxa representing the four major vertebrate pollinator groups: (a) ruby-throated hummingbird (*Archilochus colubris*), (b) lesser long-nosed bat (*Leptonycteris yerbabuenae*), (c) Namaqua rock mouse (*Micaelamys namaquensis*), and (d) bluetail day gecko (*Phelsuma cepediana*).

families and 28 orders worldwide are pollinated by bats (Kunz *et al.* 2011). Non-flying mammals such as primates, rodents, and marsupials are also known to visit at least 85 species of plants worldwide (Carthew and Goldingay 1997) (Figure 1c). In addition, flower visitation is reported for 37 lizard species, mainly island-dwelling ones (Olesen and Valido 2003) (Figure 1d).

The declines in abundance and diversity of pollinators have raised concerns worldwide, prompting a growing body of research on the extent to which reproductive success of plants is enhanced by flower-visiting animals (Garibaldi *et al.* 2013; Kleijn *et al.* 2015; Rader *et al.* 2016). However, most of these studies focus on insect pollinators visiting crop flowers. The only global review of the degree of dependence of plant reproduction on pollination focused exclusively on crop plants (Klein *et al.* 2007) and it has been used extensively to value pollination services at national and international scales (Gallai *et al.* 2009; Lautenbach *et al.* 2012). Klein *et al.* (2007) reported that, throughout the world, crop pollinators are mainly bees. Nevertheless, vertebrates are essential for the reproduction of some economically important crop species such as *Hylocereus undatus* (dragon fruit) (Ortiz-Hernández and Carrillo-Salazar 2012), *Durio* spp (durian), and *Parkia* spp (beans) among others (Bumrungsri *et al.* 2008, 2009).

The best available global-scale information on the degree of dependence of wild plants on their pollinators (Ollerton *et al.* 2011) did not use empirical data on plant reproductive success but instead classified plants as either animal-dependent or not, in 42 surveyed plant communities, based on the judgement of ecologists or botanists. To our knowledge, there has never been a global meta-analysis of the extent of dependence of wild plants on animal pollinators for fruit set or seed set. Yet this measure of dependence is crucial if scientists and resource managers are to understand and begin to value pollinators for their role in wild plant pollination.

Global-scale meta-analyses have been conducted on the extent of pollen limitation (to what degree plant reproductive success can be enhanced by hand pollination) related to local and regional biodiversity patterns (Vamosi *et al.* 2006), and on the identity of important pollinators as they relate to pollination syndromes (suites of floral traits, such as odor and color, associated with particular functional groups of pollinators) (Rosas-Guerrero *et al.* 2014). However, neither of these approaches helps to evaluate the importance of current pollination to ecosystems as well as to plant communities and populations.

We present the first global assessment of the overall importance of vertebrate pollinators for plant reproduc-

tive success (fruit and seed production for both crops and wild plants), using quantitative meta-analysis. We focus on vertebrate pollinators because, unlike invertebrates, the conservation status of most pollinating vertebrate species is well characterized at the global scale, and their distributions and diversity are mapped (Jenkins *et al.* 2013), making it possible to target and prioritize conservation actions worldwide. We pose two questions: (1) what is the importance of vertebrate pollinators for plant reproductive success, and (2) how does this importance vary with vertebrate pollinator taxon, taxonomic breadth of flower visitors, geographical region, climatic domain, type of exclusion experiment, and measure used for assessing reproductive success?

### ■ A systematic review of vertebrate pollination

Using standard review protocols, we conducted a systematic literature search for studies that investigated the relationship between vertebrate flower visitors and plant sexual reproduction (Pullin and Stewart 2006). Here we describe the literature review, search strategy, the selection of potential explanatory factors, and data analysis.

#### *Literature review and search strategy*

We defined a pollinator as a regular flower visitor that transfers pollen between plants, leading to successful pollination and, ultimately, the production of seeds (Carthew and Goldingay 1997). Pollinator performance can be assessed in two ways: pollination success (contribution to pollen deposited on female flower parts) and plant reproductive success (contribution to seed set) (Ne'Eman *et al.* 2010). We included studies that quantitatively measured the latter, in terms of fruit and seed production. To retrieve these studies, we searched ISI Web of Knowledge, Scopus, CAB Abstract, and Agricola databases (from 1900 to 2016 inclusive) and relevant gray literature sources (using Google, Google Scholar, and SciELO) in both English and Spanish. We used a combination of search terms relating to potential vertebrate pollinators, measures of plant reproductive success, and pollination efficiency and effectiveness (see WebPanel 1 for full search string). Our initial search yielded 4588 articles.

After removing obviously spurious results, we screened the title and abstract of the remaining 467 articles for relevance, resulting in 389 appropriate studies. We were denied access to 11 relevant articles but we read the remaining 378 articles in full to establish their suitability for the analysis (WebFigure 1). We categorized plants that had been exposed to vertebrate pollinators through open/natural pollination as “control” (ie vertebrate pollinators present) and plants from which vertebrates were experimentally excluded, by bagging or caging, as “treatment” (ie vertebrate pollinators absent). All studies used

either fruit production or seed production as a measure of plant reproductive success (response variables).

To be included in the subsequent analysis, studies had to meet the following criteria:

(1) involve an experiment where vertebrate pollinators were excluded using a physical barrier such as mesh bags or chicken wire, and plant reproductive success was measured in the presence and absence of vertebrate pollinators; and (2) have replicated pollinator-excluded inflorescences, spatially interspersed with replicated unmanipulated inflorescences.

#### *Data analysis*

To quantify the importance of vertebrate flower visitors for plant reproductive success (question 1 above), we calculated the natural log of the response ratio ( $\ln R$ ) as a standardized effect size for each study. This expresses the proportional difference between the seed and fruit production of the treatment group and the control group (Borenstein *et al.* 2009). We used a random effects model to calculate a combined effect size across all studies. We performed a phylogenetically controlled meta-analysis to control for shared evolutionary history between plants (see WebPanel 2 for a detailed methodology).

Our analysis then focused on assessing the influence of several ecological, environmental, and experimental factors; specifically, these six explanatory variables were pollinator taxon, taxonomic breadth of flower visitors, region, climatic domain, experiment manipulation level, and measure of reproductive success (Table 1). To investigate the variability of importance for plant reproductive success among vertebrate pollinators, we classified studies according to the vertebrate pollinator taxon (bat, bird, and rodent); we included reptiles only in the overall meta-analysis due to a small sample size ( $n = 2$ ). To determine if the importance of vertebrate pollinators was dependent on the taxonomic breadth of the flower visitors, we also labelled studies as either “low” or “high”, according to whether only vertebrates, or both vertebrates and invertebrates, were observed visiting the flowers and making contact with the flowers' anthers and stigma (ie making “legitimate” pollination visits). We further classified studies into one of five regions (North America [excluding Central America], South-Central America, Asia, Africa, and Australasia) to determine if the importance of vertebrate pollinators differed among geographical regions. To determine whether there was a difference between climate domains, we characterized studies as either tropical or extra-tropical. We placed each study in one of three categories according to the manipulation level of the exclusion experiment (flower, inflorescence, and whole plant) to check whether there was a discrepancy between the different manipulations. Finally, we grouped studies according to their measure of assessing reproductive success (fruit production and seed production) to determine if these measures yielded



**Table 1. Explanatory variables included in the mixed model with subcategories for each variable.**

<i>Explanatory variables</i>	<i>Subcategories</i>	<i>Details</i>
Pollinator taxon	Bats Birds Rodents Reptiles	
Taxonomic breadth of flower visitors	High: Vertebrates and invertebrates Low: Vertebrates	The categories show plants legitimately visited by both vertebrate and invertebrate taxa versus plants legitimately visited by only vertebrate taxa
Region	North America (NA) South–Central America (SCA) Africa Asia Australasia	These represent major biogeographic regions
Climatic domain	Tropical Extra-tropical	Categorized according to latitude reported in the study. Tropical < 23°27', Extra-tropical > 23°27'
Experiment manipulation level	Flower Inflorescence Whole plant	Categories show the level of the manipulation: some flowers, or some inflorescences or the whole plants were mechanically excluded (bagged/caged)
Measure of reproductive success	Fruit production Seed production	Each category includes measures of reproductive success at fruit and seed level, respectively

different results. We calculated the effect size for each subgroup of the six explanatory variables.

Using linear regression mixed models (question 2 above), we then tested whether these factors significantly predicted the size of effects of vertebrate exclusion on plant reproductive success. Models were built using all possible combinations of five of the explanatory variables but not interactions between them; the sixth variable, a method for determining reproductive success, was added to the model as a random factor. We selected the best models as those with the lowest values of Akaike's Information Criterion (AIC). Statistical analyses were conducted in R (version 3.1.2.) with the packages “metafor” (Viechtbauer 2010) and “MuMIn” (Barton 2011) (WebPanel 2).

#### ■ Global importance of vertebrate pollinators

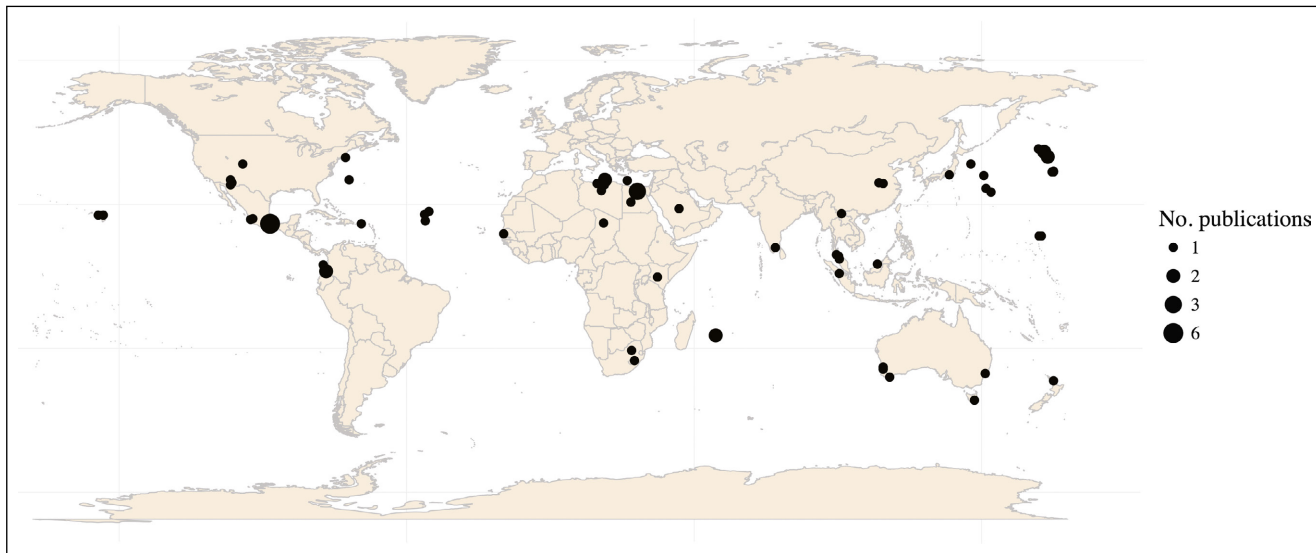
We retrieved 69 articles that satisfied the inclusion criteria. Because some of these articles investigated multiple plant species, pollinator taxa, or locations, they provided a total of 126 separate exclusion comparisons, hereafter referred to as “studies” (WebPanel 3 for a comprehensive list). The dataset included studies on 91 plant species (WebTable 1), spanning 50 genera and 35 families: 84 studies investigated bird pollinators, 27 flying mammals, 13 non-flying mammals, and 2 reptiles. Of 126 studies, 11 were from South and Central America, 37 from Africa, 36 from North America, 30 from Australasia, and 12 from Asia (Figure 2).

The exclusion of vertebrate flower visitors had a strong negative effect on plant reproduction across all studies, translating into an average reduction in fruit and seed production of 63% (confidence interval: –74.87 to –46.76) in

the absence of vertebrate pollinators. The effect size differed according to the main type of flower visitor, with bats having the strongest effect on plant reproductive success. With respect to fruit and seed production, bat-pollinated plants, bird-pollinated plants, and rodent-pollinated plants exhibited an 83% decline, a 46% decline, and a 49% decline (combined lnR), respectively (Figure 3a). The breadth of flower visitors did not have a significant effect on plant reproductive success when vertebrate pollinators were excluded. Plants pollinated by only vertebrates were subject to a 59% reduction in reproductive success whereas those pollinated by both vertebrate and invertebrate pollinators had a 61% reduction (Figure 3b).

The exclusion of vertebrate pollinators negatively affected plant reproductive success to varying degrees by region (Figure 3c) and across latitudes, where success was reduced by 71% and 45% in the tropical and extra-tropical climatic domains, respectively (Figure 3d). With regard to experimental design, the size of the negative effect of pollinator exclusion on plant reproductive success was higher when single flowers were manipulated (71%) than when inflorescences (42%) and whole plants (40%) were the experimental unit (Figure 3e), although they did not differ significantly. Additionally, in terms of fruit production and seed production, proportional reductions in plant reproductive success were almost equal (58% and 61%, respectively) (Figure 3f).

Our model selection process inferred pollinator taxon and climatic domain to be the best predictors of the size of the effect of vertebrate pollination on plant reproductive success. Four moderators – pollinator taxon, climatic domain, taxonomic breadth of flower visitors, and geographic region – all appeared in models with  $\Delta AIC_c < 6$ , models for which there is considerable support (Burnham



**Figure 2.** Location of studies featured in the meta-analysis. Locations were based on geographical coordinates provided in the publications or were georeferenced through the description of the study area provided therein. Increasing circle sizes reflect the number of publications in a specific location.

and Anderson 2002), where  $\Delta AICc$  represents the difference between the AIC value of the best model and the AIC value for each of the other models (Symonds and Moussalli 2011), corrected for small sample sizes (AICc). Pollinator taxon was included in all of the top-performing models, whereas climatic domain was included in the best model and in one of the other five models with  $\Delta AICc < 6$  (Table 2a). Pollinator taxon and climatic domain were the only predictors that had a substantial effect on the observed effect sizes, with summed AIC weights  $> 0.3$  (Newbold *et al.* 2013) (Table 2b). The taxonomic breadth of flower visitors, geographic region, and type of exclusion experiment did not seem to affect the impact of vertebrate exclusion on the reproductive success of animal-pollinated plants.

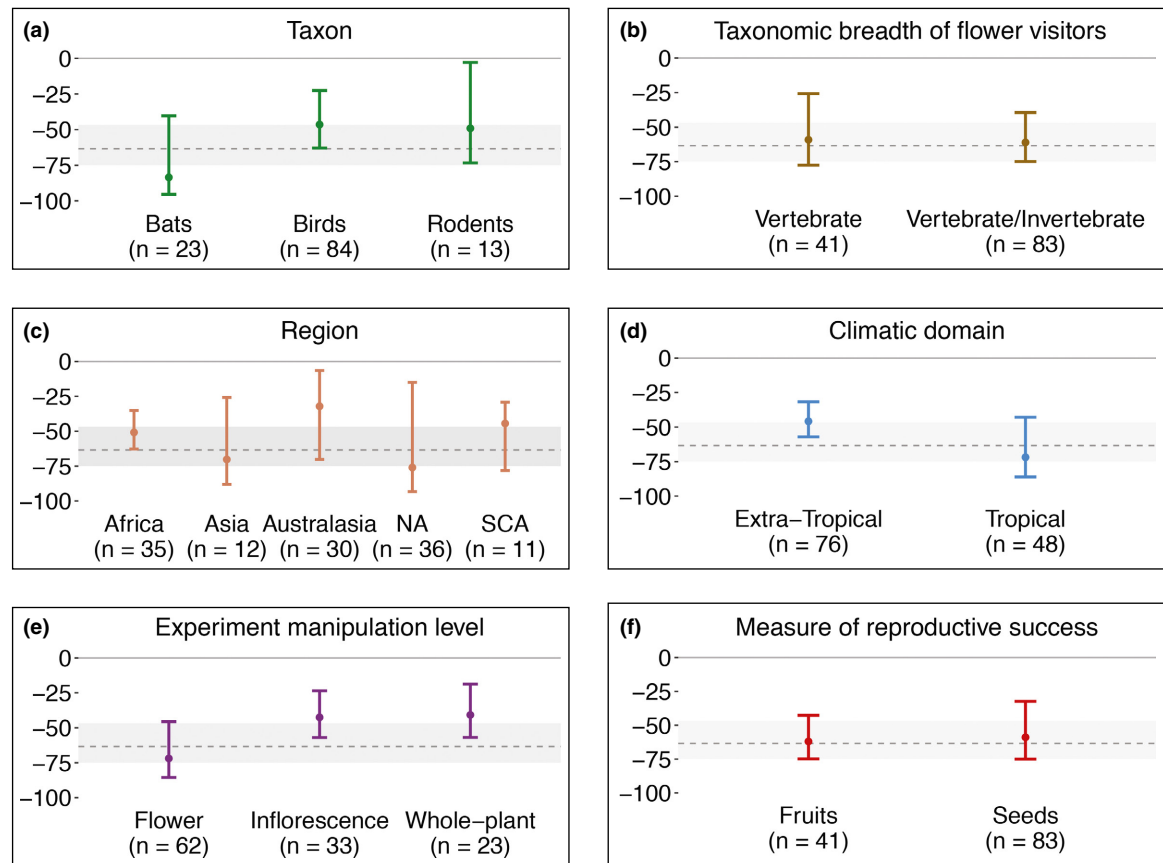
### ■ Factors predicting the importance of vertebrate pollinators

Our results show that bat-pollinated plants are more severely affected by pollinator loss than bird- or rodent-pollinated plants. The majority of plants (69%) that failed to produce fruits or seeds in vertebrate exclusion experiments were bat-pollinated species. This could be because bats are more effective than birds at moving pollen between flowers. Many bat-pollinated plants produce very large amounts of pollen, and Muchhala and Potts (2007) demonstrated that at similar flower visitation rates, bats can transfer up to four times as much pollen relative to that transferred by birds. In comparison with feathers, fur has the capacity to hold and shed more pollen grains, making reliance on bats a more secure strategy in evolutionary terms relative to birds. Pollen can be transported over long distances, a feature that is important for plants such as cacti and agave species,

which grow at low densities in arid zones (Fleming *et al.* 2009). These bat-adapted plants may represent an evolutionary “dead end” (Tripp 2010), where switching to an alternative pollinator becomes unlikely due to their inability to transport the large amount of pollen produced (Muchhala and Thomson 2010).

Our findings indicate that birds and rodents are important pollen vectors for many plants. However, we may have underestimated the magnitude of rodents’ impact on plants’ sexual reproduction for two reasons. First, studies on rodent pollinators were conducted predominantly in South Africa (and with some exceptions in Australia), resulting in a wide knowledge gap for other geographical regions. Second, our meta-analysis included only one rodent family, the Muridae (rats and mice). We consider this dataset insufficient to generalize about the global importance of non-flying mammalian pollinators on the reproductive success of animal-pollinated plants, because it excludes empirical data on many other known mammalian pollinators such as non-human primates (including lemurs), possums, and squirrels.

The second most important factor that explains the impact of vertebrate pollinators on plant reproductive success was climate domain. Vertebrate-pollinated plants inside the tropics are more dependent on pollinators than vertebrate-pollinated plants outside the tropics, conceivably due to a higher degree of plant specialization near the Equator (Olesen and Jordano 2002; Dalsgaard *et al.* 2011; Trøjelsgaard and Olesen 2013). For example, columnar cacti pollination systems range from exclusively bat-pollinated species in the tropics to species with more generalized pollinator interactions involving both diurnal and nocturnal pollinators outside the tropics (Munguia-Rosas *et al.* 2009). When plants are more specialized (that is, visited by a narrower range of pollinators), then the



**Figure 3.** Changes in plant reproductive success when vertebrates were excluded, expressed in percentages with 95% bias-corrected confidence intervals grouped by (a) pollinator taxon, (b) taxonomic breadth of flower visitors, (c) region (NA: North America; SCA: South-Central America), (d) climatic domain, (e) manipulation level of the exclusion experiment, and (f) measure used to estimate reproductive success. Categories in subgroups are shown at the bottom of graphs, and sample sizes are shown in parentheses. The overall mean percentage change in reproductive success is depicted as a dashed horizontal line with a 95% confidence interval (gray band).

removal of one pollinator species or group might be expected to have a larger impact on those plants. Dalsgaard *et al.* (2011) found higher specialization in the tropics among plant-hummingbird pollinator networks.

### ■ Pollinator dependence and pollen limitation

Our meta-analysis of exclusion experiments gauges the degree of pollinator dependence in vertebrate-pollinated plants. This measure reflects the “value” of existing vertebrate pollination, in the current contexts where the experiments took place (Figure 4), and highlights the importance of vertebrate pollinators for fruit and seed production in natural ecosystems. We recognize that experimental exclusion of vertebrate pollinators depicts a worst-case scenario of total pollinator loss for those plants relying on vertebrate pollen vectors. There is, as yet, no documented example of an animal-pollinated plant species that is at risk of extinction due to the disappearance of its dominant vertebrate pollinator. Nevertheless, the bleak scenario detailed above is plausible at the scale of individual sites. Local extinctions are known to have occurred for bees and hoverflies

(Biesmeijer 2006). The long-term survival of a plant species could conceivably be threatened when their vertebrate pollinator communities decline.

Given that we relied on exclusion experiments and not hand-pollination comparisons, our results cannot be used to determine how much pollen limitation already exists in the open-pollinated “controls”, due to previous reductions in the pollination services being provided by vertebrates when the experiments took place. The extent of pollen limitation is measured by the enhancement in plant reproductive success that can be achieved by maximizing pollination (by hand), as if pollinator populations had increased. Previous research has shown that pollen limitation is widespread (Larson and Barrett 2000; Ashman *et al.* 2004). Tropical regions may be more prone to pollen limitation than temperate regions for several reasons, including the higher incidence of animal-pollinated species in the tropics (Ollerton *et al.* 2011), as well as a positive correlation between high biodiversity and pollen limitation (Vamosi *et al.* 2006). It is not clear whether this observed pollen limitation is a result of ongoing or previous pollinator declines, or whether it reflects the ecological contexts, in which the plant-pollinator

**Table 2. (a) Explanatory variables included in the linear mixed models predicting the variation in reproductive success of plants in the presence and absence of vertebrate pollinators. (b) Relative ability of each variable to explain observed responses of reproductive success to the exclusion of vertebrate pollinators. Explanatory power is expressed as the sum of AICc weights of variables featuring in models with  $\Delta AICc < 6$ .**

(a)								
Predictors in the model								
Model rank	Climatic domain	Pollinator taxon	Taxonomic breadth of flower visitors	Region	df	AICc	$\Delta AICc$	weight
<b>1</b>	+	+			<b>9</b>	<b>550</b>	<b>0.00</b>	<b>0.52497</b>
<b>2</b>	+	+	+		<b>10</b>	<b>551</b>	<b>1.46</b>	<b>0.25327</b>
<b>3</b>		+			<b>8</b>	<b>553</b>	<b>3.53</b>	<b>0.08978</b>
<b>4</b>		+		+	<b>12</b>	<b>554</b>	<b>4.46</b>	<b>0.05657</b>
<b>5</b>		+	+		<b>9</b>	<b>555</b>	<b>5.80</b>	<b>0.02884</b>
6	+	+		+	13	556	6.39	0.02152
7		+	+	+	13	556	6.79	0.01763
8	+	+	+	+	14	558	8.52	0.00743

**Notes:** Models ranked by increasing AICc values. Best models, with  $\Delta AICc < 6$ , are shown in bold. The predictors featuring in each model are identified with the + symbol; df represents degrees of freedom.

(b)	
Variable	Sum of AICc weight
<b>Pollinator taxon</b>	<b>1.00</b>
<b>Climatic domain</b>	<b>0.82</b>
Taxonomic breadth of flower visitors	0.29
Geographical region	0.06

**Notes:** Variables with relative importance  $>0.3$  have substantial effects on the reproductive success of plants (Newbold *et al.* 2013)

nator interactions evolved. If the plants in the pollinator exclusion studies analyzed here were already experiencing pollen limitation due to pollinator decline, then the overall negative impact of vertebrate decline on fruit and seed production could be higher than we estimated.

Finally, resource reallocation at a plant level (where plants are manipulated at a flower or inflorescence scale) could potentially bias experimental results by leading to overestimates of the magnitude of the impact of vertebrate exclusion (Knight *et al.* 2006). However, the absence of significant differences in plant reproductive success among studies subjected to different experiment manipulation levels showed that our estimated magnitude of the effect of pollinator loss on plant reproductive success is robust. Nevertheless, future studies could investigate this further by developing standardized methodologies across exclusion experiments.

### ■ Implications for ecosystems and human well-being

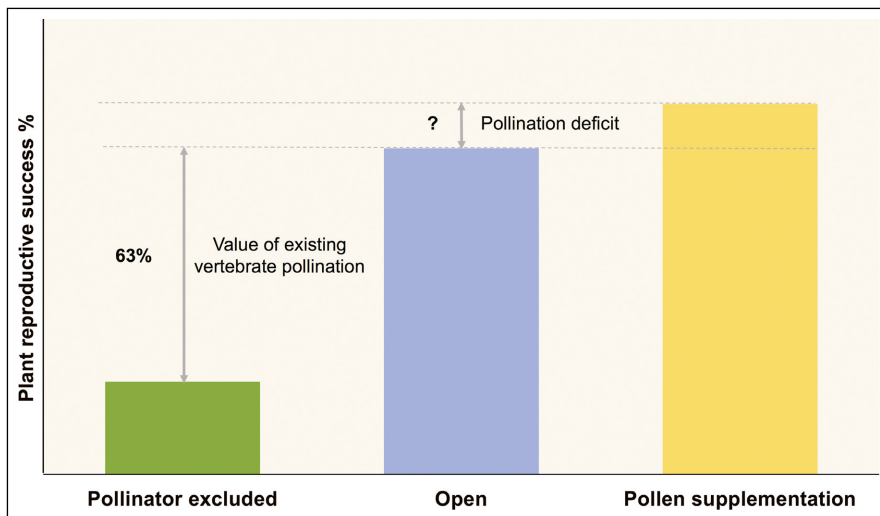
Our review emphasizes the importance of conserving vertebrate pollinators, particularly in the tropics. Vertebrate pollinator-dependent crops are an important component of tropical cultivated goods (eg pitayas, agave,

durian), and declining pollination services may result in substantial losses in revenue. Despite their reduced species richness, bat-pollinated plants have substantial economic and social value. The loss of pollinating bats, for instance, would have major consequences for the reproduction of plants such as agave and columnar cacti, which yield high monetary-valued goods – mezcal and pitayas – in the Mexican agricultural market. Furthermore, durian (*Durio zibethinus*), which depends on bats such as flying foxes (*Pteropus* spp) for pollination (Cunningham 1991; Bumrungsri *et al.* 2009), is an extremely popular and economically important fruit in Southeast Asia.

A loss of fruits and seeds of this magnitude, especially in tropical areas, would likely have an adverse impact on animals that depend on these resources, including birds, bats, rodents, and primates, as well as many granivorous or frugivorous invertebrate species.

In the tropics, vertebrate pollinators may play important roles not only in the regeneration and restoration of degraded natural systems but also in the long-term maintenance of both natural and agricultural systems. However, because many of these roles are poorly understood (such as the consequences of reduced fruit/seed sets on recruitment in future generations of plants), community-level empirical data on the pollination





**Figure 4.** Conceptual illustration of experimental results from testing the impact of both pollinator exclusion and pollen supplementation (usually by hand pollination) on plant reproductive success. This illustrates the difference between pollen limitation caused by lack of pollinators or pollen donors in the environment (leading to pollination deficit) and the value of existing open pollination in the given environment. Here we measure the value of existing pollination services to plant reproductive success.

systems of plants and their vertebrate pollinators are urgently needed. Future research should also attempt to identify the habitat preferences of and potential threats to dominant vertebrate pollinator taxa.

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### ■ References

Anderson SH. 2003. The relative importance of birds and insects as pollinators of the New Zealand flora. *NZ J Ecol* 27: 83–94.

Ashman T-L, Knight TM, Steets JA, *et al.* 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85: 2408–21.

Barton K. 2011. MuMIn: multi-model inference. R package version 1.0; <https://cran.r-project.org/web/packages/MuMIn/index.html>. Viewed 2 Jun 2017.

Bernardello G, Anderson GJ, Stuessy TF, and Crawford DJ. 2006. The angiosperm flora of the Archipelago Juan Fernandez (Chile): origin and dispersal. *Can J Bot* 84: 1266–81.

Biesmeijer JC. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313: 351–54.

Borenstein M, Hedges LV, Higgins JPT, and Rothstein HR. 2009. Introduction to meta-analysis. Chichester, UK: John Wiley & Sons.

Bumrungsri S, Harbit A, Benzie C, *et al.* 2008. The pollination ecology of two species of *Parkia* (Mimosaceae) in southern Thailand. *J Trop Ecol* 24: 467–75.

Bumrungsri S, Sripaoraya E, Chongsiri T, *et al.* 2009. The pollination ecology of durian (*Durio zibethinus*, Bombacaceae) in southern Thailand. *J Trop Ecol* 25: 85–92.

Burnham KP and Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. New York, NY: Springer-Verlag.

Carthew SM and Goldingay RL. 1997. Non-flying mammals as pollinators. *Trends Ecol Evol* 12: 104–08.

Cunningham SA. 1991. Experimental-evidence for pollination of *Banksia* spp by nonflying mammals. *Oecologia* 87: 86–90.

Dalsgaard B, Magård E, Fjeldså J, *et al.* 2011. Specialization in plant–hummingbird networks is associated with species richness, contemporary precipitation and Quaternary climate-change velocity. *PLoS ONE* 6: e25891.

Fleming TH and Muchhala N. 2008. Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. *J Biogeogr* 35: 764–80.

Fleming TH, Geiselman C, and Kress WJ. 2009. The evolution of bat pollination: a phylogenetic perspective. *Ann Bot* 104: 1017–43.

Gallai N, Salles JM, Settele J, and Vaissiere BE. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol Econ* 68: 810–21.

Garibaldi LA, Steffan-Dewenter I, Winfree R, *et al.* 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339: 1608–11.

Jenkins CN, Pimm SL, and Joppa LN. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *P Natl Acad Sci USA* 110: E2602–10.

Kato M and Kawakita A. 2004. Plant–pollinator interactions in New Caledonia influenced by introduced honey bees. *Am J Bot* 91: 1814–27.

Kleijn D, Winfree R, Bartomeus I, *et al.* 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat Commun* 6: art7414.

Klein AM, Vaissiere BE, Cane JH, *et al.* 2007. Importance of pollinators in changing landscapes for world crops. *P Roy Soc B-Biol Sci* 274: 303–13.

Knight TM, Steets JA, and Ashman TL. 2006. A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. *Am J Bot* 93: 271–77.

Kunz TH, de Torre EB, Bauer D, *et al.* 2011. Ecosystem services provided by bats. In: Ostfeld RS and Schlesinger WH (Eds). Year in ecology and conservation biology. Hoboken, NJ: Wiley.

Larson BMH and Barrett SCH. 2000. A comparative analysis of pollen limitation in flowering plants. *Biol J Linnean Soc* 69: 503–20.

Lautenbach S, Seppelt R, Liebscher J, and Dormann CF. 2012. Spatial and temporal trends of global pollination benefit. *PLoS ONE* 7: e35954.

Muchhala N and Potts MD. 2007. Character displacement among bat-pollinated flowers of the genus *Burmeistera*: analysis of



- mechanism, process and pattern. *P Roy Soc B-Biol Sci* **274**: 2731–37.
- Muchhala N and Thomson JD. 2010. Fur versus feathers: pollen delivery by bats and hummingbirds and consequences for pollen production. *Am Nat* **175**: 717–26.
- Munguia-Rosas MA, Sosa VJ, Ojeda MM, and De-Nova JA. 2009. Specialization clines in the pollination systems of agaves (Agavaceae) and columnar cacti (Cactaceae): a phylogenetically controlled meta-analysis. *Am J Bot* **96**: 1887–95.
- Nabhan S. 1997. Services provided by pollinators. In: Daily GC (Ed). *Nature's services: societal dependence of natural ecosystems*. Washington, DC: Island Press.
- Ne'Eman G, Jürgens A, Newstrom-Lloyd L, *et al.* 2010. A framework for comparing pollinator performance: effectiveness and efficiency. *Biol Rev* **85**: 435–51.
- Newbold T, Scharlemann JPW, Butchart SHM, *et al.* 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. *P Roy Soc B-Biol Sci* **280**: 20122131.
- Olesen JM and Jordano P. 2002. Geographic patterns in plant–pollinator mutualistic networks. *Ecology* **83**: 2416–24.
- Olesen JM and Valido A. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends Ecol Evol* **18**: 177–81.
- Ollerton J, Winfree R, and Tarrant S. 2011. How many flowering plants are pollinated by animals? *Oikos* **120**: 321–26.
- Ortiz-Hernández YD and Carrillo-Salazar JA. 2012. Pitahaya (*Hylocereus* spp.): a short review. *Comun Sci* **3**: 220–37.
- Potts SG, Biesmeijer JC, Kremen C, *et al.* 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* **25**: 345–53.
- Potts SG, Imperatriz-Fonseca V, Ngo HT, *et al.* 2016. The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. *Nature* **540**: 220–29.
- Pullin AS and Stewart GB. 2006. Guidelines for systematic review in conservation and environmental management. *Conserv Biol* **20**: 1647–56.
- Rader R, Bartomeus I, Garibaldi LA, *et al.* 2016. Non-bee insects are important contributors to global crop pollination. *P Natl Acad Sci USA* **113**: 146–51.
- Regan EC, Santini L, Ingwall-King L, *et al.* 2015. Global trends in the status of bird and mammal pollinators. *Conserv Lett* **8**: 397–403.
- Rosas-Guerrero V, Aguilar R, Marten-Rodriguez S, *et al.* 2014. A quantitative review of pollination syndromes: do floral traits predict effective pollinators? *Ecol Lett* **17**: 388–400.
- Symonds MRE and Moussalli A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol* **65**: 13–21.
- Tripp EA. 2010. Taxonomic revision of *Ruellia* section *Chiropterophila* (Acanthaceae): a lineage of rare and endemic species from Mexico. *Syst Bot* **35**: 629–61.
- Trøjelsgaard K and Olesen JM. 2013. Macroecology of pollination networks. *Glob Ecol Biogeogr* **22**: 149–62.
- Vamosi JC, Knight TM, Steets JA, *et al.* 2006. Pollination decays in biodiversity hotspots. *P Natl Acad Sci USA* **103**: 956–61.
- Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. *J Stat Softw* **36**; doi.org/10.18637/jss.v036.i03.
- Wester P. 2009. Mice pollinators in the Cederberg. The first field observations with photographic documentation of rodent pollination in South Africa. *Veld Flora* **95**: 82–85.
- Whelan CJ, Wenny DG, and Marquis RJ. 2008. Ecosystem services provided by birds. *Ann NY Acad Sci* **1134**: 25–60.
- Zoeller KC, Steenhuisen SL, Johnson SD, and Midgley JJ. 2016. New evidence for mammal pollination of *Protea* species (Proteaceae) based on remote-camera analysis. *Aust J Bot* **64**: 1–7.

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