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

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## Abstract

Vertebrate pollinators are increasingly threatened worldwide, but little is known about the potential consequences of their declines for plants and wider ecosystems. We present the first global assessment of the importance of vertebrate pollinators for zoophilous plant reproduction. Our meta-analysis of 126 experiments on plants revealed that excluding vertebrate pollinators reduced fruit and/or seed production by 63% on average. We found bat-pollinated plants to be more dependent on pollinators than bird-pollinated plants (an average 84% reduction in fruit/seed production when bats were being excluded, compared to 46% when birds were excluded). Dependence on vertebrate pollinators for fruit/seed production was greater in the tropics than at higher latitudes. With such a large potential impact of vertebrate pollinator loss, there is a clear need for prompt, effective conservation action for threatened flower-visiting vertebrate species. More research is needed on how such changes might affect wider ecosystems.

### In a nutshell:

- We present the first global assessment of 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.
- Plants in the tropics and bat-pollinated plants are more reliant on vertebrate pollination than temperate plants and those visited 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.

Animal pollination is necessary in the life cycle of many plant species. It is estimated that 87.5% of the world’s flowering plant species are animal pollinated (Ollerton *et al.* 2011), with 75% of the world’s major crops species benefitting to some degree from animal pollination (Klein *et al.* 2007). Animal pollinated plants are also used for medicines, forage and 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 attention is paid to insect pollinators, the role of vertebrate pollinators is widely recognized. A recent global study revealed that both mammal and bird pollinators are becoming increasingly threatened with extinction over time, with an average of 2.5 species per year having moved one Red List category towards extinction in recent decades (Regan *et al.* 2015). These bird and mammal pollinator declines 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 Nectarinidae (sunbirds), Trochilidae (hummingbirds), Meliphagidae (honeyeaters) and Loridae (lories)(Figure 1a). Birds pollinate about 5.4% of the 960 cultivated plants species for which pollinators are known (Nabhan  S. 1997) and typically pollinate 5% of a region’s flora and 10% of an island flora (Anderson 2003; Kato and Kawakita 2004; Bernardello *et al.* 2006). Amongst 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), found throughout the Neotropics (Fleming and Muchhala 2008)(Figure 1b). Approximately 528 plant species in 67 families and 28 orders worldwide are pollinated by bats (Kunz *et al.* 2011). Non-flying mammals such as primates, rodents and marsupials also are known to visit at least 85 species of plants worldwide (Carthew and Goldingay 1997)(Figure 1c). Flower visitation is reported for 37 species of lizard, mainly island-dwelling species (Olesen and Valido 2003)(Figure 1d).

The declines in abundance and diversity of pollinators has 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, the vast majority 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) documented that crop pollinators are mainly bees, throughout the world. However, vertebrates are known to be 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) amongst others (Bumrungsri *et al.* 2008, 2009).

The best global-scale information available about the degree of dependence on pollinators on wild plants was provided by Ollerton *et al*. (2011). These authors did not use empirical data on plant reproductive success, but 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 any animal pollinators for fruit set, or seed set. Yet this measure of dependence is crucial if we are to understand, perhaps even begin to value, pollinators for their role in wild plant pollination.

Global-scale meta-analyses have been conducted on the extent of pollen limitation (how much 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 (Rosas-Guerrero *et al.* 2014). However, neither of these approaches help to evaluate the importance of current pollination to plant populations, communities and ecosystems.

We present the first global assessment of the overall importance of vertebrate pollinators for plant reproductive 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 globally. We pose two questions:

(1) What is the importance of vertebrate pollinators for plant reproductive success?

(2) How does this importance vary with vertebrate pollinator taxon, taxonomic breadth of flower visitors, geographical region, climatic domain, types of exclusion experiment and measure used for assessing reproductive success.

## A systematic review of vertebrate pollination

We conducted a systematic literature search for studies that looked at the relationship between vertebrate flower visitors and plant sexual reproduction, following standard systematic review protocols (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 grey 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 (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 had no access to 11 relevant articles; and read 378 articles in full to establish their suitability for the analysis (WebFigure 1). We categorized the plants that had been exposed to vertebrate pollinators through open/natural pollination as ‘control’ (i.e. vertebrate pollinators present) and those from which vertebrates were experimentally excluded, by bagging or caging, as ‘treatment’ (i.e. vertebrate pollinators absent). All these 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.

(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 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 and the control group (Borenstein *et al.* 2009). We used a random effects model to calculate a combined effect size across all the studies. We performed a phylogenetically-controlled meta-analysis to control for shared evolutionary history between plants (WebPanel 2 for detailed methodology).

Our analysis then focused on assessing the influence of several ecological, environmental and experimental factors. To investigate the variability of importance for plant reproductive success among the 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 is dependent on the taxonomic breadth of the flower visitors, we classified studies according to whether only vertebrates, or both vertebrates and insects, were observed visiting the flowers and making contact with the flowers' anthers and stigma (i.e. making legitimate pollination visits). We categorized studies as high (pollinated by vertebrate only) and low (pollinated by both vertebrate and invertebrate). We classified studies into one of five regions (North America, South-Central America, Asia, Africa, and Australasia) to determine if the importance of vertebrate pollinators differed among geographical regions.

We classified studies into one of two climatic zones (tropical and extra-tropical) to determine if there was a difference between climate domains. 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 if there was discrepancy between the different manipulations of the study plant. Lastly, we grouped studies according to their measure of assessing reproductive success (fruit production and seed production) to determine if these measures yield different results. We calculated the effect size for each subgroup of the six variables.

We then tested whether these factors significantly predicted the size of effects of excluding vertebrates on plant reproductive success, using linear regression mixed models (question 2 above). Models were built using all possible combinations of these five factors, but not interactions between them; 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.), using the packages 'metafor'(Viechtbauer 2010) and 'MuMIn' (Barton 2011)(WebPanel 2 for detailed methodology).

## Global importance of vertebrate pollinators

We retrieved 69 articles that satisfied the inclusion criteria. As some of these articles investigated multiple plant species, pollinator taxa, or locations, these 69 articles provided 126 separate exclusion comparisons, hereafter referred to as 'studies' (WebPanel 3 for list of articles included). The dataset included studies on 90 plant species (WebTable 1 for list), spanning 50 genera and 35 families: 85 studies investigated bird pollinators, 27 flying mammals and 13 non-flying mammals. Of 126 studies, eleven were from South and Central America, 37 from Africa, 36 from North America, 30 from Australasia and 12 from Asia (Figure 2).

We found a strong negative effect of the exclusion of vertebrate flower visitors on plant reproduction across all studies, translating into an average reduction in fruit and seed production of 63% (CI: -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. Bat-pollinated plants showed an 83% decline (combined lnR), bird-pollinated plants a 46% decline and plants pollinated by rodents a 49% decline in fruit and seed production (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 vertebrates only were subject to a 59% reduction in reproductive success and those pollinated by both vertebrate and invertebrate pollinators had a 61% reduction (Figure 3b).

The effect of excluding vertebrate pollinators on plant reproductive success varied by region (Figure 3c) and across latitudes as well, with reduction of 71% in the tropics and 45% in extra-tropical latitudes (Figure 3d). The size of the negative effect of excluding vertebrate pollinators on plant reproductive success also differed according to the experimental design. The effect 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, we found almost equal proportional reduction – 58% and 61% – in plants where reproductive success was measured in terms of fruit production and seed production, 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 breath of flower visitors and geographic region - all appeared in models with $\Delta$AICc < 6, models for which there is considerable support (Burnham and Anderson 2002). Pollinator taxon was included in all the top-performing models and climatic domain in the best model and in one of the other five models with $\Delta$AICc < 6 (Table 1a). 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 1b). The taxonomic breath 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 impacted by pollinator loss than those dependent on birds or rodents. The majority of plants (69%) that yielded no fruit/seed production at all in vertebrate exclusion experiments were bat-pollinated species. This could be because bats are more effective than birds at moving pollen from one flower to another. Many bat-pollinated plants produce very large amounts of pollen and Muchhala *et al* (2007) showed that at similar visitation rates, bats can transfer up to four times more pollen than birds. Their fur holds and sheds more pollen grains than feathers, making reliance on them a more secure strategy in evolutionary terms. The pollen can be transported over long distances, a feature of pollination ecology that is important for plants such as cacti and agave species, growing at low densities in arid-zones (Fleming *et al.* 2009). It has been suggested that these bat-adapted plants 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 results show that birds and rodents are important pollen vectors for many plants. However, we might 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 – 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 does not include any empirical data on many other known mammalian pollinators such as 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 in the tropics are more dependent on pollinators than those outside the tropics, conceivably due to a higher 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 day-flying 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 removal of one species or group might be expected to have a larger impact on them.  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 measures the degree of pollinator dependence in plants pollinated by vertebrates. This measure reflects the ‘value’ of existing vertebrate pollination, in the current contexts where the experiments took place (Figure 4). It 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. We do not yet have an example of an animal –pollinated plant species that is at risk due to the disappearance of its dominant vertebrate pollinator. Nevertheless, the bleak scenario is plausible at the scale of individual sites. Local extinctions are known to have occurred for bees and hoverflies (Biesmeijer 2006). It is conceivable that the long-term survival of a plant species can be threatened when their vertebrate pollinator communities decline.

As we used exclusion experiments and not hand pollination comparisons, our results do not tell us how much pollen limitation already exists in the open pollinated ‘control’ treatments, due to deficits 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, such as the higher incidence of animal pollinated species in the tropics (Ollerton *et al.* 2011), as well as 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 interactions have 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.

Lastly, resource reallocation at a plant level – where plants are manipulated at a flower or inflorescence scale – could potentially bias the experiment results by overestimating the magnitude of the impact of vertebrate exclusion (Knight *et al.* 2006). However, the lack of significant difference in reproductive success among studies subjected to different experiment manipulation level 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 homogenising methodologies across exclusion experiment studies.

## Implications for human well-being and ecosystems

Our review emphasizes the importance of conserving vertebrate pollinator, particularly in the tropics. Vertebrate pollinator-dependent crops are an important component of our tropical cultivated goods (e.g. pitayas, agave, durian), and declining pollination services may result in substantial revenue loss. Despite the low species richness of bat-pollinated plants, they have substantial economic and social value. The loss of pollinating bats, for instance, would have profound 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 and flying foxes for pollination (Cunningham 1991; Bumrungsri *et al.* 2009) is an extremely popular and economically relevant fruit in South-East Asia.

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

The rapidly disappearing tropical natural systems may also rely on vertebrate pollinators for their regeneration and restoration. However, the role of vertebrate pollinators, particularly bats, for the long-term maintenance of tropical agricultural and natural systems, is poorly understood. For instance, the magnitude of the consequences of a reduction in fruit/seed set on future generations’ recruitment is unknown. Therefore, there is an urgent need for more empirical data on the pollination systems of vertebrate-pollinated plants and their pollinators at the community level. Furthermore, future research should attempt to identify the environmental factors that underpin the distribution of dominant vertebrate pollinators in order to determine their habitat preferences and identify plausible threats.

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## FIGURE CAPTIONS

**Figure 1** Major vertebrate pollinator groups: (a) Ruby-throated Hummingbird (*Archilochus colubris*) (b) Lesser long-nosed bat (*Leptonycteris yerbabuenae*) (c) Four-striped grass mouse (*Rhabdomys pumilio*) (d) Bluetail Day Gecko (*Phelsuma cepediane*)

**Figure 2** Location of studies featuring in our meta-analysis. Locations are based on geographical coordinates given in the publications or they were georeferenced using the provided description of the study area. Increasing circle sizes reflect the number of publication in a specific location

**Figure 3** Changes in reproductive success when vertebrates were excluded expressed in percentages and 95% biased corrected confidence intervals grouped by from top left: pollinator taxon (a), taxonomic breath of flower visitors (b), region (NA: North America; SCA: South-Central America) (c), climatic domain (d), the manipulation level of the exclusion experiment (e), and the measure used to estimate reproductive success (f). 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 shows as a dotted line with 95% confidence interval (grey band).

**Table 1** (a) Explanatory variables included in the linear mixed models predicting the variation in reproductive success of plants in 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 ΔAICc<6.

**Figure 4** A conceptual illustration of results from an experiment 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 service to plant reproductive success.

## IMAGES CREDITS

Figure 1 Credits: (a) “Larry Master” www.masterimages.org , (b) “César Guzmán”, (c) in (Zoeller *et al.* 2016), (d) “Dennis Hansen”

## PANEL_1 : Regional distribution of studies and potential factors affecting the reproductive success of zoophylous plants

**Figure 2** Location of studies featuring in our meta-analysis. Locations are based on geographical coordinates given in the publications or they were georeferenced using the provided description of the study area. Increasing circle sizes reflect the number of publication in a specific location

**Panel_1 table:** Explanatory variables included in the mixed model with sub-categories for each variable.

| Explanatory Variables | Levels | Details |
|---|---|---|
| **Pollinator Taxon** | Bats<br>Birds<br>Rodents<br>Reptiles | |
| **Taxonomic breath of flower visitors** | Low: Vertebrates & Invertebrates<br>High: Vertebrates | The categories show plants legitimately visited by both vertebrate and invertebrate taxa vs plants only legitimately visited by vertebrate taxa |
| **Region** | North America (NA)<br>South-Central America (SCA)<br>Africa<br>Asia<br>Australasia | These represent major biogeographic regions |
| **Climatic domain** | Tropical<br>Extra-Tropical | Categorized according to latitude reported in the study. Tropical <23°27’, Temperate >23°27’ |
| **Experiment manipulation level** | Flower<br>Inflorescence<br>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<br>Seed production | Each category include measures of reproductive success at fruit and seed level respectively |