

1 **Global importance of vertebrate pollinators for plant**
2 **reproductive success: a meta-analysis**

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20

21 **Abstract**

22 Vertebrate pollinators are increasingly threatened worldwide, but little is known about the
23 potential consequences of their declines for plants and wider ecosystems. We present the first
24 global assessment of the importance of vertebrate pollinators for zoophilous plant
25 reproduction. Our meta-analysis of 126 experiments on plants revealed that excluding
26 vertebrate pollinators reduced fruit and/or seed production by 63% on average. We found bat-
27 pollinated plants to be more dependent on pollinators than bird-pollinated plants (an average
28 84% reduction in fruit/seed production when bats were being excluded, compared to 46%
29 when birds were excluded). Dependence on vertebrate pollinators for fruit/seed production
30 was greater in the tropics than at higher latitudes. With such a large potential impact of
31 vertebrate pollinator loss, there is a clear need for prompt, effective conservation action for
32 threatened flower-visiting vertebrate species. More research is needed on how such changes
33 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.

34 Animal pollination is necessary in the life cycle of many plant species. It is estimated that
35 87.5% of the world's flowering plant species are animal pollinated (Ollerton *et al.* 2011),
36 with 75% of the world's major crops species benefitting to some degree from animal
37 pollination (Klein *et al.* 2007). Animal pollinated plants are also used for medicines, forage
38 and materials (Potts *et al.* 2010, 2016; Ollerton *et al.* 2011) and play a crucial role in the
39 long-term maintenance of biodiversity and natural ecosystems. While much attention is paid
40 to insect pollinators, the role of vertebrate pollinators is widely recognized. A recent global
41 study revealed that both mammal and bird pollinators are becoming increasingly threatened
42 with extinction over time, with an average of 2.5 species per year having moved one Red List
43 category towards extinction in recent decades (Regan *et al.* 2015). These bird and mammal
44 pollinator declines are thought to be driven by agricultural expansion, the spread of invasive
45 alien species, hunting and fire (Regan *et al.* 2015).

46 Over 920 species of birds are known to pollinate plants (Whelan *et al.* 2008) including
47 Nectarinidae (sunbirds), Trochilidae (hummingbirds), Meliphagidae (honeyeaters) and
48 Loridae (lories)(Figure 1a). Birds pollinate about 5.4% of the 960 cultivated plants species
49 for which pollinators are known (Nabhan S. 1997) and typically pollinate 5% of a region's
50 flora and 10% of an island flora (Anderson 2003; Kato and Kawakita 2004; Bernardello *et al.*
51 2006). Amongst mammals, bats are the major pollinators, with flower-visiting bats mostly
52 found in two families: Pteropodidae (fruit bats), occurring mainly in Asia and Australia, and
53 Phyllostomidae (leaf-nosed bats), found throughout the Neotropics (Fleming and Muchhala
54 2008)(Figure 1b). Approximately 528 plant species in 67 families and 28 orders worldwide
55 are pollinated by bats (Kunz *et al.* 2011). Non-flying mammals such as primates, rodents and
56 marsupials also are known to visit at least 85 species of plants worldwide (Carthew and
57 Goldingay 1997)(Figure 1c). Flower visitation is reported for 37 species of lizard, mainly
58 island-dwelling species (Olesen and Valido 2003)(Figure 1d).

59 The declines in abundance and diversity of pollinators has raised concerns worldwide,
60 prompting a growing body of research on the extent to which reproductive success of plants
61 is enhanced by flower-visiting animals (Garibaldi *et al.* 2013; Kleijn *et al.* 2015; Rader *et al.*
62 2016). However, the vast majority of these studies focus on insect pollinators visiting crop
63 flowers. The only global review of the degree of dependence of plant reproduction on
64 pollination focused exclusively on crop plants (Klein *et al.* 2007) and it has been used
65 extensively to value pollination services at national and international scales (Gallai *et al.*
66 2009; Lautenbach *et al.* 2012). Klein *et al.* (2007) documented that crop pollinators are
67 mainly bees, throughout the world. However, vertebrates are known to be essential for the
68 reproduction of some economically important crop species such as *Hylocereus undatus*
69 (dragon fruit) (Ortiz-Hernández and Carrillo-Salazar 2012), *Durio* spp.(Durian) and *Parkia*
70 spp. (beans) amongst others (Bumrungsri *et al.* 2008, 2009).

71 The best global-scale information available about the degree of dependence on
72 pollinators on wild plants was provided by Ollerton *et al.* (2011). These authors did not use
73 empirical data on plant reproductive success, but classified plants as either animal-dependent
74 or not, in 42 surveyed plant communities, based on the judgement of ecologists or botanists.
75 To our knowledge, there has never been a global meta-analysis of the extent of dependence of
76 wild plants on any animal pollinators for fruit set, or seed set. Yet this measure of dependence
77 is crucial if we are to understand, perhaps even begin to value, pollinators for their role in
78 wild plant pollination.

79 Global-scale meta-analyses have been conducted on the extent of pollen limitation
80 (how much plant reproductive success can be enhanced by hand pollination) related to local
81 and regional biodiversity patterns (Vamosi *et al.* 2006), and on the identity of important
82 pollinators as they relate to pollination syndromes (Rosas-Guerrero *et al.* 2014). However,

83 neither of these approaches help to evaluate the importance of current pollination to plant
84 populations, communities and ecosystems.

85 We present the first global assessment of the overall importance of vertebrate
86 pollinators for plant reproductive success (fruit and seed production for both crops and wild
87 plants), using quantitative meta-analysis. We focus on vertebrate pollinators because, unlike
88 invertebrates, the conservation status of most pollinating vertebrate species is well
89 characterized at the global scale, and their distributions and diversity are mapped (Jenkins *et*
90 *al.* 2013), making it possible to target and prioritize conservation actions globally. We pose
91 two questions:

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

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

96 **A systematic review of vertebrate pollination**

97 We conducted a systematic literature search for studies that looked at the relationship
98 between vertebrate flower visitors and plant sexual reproduction, following standard
99 systematic review protocols (Pullin and Stewart 2006). Here we describe the literature
100 review, search strategy, the selection of potential explanatory factors and data analysis.

101 ***Literature review and search strategy***

102 We defined a pollinator as a regular flower visitor that transfers pollen between plants,
103 leading to successful pollination and ultimately the production of seeds (Carthew and
104 Goldingay 1997). Pollinator performance can be assessed in two ways: pollination success
105 (contribution to pollen deposited on female flower parts) and plant reproductive success
106 (contribution to seed set) (Ne'Eman *et al.* 2010). We included studies that quantitatively

107 measured the latter, in terms of fruit and seed production. To retrieve these studies, we
108 searched ISI Web of Knowledge, Scopus, CAB Abstract and Agricola databases (from 1900
109 to 2016 inclusive) and relevant grey literature sources (using Google, Google Scholar and
110 Scielo) in both English and Spanish. We used a combination of search terms relating to
111 potential vertebrate pollinators, measures of plant reproductive success, and pollination
112 efficiency and effectiveness (WebPanel 1 for full search string). Our initial search yielded
113 4588 articles.

114 After removing obviously spurious results, we screened the title and abstract of the
115 remaining 467 articles for relevance, resulting in 389 appropriate studies. We had no access
116 to 11 relevant articles; and read 378 articles in full to establish their suitability for the analysis
117 (WebFigure 1). We categorized the plants that had been exposed to vertebrate pollinators
118 through open/natural pollination as ‘control’ (i.e. vertebrate pollinators present) and those
119 from which vertebrates were experimentally excluded, by bagging or caging, as ‘treatment’
120 (i.e. vertebrate pollinators absent). All these studies used either fruit production or seed
121 production as a measure of plant reproductive success (response variables).

122 To be included in the subsequent analysis studies had to meet the following criteria:
123 (1) Involve an experiment where vertebrate pollinators were excluded using a physical barrier
124 such as mesh bags or chicken wire, and plant reproductive success was measured in the
125 presence and absence of vertebrate pollinators.
126 (2) Have replicated pollinator-excluded inflorescences, spatially interspersed with replicated
127 unmanipulated inflorescences.

128 ***Data Analysis***

129 To quantify the importance of vertebrate flower visitors for plant reproductive success
130 (question 1 above), we calculated the natural log of response ratio ($\ln R$) as a standardized
131 effect size for each study. This expresses the proportional difference between the seed and

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

136 Our analysis then focused on assessing the influence of several ecological,
137 environmental and experimental factors. To investigate the variability of importance for plant
138 reproductive success among the vertebrate pollinators, we classified studies according to the
139 vertebrate pollinator taxon (bat, bird, and rodent). We included reptiles only in the overall
140 meta-analysis due to a small sample size ($n = 2$). To determine if the importance of vertebrate
141 pollinators is dependent on the taxonomic breadth of the flower visitors, we classified studies
142 according to whether only vertebrates, or both vertebrates and insects, were observed visiting
143 the flowers and making contact with the flowers' anthers and stigma (i.e. making legitimate
144 pollination visits). We categorized studies as high (pollinated by vertebrate only) and low
145 (pollinated by both vertebrate and invertebrate). We classified studies into one of five regions
146 (North America, South-Central America, Asia, Africa, and Australasia) to determine if the
147 importance of vertebrate pollinators differed among geographical regions.

148 We classified studies into one of two climatic zones (tropical and extra-tropical) to
149 determine if there was a difference between climate domains. We placed each study in one of
150 three categories according to the manipulation level of the exclusion experiment (flower,
151 inflorescence and whole plant) to check if there was discrepancy between the different
152 manipulations of the study plant. Lastly, we grouped studies according to their measure of
153 assessing reproductive success (fruit production and seed production) to determine if these
154 measures yield different results. We calculated the effect size for each subgroup of the six
155 variables.

156 We then tested whether these factors significantly predicted the size of effects of
157 excluding vertebrates on plant reproductive success, using linear regression mixed models
158 (question 2 above). Models were built using all possible combinations of these five factors,
159 but not interactions between them; method for determining reproductive success was added to
160 the model as a random factor. We selected the best models as those with the lowest values of
161 Akaike's Information Criterion (AIC). Statistical analyses were conducted in R (version
162 3.1.2.), using the packages 'metafor'(Viechtbauer 2010) and 'MuMIn' (Barton
163 2011)(WebPanel 2 for detailed methodology).

164 **Global importance of vertebrate pollinators**

165 We retrieved 69 articles that satisfied the inclusion criteria. As some of these articles
166 investigated multiple plant species, pollinator taxa, or locations, these 69 articles provided
167 126 separate exclusion comparisons, hereafter referred to as 'studies' (WebPanel 3 for list of
168 articles included). The dataset included studies on 90 plant species (WebTable 1 for list),
169 spanning 50 genera and 35 families: 85 studies investigated bird pollinators, 27 flying
170 mammals and 13 non-flying mammals. Of 126 studies, eleven were from South and Central
171 America, 37 from Africa, 36 from North America, 30 from Australasia and 12 from Asia
172 (Figure 2).

173 We found a strong negative effect of the exclusion of vertebrate flower visitors on plant
174 reproduction across all studies, translating into an average reduction in fruit and seed
175 production of 63% (CI: -74.87 to -46.76) in the absence of vertebrate pollinators.

176 The effect size differed according to the main type of flower visitor, with bats having the
177 strongest effect on plant reproductive success. Bat-pollinated plants showed an 83% decline
178 (combined lnR), bird-pollinated plants a 46% decline and plants pollinated by rodents a 49%
179 decline in fruit and seed production (Figure 3a). The breadth of flower visitors did not have a

180 significant effect on plant reproductive success when vertebrate pollinators were excluded.
181 Plants pollinated by vertebrates only were subject to a 59% reduction in reproductive success
182 and those pollinated by both vertebrate and invertebrate pollinators had a 61% reduction
183 (Figure 3b).

184 The effect of excluding vertebrate pollinators on plant reproductive success varied by
185 region (Figure 3c) and across latitudes as well, with reduction of 71% in the tropics and 45%
186 in extra-tropical latitudes (Figure 3d). The size of the negative effect of excluding vertebrate
187 pollinators on plant reproductive success also differed according to the experimental design.
188 The effect was higher when single flowers were manipulated (71%), than when
189 inflorescences (42%) and whole-plants (40%) were the experimental unit (Figure 3e)
190 although they did not differ significantly. Additionally, we found almost equal proportional
191 reduction – 58% and 61% – in plants where reproductive success was measured in terms of
192 fruit production and seed production, respectively (Figure 3f).

193 Our model selection process inferred pollinator taxon and climatic domain to be the
194 best predictors of the size of the effect of vertebrate pollination on plant reproductive success.
195 Four moderators - pollinator taxon, climatic domain, taxonomic breath of flower visitors and
196 geographic region - all appeared in models with $\Delta AICc < 6$, models for which there is
197 considerable support (Burnham and Anderson 2002). Pollinator taxon was included in all the
198 top-performing models and climatic domain in the best model and in one of the other five
199 models with $\Delta AICc < 6$ (Table 1a). Pollinator taxon and climatic domain were the only
200 predictors that had a substantial effect on the observed effect sizes, with summed AIC
201 weights > 0.3 (Newbold *et al.* 2013)(Table 1b). The taxonomic breath of flower visitors,
202 geographic region and type of exclusion experiment did not seem to affect the impact of
203 vertebrate exclusion on the reproductive success of animal-pollinated plants.

204 **Factors predicting the importance of vertebrate pollinators**

205 Our results show that bat-pollinated plants are more severely impacted by pollinator
206 loss than those dependent on birds or rodents. The majority of plants (69%) that yielded no
207 fruit/seed production at all in vertebrate exclusion experiments were bat-pollinated species.
208 This could be because bats are more effective than birds at moving pollen from one flower to
209 another. Many bat-pollinated plants produce very large amounts of pollen and Muchhala *et al*
210 (2007) showed that at similar visitation rates, bats can transfer up to four times more pollen
211 than birds. Their fur holds and sheds more pollen grains than feathers, making reliance on
212 them a more secure strategy in evolutionary terms. The pollen can be transported over long
213 distances, a feature of pollination ecology that is important for plants such as cacti and agave
214 species, growing at low densities in arid-zones (Fleming *et al.* 2009). It has been suggested
215 that these bat-adapted plants represent an evolutionary “dead end” (Tripp 2010), where
216 switching to an alternative pollinator becomes unlikely due to their inability to transport the
217 large amount of pollen produced (Muchhala and Thomson 2010).

218 Our results show that birds and rodents are important pollen vectors for many plants.
219 However, we might have underestimated the magnitude of rodents’ impact on plants sexual
220 reproduction for two reasons. First, studies on rodent pollinators were conducted
221 predominantly in South Africa – with some exceptions in Australia – resulting in a wide
222 knowledge gap for other geographical regions. Second, our meta-analysis included only one
223 rodent family, the Muridae (rats and mice). We consider this dataset insufficient to generalize
224 about the global importance of non-flying mammalian pollinators on the reproductive success
225 of animal-pollinated plants, because it does not include any empirical data on many other
226 known mammalian pollinators such as primates (including lemurs), possums and squirrels.

227 The second most important factor that explains the impact of vertebrate pollinators on
228 plant reproductive success was climate domain. Vertebrate-pollinated plants in the tropics are
229 more dependent on pollinators than those outside the tropics, conceivably due to a higher
230 plant specialization near the equator (Olesen and Jordano 2002; Dalsgaard *et al.* 2011;
231 Trøjelsgaard and Olesen 2013). For example, columnar cacti pollination systems range from
232 exclusively bat-pollinated species in the tropics to species with more generalized pollinator
233 interactions involving both day-flying and nocturnal pollinators outside the tropics (Munguia-
234 Rosas *et al.* 2009). When plants are more specialized – that is, visited by a narrower range of
235 pollinators – then removal of one species or group might be expected to have a larger impact
236 on them. Dalsgaard *et al.* (2011) found higher specialization in the tropics among plant-
237 hummingbird pollinator networks.

238 **Pollinator dependence and pollen limitation**

239 Our meta-analysis of exclusion experiments measures the degree of pollinator
240 dependence in plants pollinated by vertebrates. This measure reflects the ‘value’ of existing
241 vertebrate pollination, in the current contexts where the experiments took place (Figure 4). It
242 highlights the importance of vertebrate pollinators for fruit and seed production in natural
243 ecosystems. We recognize that experimental exclusion of vertebrate pollinators depicts a
244 worst-case scenario of total pollinator loss for those plants relying on vertebrate pollen
245 vectors. We do not yet have an example of an animal –pollinated plant species that is at risk
246 due to the disappearance of its dominant vertebrate pollinator. Nevertheless, the bleak
247 scenario is plausible at the scale of individual sites. Local extinctions are known to have
248 occurred for bees and hoverflies (Biesmeijer 2006). It is conceivable that the long-term
249 survival of a plant species can be threatened when their vertebrate pollinator communities
250 decline.

251 As we used exclusion experiments and not hand pollination comparisons, our results do
252 not tell us how much pollen limitation already exists in the open pollinated ‘control’
253 treatments, due to deficits in the pollination services being provided by vertebrates when the
254 experiments took place. The extent of pollen limitation is measured by the enhancement in
255 plant reproductive success that can be achieved by maximizing pollination (by hand), as if
256 pollinator populations had increased. Previous research has shown that pollen limitation is
257 widespread (Larson and Barrett 2000; Ashman *et al.* 2004). Tropical regions may be more
258 prone to pollen limitation than temperate regions, for several reasons, such as the higher
259 incidence of animal pollinated species in the tropics (Ollerton *et al.* 2011), as well as positive
260 correlation between high biodiversity and pollen limitation (Vamosi *et al.* 2006). It is not
261 clear whether this observed pollen limitation is a result of ongoing or previous pollinator
262 declines, or whether it reflects the ecological contexts in which the plant-pollinator
263 interactions have evolved. If the plants in the pollinator exclusion studies analyzed here were
264 already experiencing pollen limitation due to pollinator decline, then the overall negative
265 impact of vertebrate decline on fruit and seed production could be higher than we estimated.

266 Lastly, resource reallocation at a plant level – where plants are manipulated at a flower
267 or inflorescence scale – could potentially bias the experiment results by overestimating the
268 magnitude of the impact of vertebrate exclusion (Knight *et al.* 2006). However, the lack of
269 significant difference in reproductive success among studies subjected to different experiment
270 manipulation level showed that our estimated magnitude of the effect of pollinator loss on
271 plant reproductive success is robust. Nevertheless, future studies could investigate this further
272 by homogenising methodologies across exclusion experiment studies.

273

274 **Implications for human well-being and ecosystems**

275 Our review emphasizes the importance of conserving vertebrate pollinator, particularly
276 in the tropics. Vertebrate pollinator-dependent crops are an important component of our
277 tropical cultivated goods (e.g. pitayas, agave, durian), and declining pollination services may
278 result in substantial revenue loss. Despite the low species richness of bat-pollinated plants,
279 they have substantial economic and social value. The loss of pollinating bats, for instance,
280 would have profound consequences for the reproduction of plants such as agave and
281 columnar cacti, which yield high monetary-valued goods - mezcal and pitayas - in the
282 Mexican agricultural market. Furthermore, Durian (*Durio zibethinus*), which depends on bats
283 and flying foxes for pollination (Cunningham 1991; Bumrungsri *et al.* 2009) is an extremely
284 popular and economically relevant fruit in South-East Asia.

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

288 The rapidly disappearing tropical natural systems may also rely on vertebrate
289 pollinators for their regeneration and restoration. However, the role of vertebrate pollinators,
290 particularly bats, for the long-term maintenance of tropical agricultural and natural systems,
291 is poorly understood. For instance, the magnitude of the consequences of a reduction in
292 fruit/seed set on future generations' recruitment is unknown. Therefore, there is an urgent
293 need for more empirical data on the pollination systems of vertebrate-pollinated plants and
294 their pollinators at the community level. Furthermore, future research should attempt to
295 identify the environmental factors that underpin the distribution of dominant vertebrate
296 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 yerbabuena*) (c) Hairy-footed Gerbil (*Gerbillurus paeba*) (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 breadth 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 shown 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 $\Delta AICc < 6$.

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 Johnson & Pauw (2014) (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 Birds Rodents Reptiles	
Taxonomic breath of flower visitors	Low: Vertebrates & Invertebrates 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) 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', Temperate >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 include measures of reproductive success at fruit and seed level respectively



Figure 1 Major vertebrate pollinator groups: (a) Ruby-throated Hummingbird (*Archilochus colubris*) (b) Lesser long-nosed bat (*Leptonycteris yerbabuena*) (c) Hairy-footed Gerbil (*Gerbillurus paeba*) (d) Bluetail Day Gecko (*Phelsuma cepediane*)

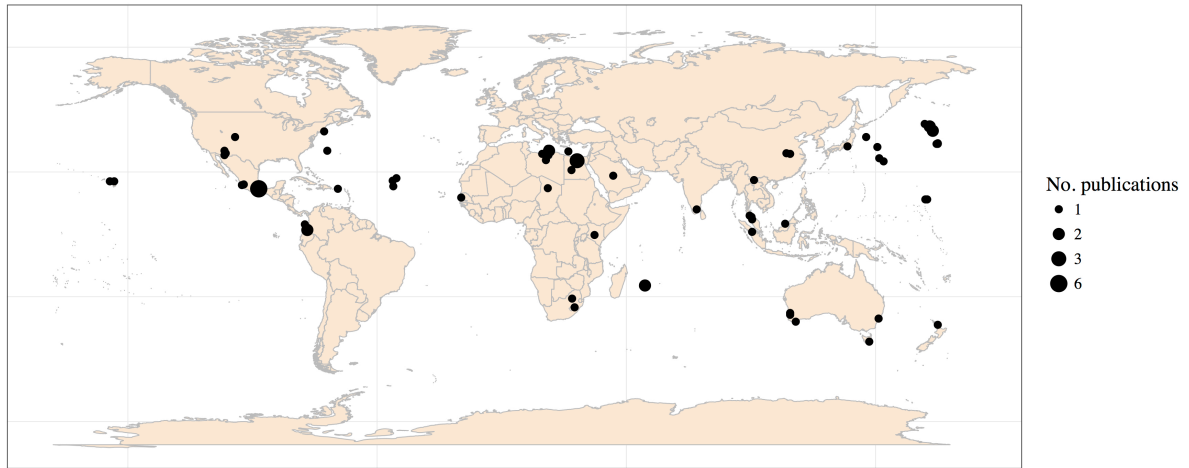


Figure 2 Location of studies featuring in our meta-analysis. Locations are based on geographical coordinates given in the publications or they were georeferenced using the provided description of the study area. Increasing circle sizes reflect the number of publication in a specific location

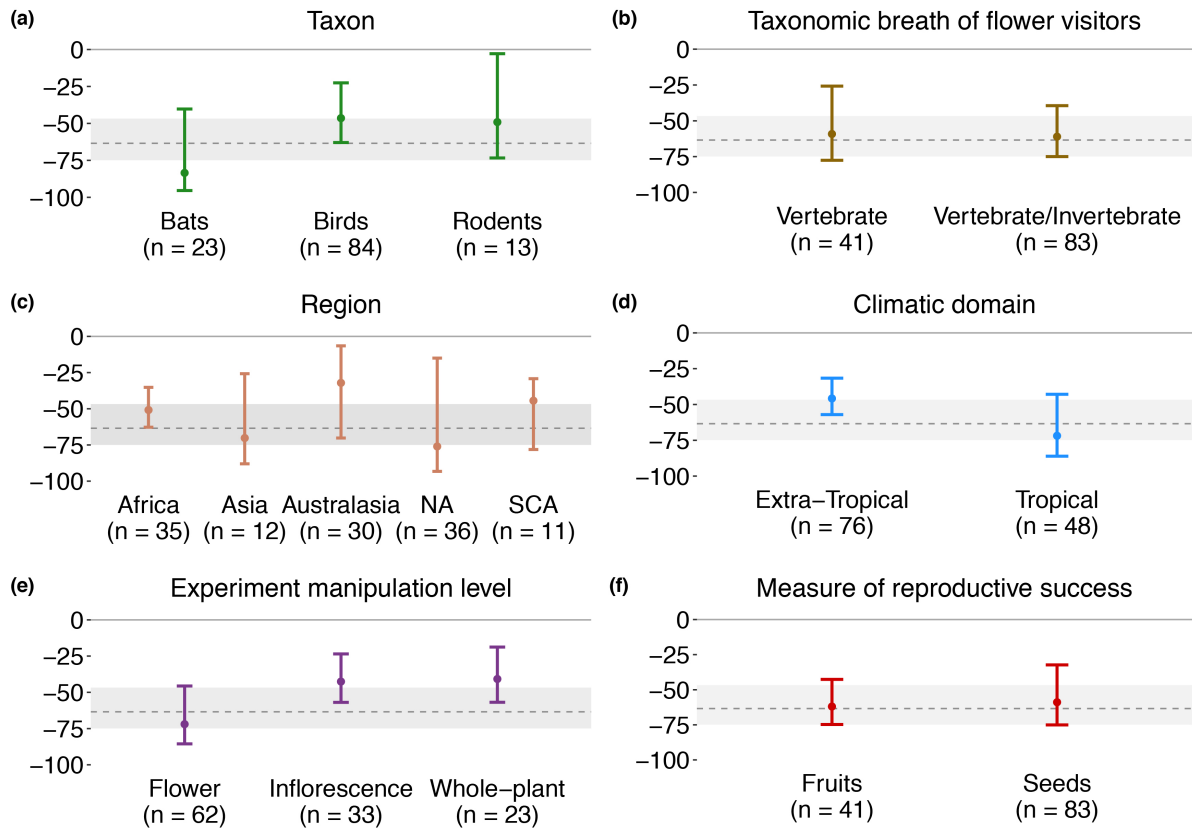


Figure 3 Changes in reproductive success when vertebrates were excluded expressed in percentages and 95% biased corrected confidence intervals grouped by from top left: pollinator taxon (a), taxonomic breath of flower visitors (b), region (NA: North America; SCA: South-Central America) (c), climatic 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 shown as a dotted line with 95% confidence interval (grey band).

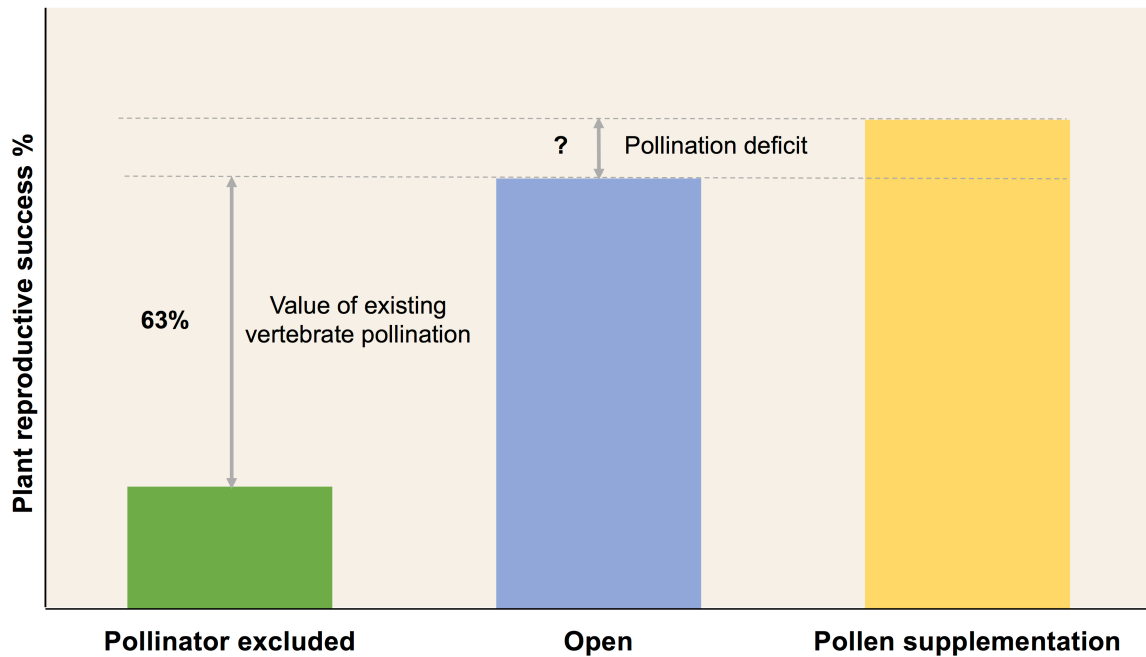


Figure 4 A conceptual illustration of results from an experiment testing the impact of both pollinator exclusion and pollen supplementation (usually by hand pollination) on plant reproductive success. This illustrates the difference between pollen limitation caused by lack of pollinators or pollen donors 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.

F Ratto et al. – Table 1

<i>Predictors in the model</i>								
<i>Model Rank</i>	<i>Climatic Domain</i>	<i>Pollinator Taxon</i>	<i>Taxonomic breath of flower visitors</i>	<i>Region</i>	<i>d.f.</i>	<i>AICc</i>	<i>ΔAICc</i>	<i>weight</i>
1	+	+			9	550	0.00	0.52497
2	+	+	+		10	551	1.46	0.25327
3		+			8	553	3.53	0.08978
4		+		+	12	554	4.46	0.05657
5		+	+		9	555	5.80	0.02884
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; *d.f.* represents degrees of freedom

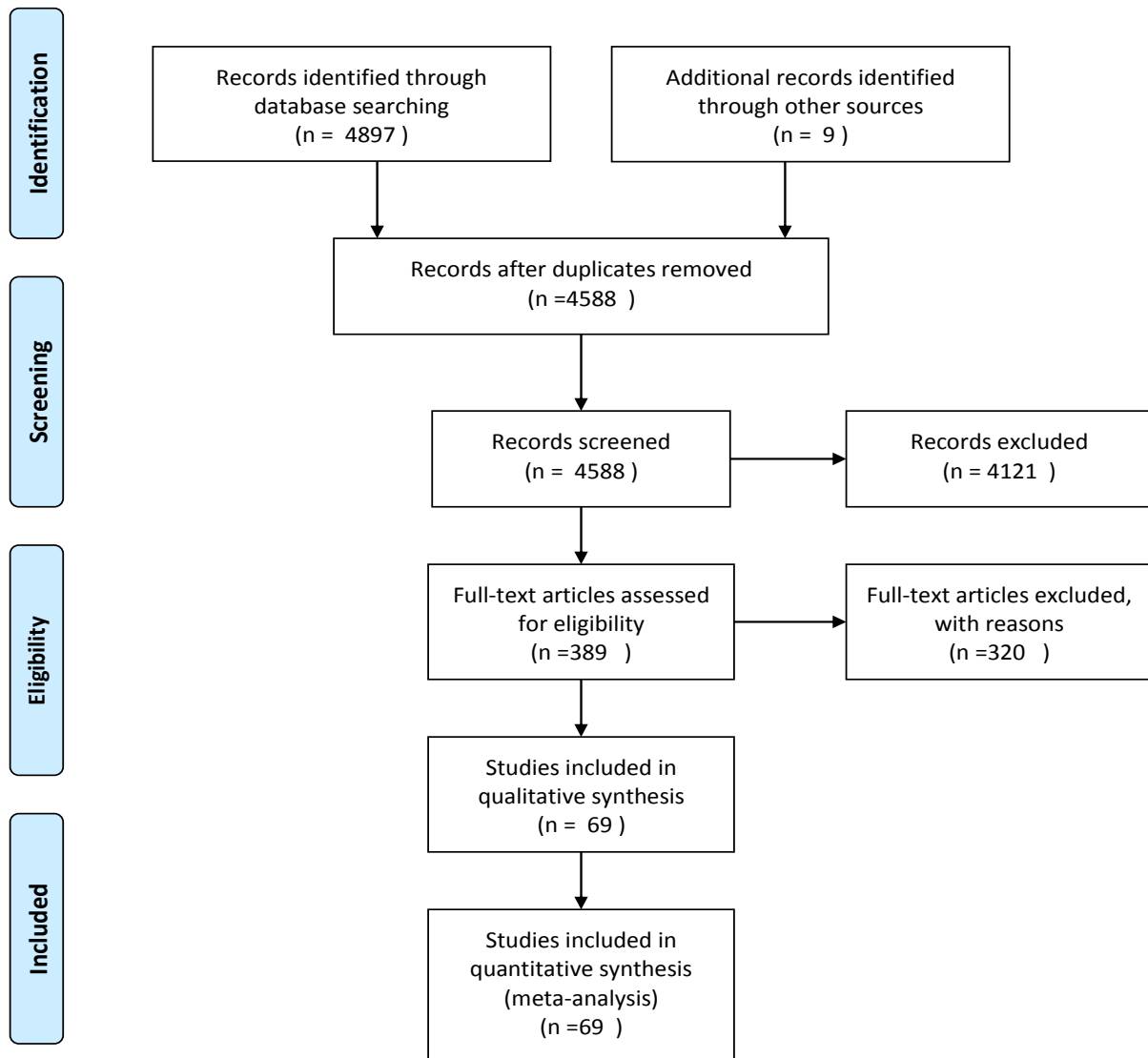
<i>Variable</i>	<i>Sum of AICc weight</i>
Pollinator taxon	1.00
Climatic Domain	0.82
Taxonomic breath of flower visitors	0.29
Geographical Region	0.06

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

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 $\Delta AICc < 6$.

SUPPORTING INFORMATION

F Ratto *et al.* - Supporting Information



WebFigure 1. Preferred Reporting Items for Systematic Review and Meta-Analysis flowchart (PRISMA), summarising the sequence of information gathering and selection. Available at <http://prisma-statement.org/PRISMAStatement/FlowDiagram.aspx>

F Ratto *et al.* - Supporting Information

WebPanel 1: Search Strings for all databases

First searches were performed in March 2015. A final search was performed in February 2016. After this, we sought unpublished data from researchers and checked databases alerts until mid 2016.

ENGLISH SEARCH

First search performed on Web of Science on 02/03/2015

pollinat* OR "flower*" OR visit* OR "pollen deposit*"

AND

bird* OR bats OR bat OR avian OR chiroptera* OR lorikeet* OR flowerpecker* OR honeyeater* OR whiteeye* OR warbler* OR hummingbird* OR sunbird* OR "diurnal pollinator*" OR nectariv* OR "nocturnal pollinator*" OR "nectar feeding" OR "flying fox*" OR lemur* OR possum* OR lizard* OR squamata OR iguania OR gekkota OR gecko* OR rodent* OR gerbil OR mammal* OR Acrobatidae OR Aotidae OR Atelidae Burramyidae OR Callaeatidae OR Callithricidae OR Cardinalidae OR Cebidae OR Cercopithecidae OR Cheirogaleidae OR Coerebidae OR Coliidae OR Columbidae OR Corvidae OR Cotingidae OR Cracidae OR Cricetidae OR Dasyuridae OR Daubentoniidae OR Dicaeini OR Didelphidae OR Emberizidae OR Fringillidae OR Furnariidae OR Galagidae OR Giraffidae OR Gliridae OR Icteridae OR Irenidae OR Lemuridae OR Lepilemuridae OR Loriinae OR Lorisidae OR Lybiidae OR Macroscelididae OR Marsupialia OR Meliphagidae OR Mimidae OR Mohoidae OR Muridae OR Mystacinidae OR Nectariniidae OR Nectariniini OR Paridae OR Parulidae OR Petauridae OR Phalangeridae OR Phelsuma OR Phoeniculidae OR Platacanthomyidae OR Pycnonotidae OR Phyllostomidae OR Picidae OR Ploceidae OR Procyonidae OR Promeropidae OR Pseudocheiridae OR Psittacidae OR Pteropodidae OR Ptilocercidae OR Scincidae OR Scincomorpha OR Sciuridae OR Strigopidae OR Sturnidae OR Sylvidae OR Tarsipedidae OR Thinocoridae OR Thraupidae OR Trochilidae OR Troglodytidae OR Tupaiidae OR Turdidae OR Tyrannidae OR Vespertilionidae OR Vireonidae OR Viverridae OR Zosteropidae

AND

Pollen OR fruit* OR seed*

Returned **2527** results

First search performed on CAB Abstract on 02/03/2015

This database accepts the same format as Web of Science so the search was the same as the original
pollinat* OR "flower*" OR visit* OR "pollen deposit*"

AND

bird* OR bats OR bat OR avian OR chiroptera* OR lorikeet* OR flowerpecker* OR honeyeater* OR whiteeye* OR warbler* OR hummingbird* OR sunbird* OR "diurnal pollinator*" OR nectariv* OR "nocturnal pollinator*" OR "nectar feeding" OR "flying fox*" OR lemur* OR possum* OR lizard* OR squamata OR iguania OR gekkota OR gecko* OR rodent* OR gerbil OR mammal* OR Acrobatidae OR Aotidae OR Atelidae Burramyidae OR Callaeatidae OR Callithricidae OR Cardinalidae OR Cebidae OR Cercopithecidae OR Cheirogaleidae OR Coerebidae OR Coliidae OR Columbidae OR Corvidae OR Cotingidae OR Cracidae OR Cricetidae OR Dasyuridae OR Daubentoniidae OR Dicaeini OR Didelphidae OR Emberizidae OR Fringillidae OR Furnariidae OR Galagidae OR Giraffidae OR Gliridae OR Icteridae OR Irenidae OR Lemuridae OR Lepilemuridae OR Loriinae OR Lorisidae OR Lybiidae OR Macroscelididae OR Marsupialia OR Meliphagidae OR Mimidae OR Mohoidae OR Muridae OR Mystacinidae OR Nectariniidae OR Nectariniini OR Paridae OR Parulidae OR Petauridae OR Phalangeridae OR Phelsuma OR Phoeniculidae OR Platacanthomyidae OR Pycnonotidae OR Phyllostomidae OR Picidae OR Ploceidae OR Procyonidae OR Promeropidae OR Pseudocheiridae OR Psittacidae OR Pteropodidae OR Ptilocercidae OR Scincidae OR Scincomorpha OR Sciuridae OR Strigopidae OR Sturnidae OR Sylvidae OR Tarsipedidae OR Thinocoridae OR Thraupidae OR Trochilidae OR Troglodytidae OR Tupaiidae OR Turdidae OR Tyrannidae OR Vespertilionidae OR Vireonidae OR Viverridae OR Zosteropidae

AND

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Web panel 2: Meta-analysis of vertebrate pollination

Search strategy

To determine whether the systematic review strategy was robust and unbiased, we quantitatively assessed the agreement between authors on study selection and exclusion. We calculated a Kappa statistic using a subset of the selected articles (50 publications per author, for two authors). We obtained a kappa value of 0.55, which corresponds to “fair agreement” and is within the acceptable range. Publication bias, the tendency for studies reporting significant results to be overrepresented in the published literature (in this case studies where the exclusion of vertebrate pollinators had a significant effect on fruit and seed set), was minimised in the systematic review process by searching for grey literature and contacting authors active in the field (see section on “Systematic review”). In addition, we estimated Rosenberg fail-safe number, which is the number of non-significant unpublished studies required to eliminate a significant overall effect size (Rosenberg 2005). We detected no evidence for publication bias, as the fails-safe number (101018) was much larger than the critical value (640).

We recorded the statistics – i.e. means, standard deviations (SD) and sample sizes – of fruit /seed production for both “control” and “treatment”. When data was presented only in figures, we extracted the data using DataThief software (Tummers 2006). We contacted the lead authors of the studies that had incomplete data, and abandoned these studies if we could not obtain the missing statistics. We could not tease apart the relative contributions from vertebrates and insects for studies using a very fine mesh; our analysis therefore excluded such studies unless we were certain that the insects were not important.

We also excluded studies that were pseudoreplicated *sensu* Hurlbert’s (1984), and only included studies that had replicated pollinator-excluded inflorescences spatially interspersed with replicated unmanipulated inflorescences. This is critical because studies that had low within-study variance arising as an artefact of the pseudo-replicated design, could have their importance inflated in a conventional meta-analytic model, which weights studies by the inverse of within-study variance (Halme *et al.* 2010). The incidence of pseudoreplicated studies nevertheless was low ($n = 7$). For studies that presented multiple years of data sampling at the same site, we used the most recent data to control for non-independence of temporal data (Gurevitch & Hedges 1993). (Hedges *et al.* 1999).

Effect size

The response ratio is calculated as: $\ln R = \ln(x_1) - \ln(x_2)$, where x_1 is the mean of reproductive success when vertebrate pollinators were absent (treatment) and x_2 is the mean of reproductive success when vertebrate pollinators were present (control). The use of natural logarithm linearizes the metric, treating changes in nominator and denominators equally and producing a normalised sampling distribution (Hedges *et al.* 1999). A response ratio cannot be calculated if the means of reproductive success were equal to zero ($n=16$ in our dataset). We therefore conducted preliminary trials following Molloy (2008), whereby a constant value (e.g. 1, 0.1, 0.001, 0.0001) was added to all estimates of reproductive success before calculating the response ratio. We concluded that adding 1 to all estimates had a negligible impact on the overall effect size. The meta-analysis was weighted by the inverse of the sample variance, which accounts for differences in sampling effort across studies.

Phylogenetic meta-analysis

To explore whether shared evolutionary history between species affected the effect size, which can violate statistical assumptions of independence (Gurevitch *et al.* 2001), we performed a phylogenetic meta-analysis using phyloMeta 1.3. The fit of the traditional and phylogenetic models were compared using Akaike Information Criterion (AIC) as in Wolowski (2014) and the former was favoured as it had better model fit. Therefore, we proceeded with the traditional meta-analysis (Lajeunesse 2011). We constructed a phylogenetic tree for plant species in our dataset by binding species into a published phylogeny (Zanne *et al.* 2014) as polytomies at the genus level, using the R package pez (Pearse *et al.* 2015). The tree was then pruned to remove any species not in our dataset (See Appendix S3 for

F Ratto *et al.* - Supporting Information**WebPanel 3: List of studies included in the final analysis**

- 1
Aizen, M.A. (2005). Breeding system of *Tristerix corymbosus* (Loranthaceae), a winter-flowering mistletoe from the southern Andes. *Aust. J. Bot.*, 53, 357-361.
2.
Anderson, S.H. (2003). The relative importance of birds and insects as pollinators of the New Zealand flora. *New Zeal J Ecol*, 27, 83-94.
3.
Arena, G., Symes, C.T. & Witkowski, E.T.F. (2013). The birds and the seeds: opportunistic avian nectarivores enhance reproduction in an endemic montane aloe. *Plant Ecol.*, 214, 35-47.
4.
Arizaga, S., Ezcurra, E., Peters, E., de Arellano, F.R. & Vega, E. (2000). Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert. II. The role of pollinators. *Am. J. Bot.*, 87, 1011-1017.
5.
Aslan, C.E. (2015). Pollination of the Endangered Arizona Hedgehog Cactus (*Echinocereus arizonicus*). *Am. Midl. Nat.*, 173, 61-72.
6.
Aslan, C.E., Zavaleta, E.S., Tershy, B., Croll, D.O.N. & Robichaux, R.H. (2014). Imperfect Replacement of Native Species by Non-Native Species as Pollinators of Endemic Hawaiian Plants. *Conserv. Biol.*, 28, 478-488.
7.
Aximoff, I.A. & Freitas, L. (2010). Is pollen removal or seed set favoured by flower longevity in a hummingbird-pollinated *Salvia* species? *Ann. Bot.*, 106, 413-419.
8.
Biccard, A. & Midgley, J.J. (2009). Rodent pollination in *Protea nana*. *S. Afr. J. Bot.*, 75, 720-725.
9.
Brown, M., Downs, C.T. & Johnson, S.D. (2009). Pollination of the red hot poker *Kniphofia caulescens* by short-billed opportunistic avian nectarivores. *S. Afr. J. Bot.*, 75, 707-712.
10.
Brown, M., Downs, C.T. & Johnson, S.D. (2010). Pollination of the red-hot poker *Kniphofia laxiflora* (Asphodelaceae) by sunbirds. *S. Afr. J. Bot.*, 76, 460-464.
11.
Bumrungsri, S., Harbit, A., Benzie, C., Carmouche, K., Sridith, K. & Racey, P. (2008). The pollination ecology of two species of *Parkia* (Mimosaceae) in southern Thailand. *J. Trop. Ecol.*, 24, 467-475.
12.
Bumrungsri, S., Sripaoraya, E., Chongsiri, T., Sridith, K. & Racey, P.A. (2009). The pollination ecology of durian (*Durio zibethinus*, Bombacaceae) in southern Thailand. *J. Trop. Ecol.*, 25, 85-92.
13.
Carpenter, F.L. (1976). Plant pollinator interactions in Hawaii: pollination energetics of *Metrosideros collina* (Myrtaceae). *E.S.A.*, 57 (6), 1125-1144.
14.
Casas, A., Valiente-Banuet, A., Rojas-Martinez, A. & Davila, P. (1999). Reproductive biology and the process of domestication of the columnar cactus *Stenocereus stellatus* in central Mexico. *Am. J. Bot.*, Apr 1999. v. 86 (4), 534-542.
15.
Celebrezze, T. & Paton, D.C. (2004). Do introduced honeybees (*Apis mellifera*, Hymenoptera) provide full pollination service to bird-adapted Australian plants with small flowers? An experimental study of *Brachyloma ericoides* (Epacridaceae). *Austral Ecol.*, 29, 129-136.
- 16.

F Ratto et al. - Supporting Information**WebTable 1. List of Plant species included in the analysis**

Plant Species	Plant family	Crop or Wild
<i>Aloe greatheadii</i> var. <i>davyana</i>	Xanthorrhoeaceae	Wild
<i>Agave Macroacantha</i>	Agavaceae	Wild
<i>Aloe divaricata</i>	Liliaceae	Wild
<i>Aloe marlothii</i>	Xanthorrhoeaceae	Wild
<i>Aloe peglerae</i>	Xanthorrhoeaceae	Wild
<i>Aloe plicatilis</i>	Xanthorrhoeaceae	Wild
<i>Alseuosmia macrophylla</i>	Alseuosmiaceae	Wild
<i>Banksia attenuata</i>	Proteaceae	Wild
<i>Banksia brownii</i>	Proteaceae	Wild
<i>Banksia ericifolia</i>	Proteaceae	Wild
<i>Banksia integrifolia</i>	Proteaceae	Wild
<i>Banksia littoralis</i>	Proteaceae	Wild
<i>Banksia menziesii</i>	Proteaceae	Wild
<i>Banksia prionotes</i>	Proteaceae	Wild
<i>Banksia spinulosa</i>	Proteaceae	Wild
<i>Billbergia horrida</i>	Bromeliaceae	Wild
<i>Brachyloma ericoides</i>	Epacridaceae	Wild
<i>Carnegiea gigantea</i>	Cactaceae	Wild
<i>Ceiba pentandra</i>	Bombaceae	Crop/Wild
<i>Clermontia hawaiiensis</i>	Campanulaceae	Wild
<i>Clermontia montis-loa</i>	Campanulaceae	Wild
<i>Clermontia parviflora</i>	Campanulaceae	Wild
<i>Colchicum coloratum</i>	Colchicaceae	Wild
<i>Colchicum hantamense</i>	Colchicaceae	Wild
<i>Colchicum scabromarginatum</i>	Colchicaceae	Wild
<i>Delphinium nelsoni</i>	Ranunculaceae	Wild
<i>Durio grandiflorus</i>	Bombaceae	Wild
<i>Durio oblongus</i>	Bombaceae	Wild
<i>Durio zibethinus</i>	Bombaceae	Crop
<i>Echinocereus arizonicus</i>	Cactaceae	Wild
<i>Encholirium vogelii</i>	Bromeliaceae	Wild
<i>Eriobotrya japonica</i>	Rosaceae	Wild
<i>Eucalyptus globulus</i>	Myrtaceae	Wild
<i>Fouquieria splendens</i>	Fouquieriaceae	Wild
<i>Geniostoma ligustrifolium</i>	Loganiaceae	Wild
<i>Hylocereus undatus</i>	Cactaceae	Crop
<i>Ipomopsis aggregata</i>	Pomeliaceae	Wild
<i>Isertia laevis</i>	Rubiaceae	Wild
<i>Kniphofia caulescens</i>	Asphodelaceae	Wild
<i>Kniphofia laxiflora</i>	Asphodelaceae	Wild