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1 **The worldwide importance of honey bees as pollinators in natural habitats**

2

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24 **Abstract.** The western honey bee (*Apis mellifera*) is the most frequent floral visitor of crops
25 worldwide, but quantitative knowledge of its role as a pollinator outside of managed habitats is
26 largely lacking. Here we use a global data set of 80 published plant-pollinator interaction
27 networks as well as pollinator effectiveness measures from 34 plant species to assess the
28 importance of *A. mellifera* in natural habitats. *Apis mellifera* is the most frequent floral visitor in
29 natural habitats worldwide, averaging 13% of floral visits across all networks (range 0 – 85%),
30 with 5% of plant species recorded as being exclusively visited by *A. mellifera*. For 33% of the
31 networks and 49% of plant species, however, *A. mellifera* visitation was never observed,
32 illustrating that many flowering plant taxa and assemblages remain dependent on non-*A.*
33 *mellifera* visitors for pollination. *Apis mellifera* visitation was higher in warmer, less variable
34 climates and on mainland rather than island sites, but did not differ between its native and
35 introduced ranges. With respect to single-visit pollination effectiveness, *A. mellifera* did not
36 differ from the average non-*A. mellifera* floral visitor, though it was generally less effective than
37 the most effective non-*A. mellifera* visitor. Our results argue for a deeper understanding of how
38 *A. mellifera*, and potential future changes in its range and abundance, shape the ecology,
39 evolution, and conservation of plants, pollinators, and their interactions in natural habitats.
40

41 **1. Introduction**

42 The western honey bee (*Apis mellifera* L.) provides highly valued pollination services for a wide
43 variety of agricultural crops [1], and ranks as the most frequent single species of pollinator for
44 crops worldwide [2]. A long history of domestication and intentional transport of *A. mellifera* by
45 humans has resulted in its current cosmopolitan distribution that includes all continents except
46 Antarctica and many oceanic islands. Given the advanced state of knowledge concerning this
47 species and its role in agriculture, it seems surprising that the importance of *A. mellifera* as a
48 pollinator in natural habitats remains poorly understood [3–5].

49 Clarifying the role of *A. mellifera* as a pollinator in natural habitats is important for
50 several reasons. First, animal-mediated pollination represents a vital ecosystem service [6,7]; an
51 estimated 87.5% of flowering plant species are pollinated by animals [8]. Quantification of the
52 pollination services provided by the cosmopolitan, super-generalist *A. mellifera* [9] will thus
53 provide insight into the functioning of many terrestrial ecosystems. Second, non-*A. mellifera*
54 pollinators are declining as a result of habitat loss, habitat degradation, and other factors
55 including pesticides, pathogens, parasites, and climate change [10–12]. In cases where *A.*
56 *mellifera* populations can withstand these perturbations, the degree to which they replace
57 pollination services formerly performed by extirpated pollinators [13–17] deserves scrutiny.
58 Third, recent increases in the mortality of managed *A. mellifera* colonies in some regions of the
59 world [11,18] may extend to populations of free-living *A. mellifera* [19–21]. Threats to *A.*
60 *mellifera* populations could thus affect the reproduction and population dynamics of plants in
61 natural areas, with potential shifts in the composition of plant assemblages [22,23], and in turn,
62 the ecosystem services (e.g., carbon sequestration, soil retention) that these plants provide.
63 Lastly, where introduced populations of *A. mellifera* attain high densities [24–26], they may

64 compete with other pollinators [27–29] or compromise plant reproductive success [30]. These
65 phenomena are of broad ecological, evolutionary, and conservation importance, but to our
66 knowledge, there currently exists no global quantitative synthesis of the numerical importance of
67 *A. mellifera* as a pollinator in natural ecosystems in their native or introduced ranges.

68 Here, we address questions concerning the importance of *A. mellifera* by exploiting a
69 recent trend in pollination research—the documentation of community-level, plant-pollinator
70 interaction networks (hereafter “pollination networks”). Quantitative pollination network studies
71 document the identity and frequency of each type of pollinator visiting each plant species within
72 a locality [31]. Network data are used to address a variety of questions (e.g., [32–34]), but key
73 for our goals here, they provide an underutilised opportunity to gauge the importance of *A.*
74 *mellifera* in natural habitats, particularly because the role of *A. mellifera* has rarely been the
75 focus of these studies [25,26,35]. We compiled a database of 80 quantitative pollination
76 networks from natural habitats worldwide. To further assess the importance of *A. mellifera* as a
77 pollinator, we also compiled data on per-visit pollination effectiveness of *A. mellifera* relative to
78 other floral visitors from studies of 34 plant species.

79 Our meta-analyses address three interrelated lines of inquiry concerning the ecological
80 importance of *A. mellifera* in natural habitats. (i) What proportions of floral visits are contributed
81 by *A. mellifera* foragers to individual networks worldwide, and to individual plant species within
82 networks? (ii) What environmental factors govern the relative contribution of *A. mellifera* to
83 community-level floral visitation, and do levels of visitation differ between its native and
84 introduced ranges? (iii) Given that pollination network studies often use visitation frequency as a
85 proxy for pollinator importance (e.g., [36]), how does the per-visit pollination effectiveness of *A.*
86 *mellifera* compare to the effectiveness of other floral visitors?

87

88 **2. Material and Methods**

89 *(a) Database for network synthesis*

90 We used two approaches to compile our dataset of pollination networks. First, we performed a
91 literature search using the ISI Web of Science database with the search terms [pollinat*
92 network], [pollinat* web], and [pollinat* visit* community], examining all studies available as of
93 August 2016. Second, we downloaded all pollination network data from the Interaction Web
94 Database of the National Center for Ecological Analysis and Synthesis website
95 (<http://data.nceas.ucsb.edu/>) and the Web of Life Ecological Networks Database
96 (<http://www.web-of-life.es/>) available as of December 2014. We collected all studies and plant-
97 pollinator interaction network datasets that documented visitation frequency (i.e., number of
98 individuals observed contacting flowers or number of floral contacts per unit time) between each
99 pair of plant and pollinator taxa. We defined a network as the sum of recorded plant-pollinator
100 interactions in all sites from a single study that fell within a 50-km diameter circle, regardless of
101 the number of sites that constitute the network. Sites within the same study that are separated by
102 more than 50 km were treated as separate networks. When we encountered networks from
103 different studies that were less than 50 km apart, we excluded those that sampled a smaller
104 number of plant or pollinator taxa, or documented fewer interactions. We chose 50 km as a
105 threshold to avoid over-representing studies that include many networks within a locality (e.g.,
106 [32,37]), while keeping separate those networks originating from distinct localities within the
107 same geographic region, such as networks documented on different islands from the same
108 archipelago (e.g., [38]). When studies included multiple years of data collection at the same sites
109 using the same protocols, we pooled data from all study years into a single network.

110 All networks retained for analyses met the following criteria. The data were collected in
111 natural habitats, here defined as largely unmanaged assemblages of plant species where the
112 identities and relative abundances of plant species are not purposefully manipulated (thus
113 excluding, for example, agricultural, urban, and experimental habitats; see the electronic
114 supplementary material, table S1-1). Each network consisted of observations on five or more
115 plant species when pooled across the sites making up an individual study. All networks
116 documented a broad range of pollinators; studies with a narrow taxonomic scope (e.g. social
117 bees, bird pollinators with incidental observations of *A. mellifera*) or those that *a priori* excluded
118 *A. mellifera* were not included. We also excluded networks from sites that were known to be
119 heavily influenced by *A. mellifera* colonies stocked for adjacent agricultural pollination. Thus,
120 our estimates of the numerical importance of *A. mellifera* may be conservative with respect to
121 mosaic landscapes where natural habitats are intermixed with agricultural fields with managed *A.*
122 *mellifera* colonies [39]. We did not *a priori* exclude networks from localities outside of the
123 presumed climatic niche of *A. mellifera* [40], or where *A. mellifera* was never introduced. In all,
124 we obtained 80 networks (see the electronic supplementary material, table S1-1) from 60 peer-
125 reviewed studies and three graduate theses [37,41,42]. While lacking coverage in some regions
126 (figure 1), our dataset attains geographical coverage comparable to other recent studies that
127 examine the importance and conservation of pollinators at a global scale [2,12,43].

128 For each network, we obtained the following data from their associated publications or
129 from study authors when data were not available from publications: latitude, longitude, and final
130 year of data collection. When these data were not available and authors could not be reached, we
131 used the approximate geographical centre of the study locality listed in the publication, and the
132 year of publication as the last year of data collection. We defined the native status of *A. mellifera*

133 based on [40] and [44]; although we caution that the native status of *A. mellifera* in the British
134 Isles and northern Europe remains unresolved. We also extracted the following information from
135 each study, when available: the proportion of all floral visits contributed by *A. mellifera* (in two
136 networks this metric was estimated by calculating the proportion of the total visitation rate,
137 summed across plant species, contributed by *A. mellifera*; see the electronic supplementary
138 material, table S1-1), the proportion of plant species receiving at least one visit by *A. mellifera*,
139 and the rank of *A. mellifera* with respect to both the proportion of all floral visits contributed and
140 the proportion of plant species visited. Additionally, we used geographic information system
141 (GIS) analysis to obtain elevation data and bioclimatic variables ([45],
142 <http://www.worldclim.org>) for each network based on its GPS coordinates. We also categorised
143 each network as being on an island or a mainland; the latter category includes all continents as
144 well as islands > 200,000 km², namely Great Britain (United Kingdom), Honshu (Japan), and
145 Greenland. For studies for which raw data were not available, we contacted the corresponding
146 authors to request data, or, in cases where data could not be shared, requested summary statistics
147 on plant-pollinator interactions. When raw numeric data were unavailable from the publication
148 or from authors, we used ImageJ to extract data from figures, where possible (see the electronic
149 supplementary material, table S1-1). Due to the different methodologies and data reported by
150 each study, not all of the abovementioned variables were extracted from all networks.

151 *(b) Frequency and patterns of Apis mellifera visitation*

152 We calculated the global mean and median proportion of all floral visits contributed by *A.*
153 *mellifera*, using each network as a data point (n = 80 networks). Calculations were repeated after
154 excluding networks that documented no *A. mellifera* visits, in order to examine the role of *A.*
155 *mellifera* specifically in localities where it occurs. Additionally, we examined plant species in 41

156 networks in which (i) *A. mellifera* was present, and (ii) data on the number of visits contributed
157 by *A. mellifera* and non-*A. mellifera* visitors were available for each plant species. Across these
158 networks, we calculated the mean and median proportion of plant species that were (i) not visited
159 by *A. mellifera*, (ii) numerically dominated by *A. mellifera* (i.e., *A. mellifera* contributing $\geq 50\%$
160 of all floral visits), and (iii) visited exclusively by *A. mellifera*. Because plant species receiving
161 few visits overall may tend to have extreme values of proportion of visits by *A. mellifera*, we
162 restricted the analysis to 834 plant taxa with ≥ 10 visits recorded. Additionally, to aid in
163 visualizing the distribution of the numerical importance of *A. mellifera* across plant species, we
164 also calculated for each network the proportion of plant species that fell into each of 10 bins with
165 respect to the proportion of visits contributed by *A. mellifera* (range = 0 - 1; bin width = 0.1). We
166 then constructed a histogram by calculating the mean and 95% confidence intervals of each bin
167 across all 41 networks.

168 (c) *Environmental correlates of Apis mellifera visitation frequency*

169 We constructed multiple regression models to identify environmental factors that best explain
170 variation in the visitation frequency of *A. mellifera* among networks. The response variable in
171 these regression models was the proportion of all floral visits in each network contributed by *A.*
172 *mellifera*. Due to the strongly non-normal distribution of the data as well as the presence of
173 numerous zeroes, we performed zero-inflated, multiple beta regression using package *gamlss*
174 [46] in R (version 3.3.1 [47]). One network located above the Arctic Circle [48] was excluded
175 from this analysis because bioclimatic data were unavailable (hence, $n = 79$). We note that the
176 exclusion of networks with no *A. mellifera* visits did not qualitatively alter our results (see the
177 electronic supplementary material, table S2-1).

178 To incorporate bioclimatic variables [45], we first performed principal components
179 analysis (PCA) to avoid constructing models with highly collinear terms. We performed one
180 PCA for the 11 variables measuring temperature, and a separate PCA for the eight bioclimatic
181 variables measuring precipitation (see the electronic supplementary material, table S3). We then
182 reduced bioclimatic variables to the first two principal components of the temperature and
183 precipitation variables, which accounted for 86% and 89% of the variance, respectively. We
184 constructed a full model containing the following explanatory variables, without interactions:
185 latitude, longitude, altitude, land category (mainland versus island), and the first two principal
186 components of temperature and precipitation variables. We used R package *glmulti* [49] to
187 generate all possible permutations of the full model on which to perform zero-inflated, multiple
188 beta regression; and then selected the best-fit model using corrected Akaike's Information
189 Criterion (AICc) scores. We also used the best-fit environmental model to address whether the
190 proportion of visits contributed by *A. mellifera*, after accounting for environmental factors, was
191 affected by (i) *A. mellifera* native status (native versus introduced), and (ii) year of data
192 collection.

193 *(d) Pollination effectiveness*

194 We used two approaches to compile data on pollination effectiveness. First, we performed a
195 literature search using the ISI Web of Science database with the search term [pollinat*] in
196 combination with one of the following terms: [efficiency], [effectiveness], ["pollen deposition"],
197 ["seed set"], ["fruit set"], or ["pollination biology of"], examining all studies available as of
198 August 2016. Second, we examined the literature cited sections of each of the studies found
199 through the first approach for additional studies not captured in the initial literature search. Data
200 points in this analysis consist of studies of focal plant species that compared *A. mellifera* and at

201 least one other pollinator taxon with respect to pollen deposition, seed set, or fruit set resulting
202 from single floral visits [50]. We used seed set data whenever available because it is most
203 directly related to plant reproductive fitness [51], fruit set when seed counts were unavailable,
204 and pollen deposition when measures of seed and fruit set were unavailable. When raw data were
205 unavailable, we used ImageJ to extract data from figures. In all, we obtained 32 studies reporting
206 single-visit pollination effectiveness data for 34 plant species, spanning 22 plant families (see the
207 electronic supplementary material, table S1-2). Of these, 18 plant species in 15 families were
208 undomesticated, and 16 plant species in 7 families were grown in agricultural settings. For each
209 plant species considered, we divided the pollination effectiveness of *A. mellifera* by the mean
210 effectiveness of all other visitors studied to obtain the relative effectiveness of *A. mellifera*. We
211 also divided *A. mellifera* effectiveness by that of the most effective non-*A. mellifera* visitor. We
212 then used one-sample *t*-tests to examine whether the pollination effectiveness of *A. mellifera*
213 differed significantly from that of the average, or the most effective, non-*A. mellifera* floral
214 visitor.

215 **3. Results**

216 *(a) Frequency and patterns of Apis mellifera visitation*

217 *Apis mellifera* was recorded in 88.89% (16/18) of the pollination networks from its native range
218 and in 61.29% (38/62) of the networks from its introduced range (figure 1; see also the electronic
219 supplementary material, table S1-1). Across all networks, the mean proportion of visits
220 contributed by *A. mellifera* was 12.64% (figure 2a; median = 1.56%); among the 54 networks in
221 which *A. mellifera* was recorded, this proportion increased to 18.72% (median = 8.13%). *Apis*
222 *mellifera* was the most frequent floral visitor in 17 networks and visited the most plant species in
223 14 networks.

224 Across 41 networks in which *A. mellifera* was present and the proportion of visits to each
225 plant species by *A. mellifera* was recorded, we found a positively skewed distribution of the
226 proportion of visits contributed by *A. mellifera* to individual plant species (figure 2b). *Apis*
227 *mellifera* was the only documented visitor to 4.48% of plant taxa (median = 0%, range = 0%–
228 66.67%) and contributed the majority ($\geq 50\%$) of visits to 17.28% of plant taxa (median = 0%,
229 range = 0%–100%). However, *A. mellifera* went unrecorded as a visitor to nearly half (49.38%)
230 of plant taxa (median = 47.22%, range = 0%–100%). The overall patterns we report remain
231 similar when we expand the analysis to include plant species where fewer than 10 visits were
232 recorded (i.e., those species that might be expected to produce extreme values; see the electronic
233 supplementary material, figure S4-1).

234 (b) *Environmental correlates of Apis mellifera visitation frequency*

235 The best-fit zero-inflated, multiple beta regression model of environmental variables revealed
236 that the proportion of visitation by *A. mellifera* in networks increases with the first principal
237 component of temperature variables, with higher values corresponding to higher overall
238 temperature, higher isothermality, lower annual temperature range and less seasonality (table 1;
239 further statistics are reported in the electronic supplementary material, table S2-2). *Apis mellifera*
240 visitation was also higher in mainland than island networks (table 1), but we found no effect of
241 native status on the proportion of visits contributed by *A. mellifera* (table 1). Nevertheless, it is
242 noteworthy that eight of the ten networks with the highest *A. mellifera* visitation came from
243 introduced range localities. In five of these networks [25,26,35,37,52], *A. mellifera* accounted for
244 more than half of the total visits recorded. Lastly, we found that study year was unrelated to the
245 proportion of *A. mellifera* visits in natural habitats worldwide (table 1).

246 (c) *Pollination effectiveness*

247 A literature survey of single-visit pollinator effectiveness data revealed that *A. mellifera* does not
248 differ from the average non-*A. mellifera* floral visitor, with the effectiveness of *A. mellifera*
249 averaging 90.1% that of other visitors (one sample *t*-test, $t_{33} = 1.25$, $P = 0.22$; figure 3a). On the
250 other hand, *A. mellifera* was generally less effective than the most effective non-*A. mellifera*
251 visitor, with *A. mellifera* effectiveness averaging 75.6% that of the top non-*A. mellifera* visitor
252 (one sample *t*-test, $t_{33} = 3.28$, $P = 0.0024$; figure 3b). The relative effectiveness of *A. mellifera*
253 did not differ between non-agricultural ($n = 18$) and agricultural ($n = 16$) plant species, either
254 when compared with the average non-*A. mellifera* visitor (figure 3a; Welch's two-sample *t*-test,
255 $t_{30.75} = 0.44$, $P = 0.67$) or when compared with the top non-*A. mellifera* visitor (Figure 3b;
256 Welch's two-sample *t*-test, $t_{24.46} = 0.96$, $P = 0.34$).

257

258 **4. Discussion**

259 While *A. mellifera* is acknowledged to be a widely introduced [53,54], super-generalist [55,56]
260 species that occupies a central role in many pollination networks [9,24,57], our study presents
261 the first quantitative synthesis demonstrating the importance of *A. mellifera* as a floral visitor in
262 natural habitats at a global scale. Despite considerable variance in its local abundance (figures 1,
263 2a), *A. mellifera* appears to be the most important single species of pollinator across the natural
264 systems studied, owing to its wide distribution, generalist foraging behaviour, and competence as
265 a pollinator. The numerical dominance of *A. mellifera* is further underscored by our finding that,
266 in a subset of 68 networks with sufficient taxonomic resolution, the average proportion of floral
267 visits contributed by *A. mellifera* was more than double that contributed by all bumble bee
268 species (Apidae: *Bombus*) combined (*A. mellifera* mean = 13.79%, *Bombus* mean = 6.26%, $P =$

269 0.055; see the electronic supplementary material, S5). Given that *Bombus* is the only other
270 pollinator genus comparable to *A. mellifera* with respect to both local importance and global
271 distribution [7,9,54], it seems unlikely that any other single pollinator species contends with *A.*
272 *mellifera* with respect to worldwide numerical importance in natural habitats. That said, with
273 appropriate data, it would be instructive to compare the worldwide importance of *A. mellifera*
274 with that of other cosmopolitan and widely introduced pollinator taxa, such as the hover fly
275 (Syrphidae) species *Syrphus ribesii* (L.) and *Eristalis tenax* (L.) [58], or with that of pollinator
276 taxa that numerically dominate pollination networks in key biomes, such as stingless bees
277 (Apidae: Meliponini) in tropical ecosystems [24,59].

278 We quantify for the first time that despite the global distribution and often high local
279 abundance of *A. mellifera*, it is a frequent visitor to only a minority of insect-pollinated plant
280 species (figure 2b). Even in networks where more than half of all visits are contributed by *A.*
281 *mellifera*, ca. 16% of the plant species, on average, receive fewer than 10% of their visits from *A.*
282 *mellifera* (see the electronic supplementary material, figure S4-2). Although individual *A.*
283 *mellifera* colonies are known to forage extensively on only a fraction of the plant species
284 available at any given time [60], the skewed pattern of floral visitation documented here (figure
285 2b) is nonetheless surprising given that *A. mellifera* has the greatest diet breadth of any pollinator
286 species studied [55,56]. This result underscores the importance of maintaining robust, diverse
287 assemblages of non-*A. mellifera* pollinators to provide pollination services for the majority of
288 flowering plant species in natural habitats.

289 From a different perspective, *A. mellifera* often numerically dominated a portion of the
290 plant species in a given network. While non-*A. mellifera* pollinators may find such plant taxa
291 inherently unprofitable in some cases, they may be displaced by *A. mellifera* via interference or

292 exploitative competition in other cases (e.g., [61]). In instances where *A. mellifera* numerically
293 dominates plant species belonging to the “core” of a pollination network (i.e., the subset of
294 locally abundant plant species that are visited by a variety of pollinator taxa [31,62]), they may
295 exert a strong influence on co-occurring pollinators [39]. While this phenomenon has been
296 documented in the native range of *A. mellifera* [39], it may be especially consequential in its
297 introduced range, where plant species numerically dominated by *A. mellifera* presumably
298 coevolved with, and supply food for, native pollinators [63]. Our results thus suggest that *A.*
299 *mellifera* may disrupt interactions between plants and other pollinators in many areas, including
300 localities where *A. mellifera* attains only modest abundance (see the electronic supplementary
301 material, S4-3).

302 Our analyses of how *A. mellifera* visitation correlates with environmental variables
303 revealed significant associations with climatic and geographical predictors, but no effect of
304 native status (table 1). Release from pathogens and parasites can contribute to the success of
305 introduced species [64], but this mechanism may be less important for *A. mellifera* given that
306 major pathogens and parasites have spread worldwide with the trafficking of managed colonies
307 [17, 18]. Nevertheless, the majority of networks with the highest proportion of *A. mellifera* visits
308 come from introduced range localities. Researchers have long recognised the potential for
309 introduced *A. mellifera* to impact co-occurring pollinators (e.g., [29,65]) and plants (e.g., [66]) at
310 the local scale. Numerical dominance of introduced *A. mellifera* may also lead to
311 homogenisation [67] of pollinator faunas, and of pollination networks, across large spatial scales.
312 Accordingly, further studies are needed to clarify why *A. mellifera* reaches high levels of
313 abundance in some parts of its introduced range (e.g., [25,26]) and how variation in its local
314 abundance affects native plants and pollinators.

315 Despite recent increases in the mortality of managed *A. mellifera* colonies in Europe and
316 North America [68,69], our analyses found that study year was unrelated to the proportion of *A.*
317 *mellifera* visits in natural habitats worldwide (table 1). Agents responsible for increased
318 mortality in managed colonies can affect wild or feral *A. mellifera* colonies [19–21], but ongoing
319 research suggests that unmanaged *A. mellifera* populations may be better able to cope with
320 parasites and pathogens compared to managed populations [70]. In our pollination networks, the
321 degree to which *A. mellifera* foragers originated from managed versus unmanaged colonies
322 likely varies. However, in one network numerically dominated by *A. mellifera* [37], genetic
323 testing indicated that the majority of *A. mellifera* foragers were derived from feral, Africanised
324 colonies [71].

325 Most network studies equate visitation frequency with the importance of a particular
326 pollinator, but pollination biologists usually define pollinator importance as the per-visit
327 effectiveness multiplied by visitation frequency [50]. Our survey of pollinator effectiveness
328 estimates involving *A. mellifera* (figure 3) suggests that the average importance of *A. mellifera* as
329 a pollinator is satisfactorily estimated by its visitation frequency. However, given that *A.*
330 *mellifera* exhibits poor effectiveness at pollinating certain plant taxa [57,72], additional studies
331 are needed to demonstrate the importance of *A. mellifera* as a pollinator of any particular plant
332 species. Repeated visits by abundant pollinators, for example, can damage flowers and reduce
333 reproductive success [73]. On plant species where *A. mellifera* attains high visitation rates,
334 negative relationships between visitation frequency and plant reproductive fitness may occur
335 [39] and are worthy of investigation [74].

336 As a numerically abundant, super-generalist pollinator, *A. mellifera* may influence the
337 fitness [27] and behaviour [63] of competing pollinators, enhance [15] or reduce [30] plant

338 reproduction, and facilitate the spread of non-native weeds [75] and pathogens [76]. Given the
339 ecological importance of *A. mellifera*, changes in its distribution and abundance may impact the
340 evolutionary trajectory of co-occurring animal-pollinated plants [77] and pollinators. Our study
341 quantifies the current importance of *A. mellifera* in natural communities, and also highlights the
342 vital importance of non-*A. mellifera* pollinators, whose key role in maintaining ecosystem
343 function cannot be replaced by *A. mellifera*. Our study underscores the need for more data on
344 how *A. mellifera*, and potential changes in its range and population size, shape the ecology,
345 evolution, and conservation of plants, pollinators, and their interactions in natural habitats on
346 local and global scales.

347

348 **Data Accessibility**

349 Project data are made available in the electronic supplementary material.

350

351 **Author Contributions**

352 The study was conceived by K.-L.J.H., D.A.H. and J.R.K. Data were collected by K.-L.J.H.,
353 J.M.K., M.A, and J.R.K. Data analysis was conducted by K.-L.J.H. All authors contributed to the
354 writing of the manuscript and gave final approval for publication.

355

356 **Competing Interests**

357 We have no competing interests.

358

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377

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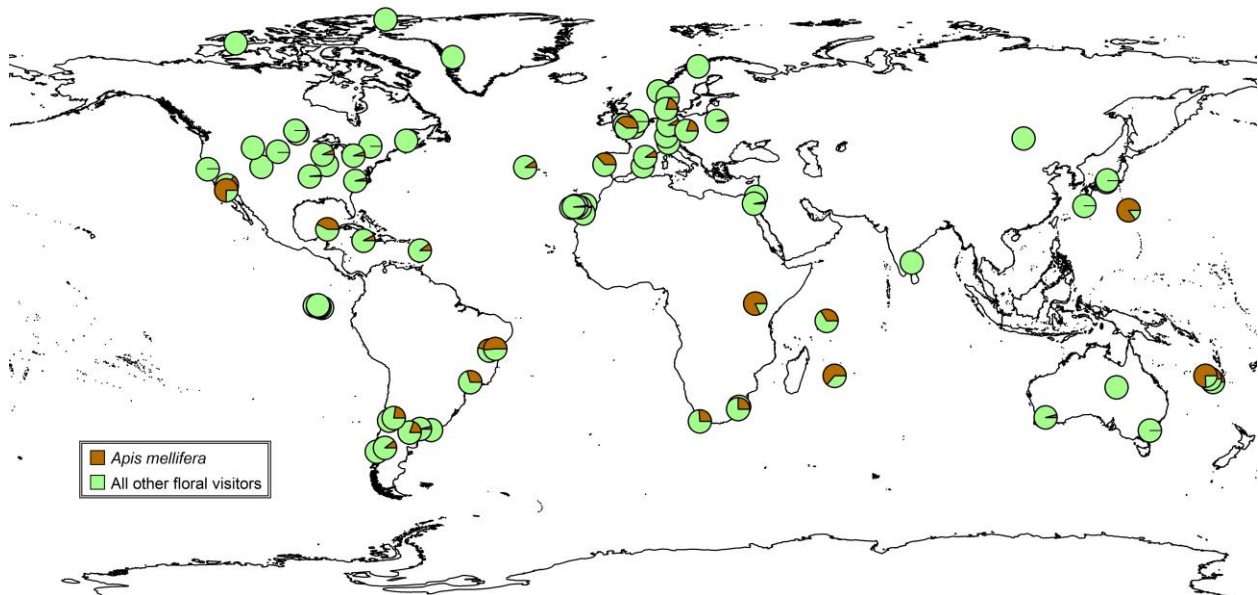
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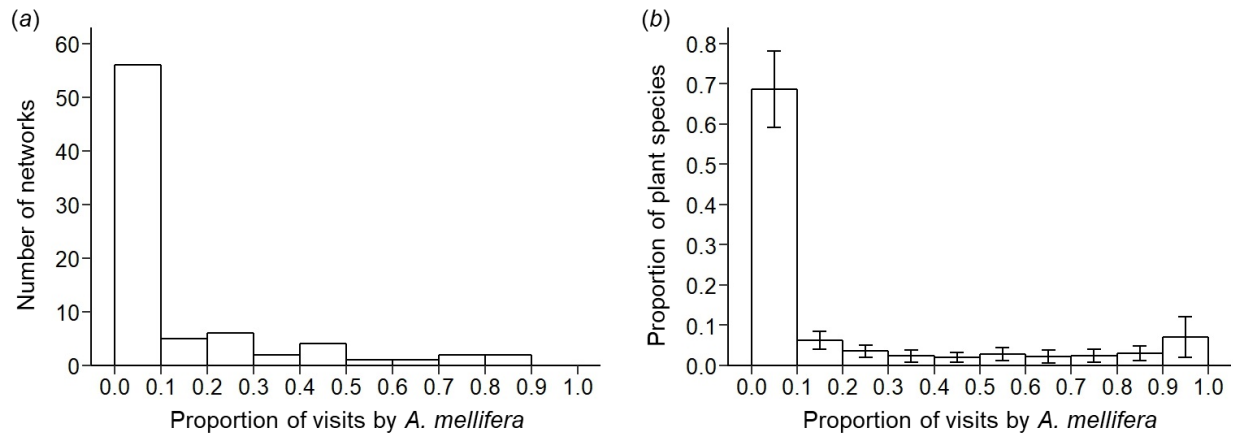
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576 **Figures and Tables**



577

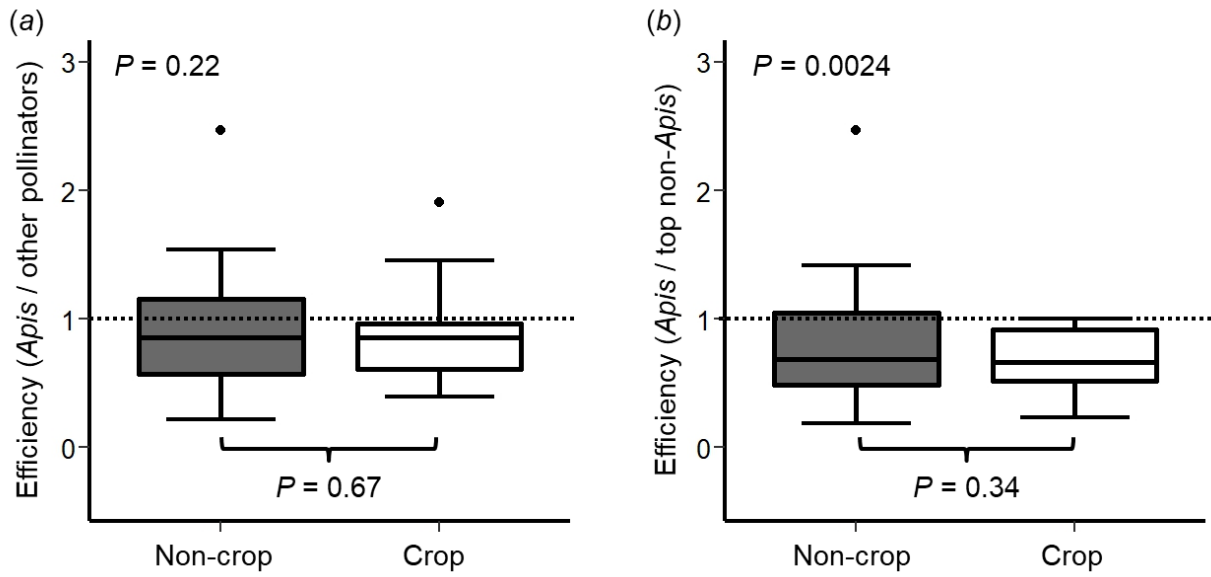
578 **Figure 1.** Proportion of all floral visits contributed by the western honey bee (*Apis mellifera*) in
579 80 plant-pollinator interaction networks in natural habitats worldwide. *Apis mellifera* is generally
580 considered a native species in Europe, the Middle East, and Africa; and introduced elsewhere.
581



582

583 **Figure 2.** The distribution of the proportion of floral visits contributed by the western honey bee
 584 (*Apis mellifera*) (a) across 80 plant-pollinator interaction networks in natural habitats worldwide,
 585 and (b) across plant species in 41 networks where *A. mellifera* was documented and where the
 586 numbers of visits to each plant species by *A. mellifera* and other floral visitors were available.
 587 Bars show the mean value of each bin across networks; whiskers show 95% confidence intervals.

588



589

590 **Figure 3.** Average single-visit pollination effectiveness of the western honey bee (*Apis*
 591 *mellifera*) relative to (a) the mean effectiveness of all other floral visitor taxa, and (b) the
 592 effectiveness of the most effective non-*A. mellifera* taxon. *P*-values at the bottom-centre of each
 593 panel reflect two-sample *t*-test comparisons of *A. mellifera* relative effectiveness in non-crop (n =
 594 18) versus crop (n = 16) plant species; *P*-values at the top-left reflect one-sample *t*-test
 595 comparisons of *A. mellifera* to the mean or most effective non-*A. mellifera* pollinator after
 596 combining data from non-crop and crop plant species. Boxes show central 50% of data and
 597 median; whiskers show quartiles $\pm 1.5 \times$ interquartile range, or most extreme values of data,
 598 whichever is closest to median. Points indicate extreme values.

599

600 **Table 1.** The best-fit, zero-inflated, multiple beta regression models relating environmental
601 variables to the proportion of visits contributed by the western honey bee (*Apis mellifera*) in
602 plant-pollinator interaction networks worldwide (n = 79 networks where bioclimatic variables
603 were available). Temperature PC1 increases with overall temperature and isothermality, and
604 decreases with temperature seasonality and annual range. Models examining the influence of *A.*
605 *mellifera* native status and last year of study on proportion of visits by *A. mellifera* were
606 constructed by adding these two variables to the best-fit model of environmental variables.

607

Model (Δ AICc) / Variable	Estimate	t value	P value
Bes-fit environmental model ("BFEM") (Δ AICc = 0)	Cox-Snell $R^2 = 0.19$		
Temperature PC1	$\mu = 0.39$	4.24	< 0.001
Land category (mainland = 1, island = 0)	$\mu = 0.81$	2.27	0.026
BFEM + <i>Apis</i> native status (Δ AICc = 1.39)	Cox-Snell $R^2 = 0.20$		
Temperature PC1	$\mu = 0.41$	4.31	< 0.001
Land category (mainland = 1, island = 0)	$\mu = 0.74$	2.04	0.045
<i>Apis</i> native status (native = 1, introduced = 0)	$\mu = 0.31$	0.99	0.33
BFEM + last study year (Δ AICc = 2.25)	Cox-Snell $R^2 = 0.19$		
Temperature PC1	$\mu = 0.39$	4.75	< 0.001
Land category (mainland = 1, island = 0)	$\mu = 0.81$	2.26	0.026
Last study year (years CE)	$\mu = 0.0056$	0.31	0.76
BFEM + <i>Apis</i> native status + last study year (Δ AICc = 3.75)	Cox-Snell $R^2 = 0.20$		
Temperature PC1	$\mu = 0.41$	4.95	< 0.001
Land category (mainland = 1, island = 0)	$\mu = 0.74$	2.03	0.046
<i>Apis</i> native status (native = 1, introduced = 0)	$\mu = 0.30$	0.96	0.34
Last study year (years CE)	$\mu = 0.0041$	0.23	0.82

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