

**Gradual replacement of wild bees by honeybees
in flowers of the Mediterranean Basin over the last 50 years**

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1 **Abstract**

2 Current evidence for generalized pollinator decline largely originates from mid-latitude
3 regions in North America and Europe. Unacknowledged geographical heterogeneity in
4 pollinator trends, in combination with geographical biases in pollinator studies, can
5 produce distorted extrapolations and limit understanding of pollinator responses to
6 environmental changes. In contrast to the severe declines experienced in some well-
7 investigated European and North American regions, honeybees seem to have increased in
8 recent years over large expanses of the Mediterranean Basin. Since honeybees can have
9 negative impacts on wild bees, the hypothesis was formulated that if honeybees are
10 actually increasing in the Mediterranean Basin, then an extensive, biome-wide alteration
11 in the composition of bee pollinator assemblages may be currently underway there,
12 involving a progressive reduction in the importance of wild bees as pollinators. This
13 hypothesis was tested using a large data sample gathered from published investigations on
14 the composition of bee pollinators of wild and cultivated plants conducted between 1963-
15 2017 in the Mediterranean Basin. Over this period, honeybee colonies increased
16 exponentially and wild bees were gradually replaced by honeybees in flowers of wild and
17 cultivated plants. Mean estimated proportion of wild bees at flowers roughly
18 quadruplicated that of honeybees at the beginning of the period considered, the
19 proportions of both groups becoming roughly similar fifty years later. The Mediterranean
20 Basin is a world biodiversity hotspot for wild bees and wild bee-pollinated plants, and the
21 ubiquitous rise of honeybees to dominance as pollinators could in the long run undermine
22 the diversity of plants and wild bees, as well as their mutualistic relationships in the
23 region.

24 *“El sur también existe”*

25 Joan Manuel Serrat, singer and songwriter

26

27 **Introduction**

28 The structure and dynamics of ecological communities can vary tremendously across
29 biomes and continents. Critical elements of ecological knowledge will thus be closely tied
30 to the particular location where it is attained, and attempts at generalizations which are
31 based on limited, spatially biased ecological data may produce distorted or erroneous
32 inferences (Martin et al. 2012, Culumber et al. 2019). Unawareness of geographical
33 sampling biases has been pointed out as one possible cause of erroneous extrapolations
34 related to the notions of “pollinator decline” and “pollination crisis” (Ghazoul 2005,
35 Archer 2014, Herrera 2019, Jamieson et al. 2019), two topics that have recently elicited
36 considerable academic and popular interest because of the importance of animal
37 pollination for the reproduction of many wild and crop plants (Ollerton et al. 2014,
38 Senapathi et al. 2015, Breeze et al. 2016, Ollerton 2017). Evidence for the widely held
39 view of a generalized pollinator decline is strongly biased geographically, as it mostly
40 originates from a few mid-latitude regions in Europe and North America (Rodger et al.
41 2004, Ghazoul 2005, Winfree et al. 2009, Archer 2014, Hung et al. 2018, Nicholson and
42 Egan 2019). Mounting evidence indicates, however, that pollinator declines are not
43 universal; that the sign and magnitude of temporal trends in pollinator abundance may
44 differ among pollinator groups, continents or regions; and that taxonomic and
45 geographical biases in pollinator studies in combination with unrecognized patterns of
46 geographical or taxonomic differences in pollinator trends are bound to limit a realistic
47 understanding of pollinator responses to environmental changes and the causal

48 mechanisms involved (Aizen and Harder 2009, Potts et al. 2010, Hofmann et al. 2018,
49 Herrera 2019, Jamieson et al. 2019, Thomson 2019).

50 Even for well-studied social bees, data supporting a general decline are
51 geographically biased (Archer et al. 2014, Ollerton 2017, Hung et al. 2018). For example,
52 in thoroughly studied North America and mid-western Europe the number of honey bee
53 colonies has experienced severe declines, but the trend is apparently reversed in the less
54 investigated areas of southernmost Europe, where honeybees seems to be increasing over
55 large expanses in the last few decades (Aizen and Harder 2009: Fig. S1, Potts et al. 2010,
56 vanEngelsdorp and Meixner 2010). Honeybees can have strong negative impacts on wild
57 bee populations in both natural and anthropogenic scenarios (Shavit et al. 2009, Lindström
58 et al. 2016, Torné-Noguera et al. 2016, Herrera 2019, Ropars et al. 2019, Valido et al.
59 2019). I thus formulated the hypothesis that, if the abundance of managed honeybees has
60 been actually increasing in the Mediterranean Basin over the last decades, then a profound
61 biome-wide alteration in the composition of bee pollinator assemblages could be currently
62 underway there, involving a progressive replacement of wild bees by honeybees in
63 flowers. This paper verifies this hypothesis using data from a large sample of published
64 investigations on the composition of bee pollinators of wild and cultivated plants,
65 conducted during the last 50 years throughout the Mediterranean Basin. Results of this
66 study stress the importance of broadening the geographical scope of current investigations
67 on pollinator trends, while at the same time issue a warning on the perils of uncritically
68 importing to Mediterranean ecosystems honeybee conservation actions specifically
69 designed for the contrasting situations that prevails in temperate-climate European or
70 North American countries.

71 **Material and methods**

72 *The data*

73 The literature on floral biology, pollination ecology, plant-pollinator interactions and crop
74 pollination was searched for field studies conducted during 1960-2019 in the
75 Mediterranean Basin and providing quantitative data on the relative abundance of
76 honeybees and wild bees at flowers of insect-pollinated plants, either wild-growing or
77 cultivated. Preliminary searches showed that studies conducted before 1960 quite rarely
78 reported quantitative data on bee abundance at flowers. The literature screening used
79 searches in Web of Science, Google Scholar and my personal database of plant-pollinator
80 studies. To improve the chances of obtaining a representative, geographically
81 comprehensive coverage of all regions surrounding the Mediterranean Sea (i.e., African,
82 Asian and European shores), literature searches were conducted using terms in English,
83 French, Italian, Portuguese and Spanish. For inclusion in this study I considered
84 exclusively field investigations where (1) quantitative data were provided on relative
85 numbers of wild bees and honeybees based on direct visual counts or standardized
86 collections at flowering individuals or flowering patches of single plant species.
87 Investigations at the plant community level or providing semiquantitative or subjective
88 abundance scores of bee abundance were thus excluded; and (2) the year(s) on which bee
89 abundance data had been originally collected in the field was unambiguously stated. In a
90 few publications where information from two or more study years had been pooled into a
91 single estimate of wild bee and honeybee abundances, but the data were otherwise
92 suitable, the average year was used. A total of 336 estimates of wild bee and honeybee
93 abundance at the flowers of 200 plant species were gathered from 136 different literature
94 sources. Each data record corresponded to a unique combination of plant species x
95 sampling year x sampling location. The data had been collected in the field between 1963–

96 2017 in 13 different countries surrounding the Mediterranean Sea (Fig. 1). Information on
97 plant type (wild-growing vs. cultivated) and taxonomic affiliation (plant family) was also
98 incorporated into the data set.

99 The complete data set including literature sources is presented in Table S1, electronic
100 supplementary material. Most records originate from Spain, Italy, Algeria and Egypt (159,
101 59, 33 and 21, respectively; Fig. 1). The median of the distribution of study years was
102 1996 (interquartile range = 1986-2008). There were 106 and 230 records for cultivated
103 and wild-growing plants, respectively. A total of 54 plant families were represented in the
104 sample, with most species belonging to Fabaceae, Lamiaceae, Asteraceae, Rosaceae and
105 Cistaceae; 51, 34, 32, 30 and 25 records, respectively).

106 Trends in honeybee abundance in the Mediterranean Basin over the period considered
107 in this study were assessed using information gathered from the Food and Agriculture
108 Organization (FAO) of the United Nations databases (FAOSTAT;
109 <http://www.fao.org/faostat>). This data source has been used previously in some historical
110 reviews of honeybee abundance (e.g., Aizen and Harder 2009, vanEngelsdorp and
111 Meixner 2010). Number of honeybee colonies per country and year for the period
112 1963-2017 was obtained from FAOSTAT (accessed 25 September 2019) for each of the
113 13 Mediterranean countries with estimates of wild bee and honeybee relative abundances
114 in my data set (Fig. 1). Comparable abundance figures were obtained by dividing the
115 number of honeybee colonies by the land surface of the country (obtained also from
116 FAOSTAT), which provided estimates of honeybee colonies/km² per country and year.

117 *Statistical analyses*

118 The original figures of bee abundance at flowers found in the literature were transformed
119 to proportions of wild bees (p_{wb}) and honeybees ($p_{hb} = 1 - p_{wb}$) relative to all bees
120 combined. For the purpose of statistical analyses, the log-odds that one randomly chosen

121 bee found at flowers was a wild bee rather than a honeybee was estimated for each data
122 record using the logit transformation, $\text{logit}(p_{wb}) = \log(p_{wb}/p_{hb})$. Since the logit function is
123 undefined for $p = 0$ or 1 , proportions were remapped to the interval $(0.05, 0.95)$ prior to the
124 transformation.

125 The null hypothesis that the relative proportions of wild and honeybees at flowers
126 were unrelated to the year on which the data had been collected was tested by fitting a
127 linear mixed effect model. $\text{Logit}(p_{wb})$ was the response variable, and data collection year
128 (treated as a continuous numerical variable), plant type (two-level factor, wild-growing *vs.*
129 cultivated) and their interaction were included as fixed effects. Country of origin, plant
130 family and plant species were included as random effects to statistically control for, on
131 one side, the effects of likely taxonomic and geographical correlations in the data and, on
132 the other, the unbalanced distribution of data across countries and plant taxonomic groups.
133 The existence of a long-term trend in honeybee abundance in the Mediterranean Basin as a
134 whole was tested by fitting a linear mixed model to the FAOSTAT colony density data
135 (log-transformed). Year (as a numerical variable) was the single fixed effect, and country
136 was included in the model as a random effect to account for the correlated data of the
137 same country. Linear mixed models allow drawing conclusions on fixed effects with
138 reference to a broad inference space whose scope transcends the specific samples studied
139 (McLean et al. 1991, Bolker 2015). In the present instance, the universe of all countries
140 and plant species in the Mediterranean Basin that could have been sampled for this study
141 represents the broad inference space (Schabenberger and Pierce 2001). Conclusions on
142 long-term trends in honeybee abundance and $\text{logit}(p_{wb})$, including predicted marginal
143 effects, will thus refer to such inference space.

144 All statistical analyses were carried out using the R environment (R Core Team
145 2018). Linear mixed models were fitted with the lmer function in the lme4 package (Bates

146 et al. 2015). Statistical significance of fixed effects was assessed using analysis of
147 deviance-based, Type II Wald chi-square tests using the Anova function in the car package
148 (Fox and Weisberg 2011). The function ggpredict from the ggeffects package (Lüdtke
149 2018) was used to compute marginal effects of year on $\text{logit}(p_{wb})$ separately for wild-
150 growing and cultivated plants.

151 **Results**

152 Estimated density of managed honeybee colonies tended to increase steadily over the
153 1963-2017 period in most Mediterranean countries considered in this paper (Fig. 2). The
154 linear mixed model fitted to colony density data (log-transformed), with year as fixed
155 effect and country as random effect, revealed a highly significant linear effect of year on
156 colony density (Chi-squared = 412.9, $P < 10^{-16}$). The estimated linear trend for the whole
157 Mediterranean Basin obtained from this model is depicted by the blue line in Fig. 2.
158 Linearity of the estimated relationship on the logarithmic scale reveals an exponential
159 increase in the density of honeybee colonies in the region over the period considered.

160 For all years, countries and plant species combined, the logarithm of the ratio between
161 proportions of wild bees and honeybees at flowers [$\text{logit}(p_{wb})$] encompassed the whole
162 range of possible values, and there was extensive overlap between cultivated and wild-
163 growing plants (Fig. 3). Wild bees tended to be proportionally more abundant in flowers
164 of wild-growing plants, with mean $\text{logit}(p_{wb})$ differing significantly between cultivated
165 and wild-growing plants (Chi-squared = 18.96, $P = 0.000013$, Kruskal-Wallis rank sum
166 test). For all the data combined (“naïve” least-squares regression fitted to the data; Fig.
167 4A), there existed a statistically significant, negative relationship between $\text{logit}(p_{wb})$ and
168 year of study ($r_s = -0.139$, $N = 336$, $P = 0.011$, Spearman rank correlation), thus
169 suggesting a declining temporal trend in the importance of wild bees at flowers relative to
170 honeybees over the period considered (Fig. 4A). The reality of this trend was corroborated

171 and strengthened after accounting statistically for correlations underlying the data and
172 unbalanced distribution across plant types, countries, plant families and plant species.

173 Results of the linear mixed model testing for the effect of year of study on $\text{logit}(p_{wb})$
174 are summarized in Table 1. After statistically accounting for plant type (wild-growing *vs.*
175 cultivated), country, plant family and plant species, there was a highly significant negative
176 effect of study year on $\text{logit}(p_{wb})$. The effect was similar for wild-growing and cultivated
177 species, as denoted by the statistical nonsignificance of the year x plant type interaction.
178 After statistically accounting for the rest of effects in the model, the effect of plant type on
179 $\text{logit}(p_{wb})$ was only marginally significant (Table 1). Mean predicted marginal effects of
180 year on $\text{logit}(p_{wb})$, computed separately for wild-growing and cultivated plants, illustrate a
181 linear decline in $\text{logit}(p_{wb})$ over the study period (Fig. 4B). In 1963, the data-predicted
182 proportion of wild bees at flowers roughly quadruplicated that of honeybees, while the
183 proportions of both groups had become roughly similar in 2017. This long-term
184 replacement of wild bees by honeybees at flowers occurred at similar rates in wild and
185 cultivated plants, as shown by the parallel predicted marginal effects (Fig. 4B).

186 **Discussion**

187 Previous studies that have examined long-term trends in honeybee colony numbers from a
188 wide geographical perspective have shown that (1) there is not any hint of honeybees
189 declining at a planetary scale, but instead considerable evidence that the total number of
190 colonies is increasing globally and in almost every continent; (2) well documented cases
191 of honeybee decline are few and fairly restricted geographically, being mostly
192 circumscribed to parts of Europe and North America; and (3) in the thoroughly-
193 investigated European continent, severe honeybee declines affect just a few countries
194 (e.g., Austria, Germany, Sweden), while stability or increases predominate in the rest (e.g.,
195 Finland, Greece, Spain) (Aizen and Harder 2009, Potts et al. 2010, vanEngelsdorp and

196 Meixner 2010). As an illustration, Fig. 5 depicts the inverse trajectories of honeybee
197 colony density over the last half century in Spain and Germany, two representative
198 countries of Mediterranean and mid-western Europe. The analyses presented in this study
199 show that honeybee colonies have increased exponentially over the last 50 years in the
200 Mediterranean Basin, comprising areas of southern Europe, the Middle East and Northern
201 Africa. The latter two regions are prominent examples of ecologically understudied areas
202 (Martin et al. 2012) and, as far as I know, have been never considered in quantitative
203 analyses of bee population trends. The empirical evidence available, therefore, supports
204 the view that, to the extent that broad extrapolations on “pollinator decline” or “pollination
205 crisis” were inspired or supported by honeybee declines (see, e.g., Ghazoul 2005, Potts et
206 al. 2010, Ollerton 2017, for reviews), such generalizations exemplify distorted ecological
207 knowledge arising from geographically biased data (Ghazoul 2005, Martin et al. 2012,
208 Archer et al. 2014, Culumber et al. 2019).

209 Correlative and experimental evidence alike has recently shown that beyond certain
210 density threshold honeybees can have strong negative impacts on wild bee populations in
211 both natural and anthropogenic scenarios (Shavit et al. 2009, Lindström et al. 2016, Torné-
212 Noguera et al. 2016, Ropars et al. 2019, Valido et al. 2019), and that in well-preserved
213 natural areas honeybee absence is associated with substantial long-term increases in wild
214 bee populations (Herrera 2019). Much of the direct or circumstantial evidence on the
215 harmful effects of honeybees on wild bees originated in the Mediterranean Basin, which
216 motivated the hypothesis formulated in this paper of a possible replacement of wild bees
217 by honeybees in the Mediterranean running parallel to the increasing abundance of
218 honeybees. This hypothesis has been tested using literature data from highly
219 heterogeneous sources, and originally collected using an enormous variety of field
220 procedures. The data were also imbalanced with regard to observation year, country of

221 origin or plant species identity, which unavoidably combined to produce a “messy”
222 dataset. Despite these limitations, the data have verified the prediction of a gradual long-
223 term replacement of wild bees by honeybees in flowers of the Mediterranean Basin. This
224 conclusion persisted regardless of whether the hypothesis was tested “naïvely” (i.e.,
225 simple correlation on all data pooled) or by fitting a linear mixed model where major
226 sources of data “messiness” were appropriately handled by treating them as random
227 effects. Estimated marginal effects predicted from the mixed model revealed that, on
228 average, the proportion of wild bees at Mediterranean flowers roughly quadruplicated that
229 of honeybees at the beginning of the period considered ($\text{logit}(p_{wb}) \sim 1.5$) while fifty years
230 later the proportions of both groups had become roughly similar ($\text{logit}(p_{wb}) \sim 0$).

231 On average, model-predicted importance of wild bees relative to honeybees was
232 slightly lower in flowers of cultivated plants throughout the period considered, a finding
233 that seems logically related to the traditional practice of placing honeybee colonies in the
234 vicinity of orchards or cultivated land to ensure crop pollination. More difficult to
235 interpret is the close similarity between wild and cultivated plants in average replacement
236 rate of wild bees by honeybees in flowers, as denoted by parallel slopes of mean predicted
237 marginal effects of year on $\text{logit}(p_{wb})$ and the statistical nonsignificance of the year x plant
238 type interaction effect. A tentative interpretation of this finding is that the causal
239 mechanism behind temporal trends in bee composition at flowers was one and the same
240 for cultivated and wild plants, or in other words, that increasing honeybee colony density
241 affected in similarly negative ways to wild bees in flowers from anthropogenous and
242 natural habitats. Irrespective of the causal mechanism accounting for it, however, parallel
243 trends in the decline of wild bees relative to honeybees in wild and cultivated plants
244 corroborate in a broader geographical context previous findings at a regional scale
245 showing that natural Mediterranean habitats are not exempt from the negative impact of

246 increasing honeybee densities in anthropogenous habitats nearby (Magrach et al. 2017).

247 Results of this study are important because the Mediterranean Basin is a world

248 biodiversity hotspot for both wild bees and wild bee-pollinated plants (Petanidou and

249 Vokou 1993, Dafni and O'Toole 1994, Michener 2000, Petanidou and Lamborn 2005,

250 Harrison and Noss 2017). Predicting the global consequences for the Mediterranean flora

251 of the proportional decline of wild bees as floral visitors documented in this paper will

252 require extensive data, e.g., on the pollinating effectiveness of different groups of bees on

253 different plants. Nevertheless, studies conducted so far on the effectiveness of honeybees

254 and wild bees as pollinators of cultivated and wild species in the Mediterranean Basin

255 have found that wild bees generally are better pollinators than honeybees (Herrera 1987,

256 Obeso 1992, Bosch and Blas 1994, Vicens and Bosch 2000, Potts et al. 2001, Monzón et

257 al. 2004). If these limited findings are corroborated in the future by more extensive

258 investigations, then the gradual replacement of wild bees by honeybees currently

259 underway in Mediterranean flowers could translate into impaired fruit and seed production

260 and, in the case of pollen-limited wild plants, reduced population recruitment.

261 It does not seem implausible to suggest that, because of its colossal magnitude and

262 spatial extent, the exponential flood of honeybee colonies that is silently taking over the

263 Mediterranean Basin can pose serious threats to two hallmarks of the Mediterranean

264 biome, namely the extraordinary diversities of wild bees and wild bee-pollinated plants

265 (Blondel et al. 2010). The Mediterranean Basin is home to ~3300 wild bee species, or

266 about 87% of those occurring in the whole Western Palaearctic region (data taken from

267 Discover Life, <https://www.discoverlife.org/>, accessed 1 November 2019; and Kuhlmann

268 2019). Large as that percent may seem, it is likely an underestimate given the imperfect

269 knowledge of Mediterranean Africa wild bee faunas. From a conservation perspective,

270 actions advocated for promoting apiculture or enhancing honeybee populations in

271 European regions where the species is actually declining (de la Rúa et al. 2009, Cayuela et
272 al. 2011) should not be transferred uncritically to the Mediterranean Basin, as Fig. 5
273 should make clear to anyone. In the Mediterranean, such actions would be aiming at the
274 wrong conservation target and, even worse, could be indirectly threatening the unique
275 regional diversity of wild bees, wild bee-pollinated plants and their mutualistic
276 relationships.

277 **Acknowledgements**

278 This study was prompted by the troubling discrepancy between allusions to the
279 honeybees' impending demise so often found in popular media, and my subjective
280 impression in the field that managed honeybees are quickly displacing wild bees from the
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411

412 Table 1. Summary of results of the linear mixed model testing for the significance of
413 supra-annual variation in $\text{logit}(p_{wb})$, the log of the quotient between proportions of
414 wild bees and honeybees, in flowers of wild-growing and cultivated plants of the
415 Mediterranean Basin.

	Standardized parameter estimate (standard error)	Chi- squared	<i>P</i> value	Variance (95% confidence interval)
Fixed effects				
Year (Y)	-0.314 (0.137)	10.94	0.00094	
Plant type (PT)	0.566 (0.306)	3.45	0.063	
Y x PT	0.030 (0.184)	0.027	0.87	
Random effects				
Country				0.357 (0.040-1.254)
Plant family				0.389 (0.091-0.983)
Plant species				1.399 (0.896-1.997)

416

417

418 **Legends to figures**

419 Fig. 1. Distribution among 13 circum-Mediterranean countries of the $N = 336$
420 published estimates of wild bee and honeybee abundance in flowers of cultivated and
421 wild-growing plants for the period 1963-2017 considered in this study (Table S1,
422 electronic supplementary material).

423 Fig. 2. Variation over 1963-2017 in density of honeybee colonies in the 13 circum-
424 Mediterranean countries considered in this study (gray lines), and overall relationship
425 for the Mediterranean Basin as a whole (blue line; estimated from parameters obtained
426 by fitting a linear mixed model to the data with country as a random effect). Note the
427 logarithmic scale on vertical axis.

428 Fig. 3. Frequency distribution of $\text{logit}(p_{wb})$, the logarithm of the ratio between
429 proportions of wild bees and honeybees at flowers, in the $N = 336$ unique combinations
430 of plant species x sampling year x sampling location considered in this study. Bars to
431 the left and right of the vertical dashed line [$\text{logit}(p_{wb}) = 0$] correspond to situations of
432 numerical dominance at flowers of honeybees and wild bees, respectively.

433 Fig. 4. A. Relationship between $\text{logit}(p_{wb})$, the logarithm of the ratio between
434 proportions of wild bees and honeybees at flowers, and year of study. Each dot
435 corresponds to a unique combinations of plant species x sampling year x sampling
436 location ($N = 336$). The black line is the “naïve” least-squares regression fitted to the
437 data, all countries, plant species and plant types (cultivated and wild-growing)
438 combined. B. Mean marginal effects of year on $\text{logit}(p_{wb})$ for cultivated and wild-
439 growing plants, as predicted from the linear mixed model with country, plant family,
440 and plant species as random effects (Table 1).

441 Fig. 5. Variation over 1963-2017 in density of honeybee colonies in Germany an
442 Spain (gray lines), based on FAOSTAT data (see text). These two countries were

443 chosen as representatives, respectively, of thoroughly-studied, mid-western, temperate-

444 climate Europe, and insufficiently-studied, southern, Mediterranean-climate Europe.

445 The blue line depict least-squares fitted linear regressions.

446

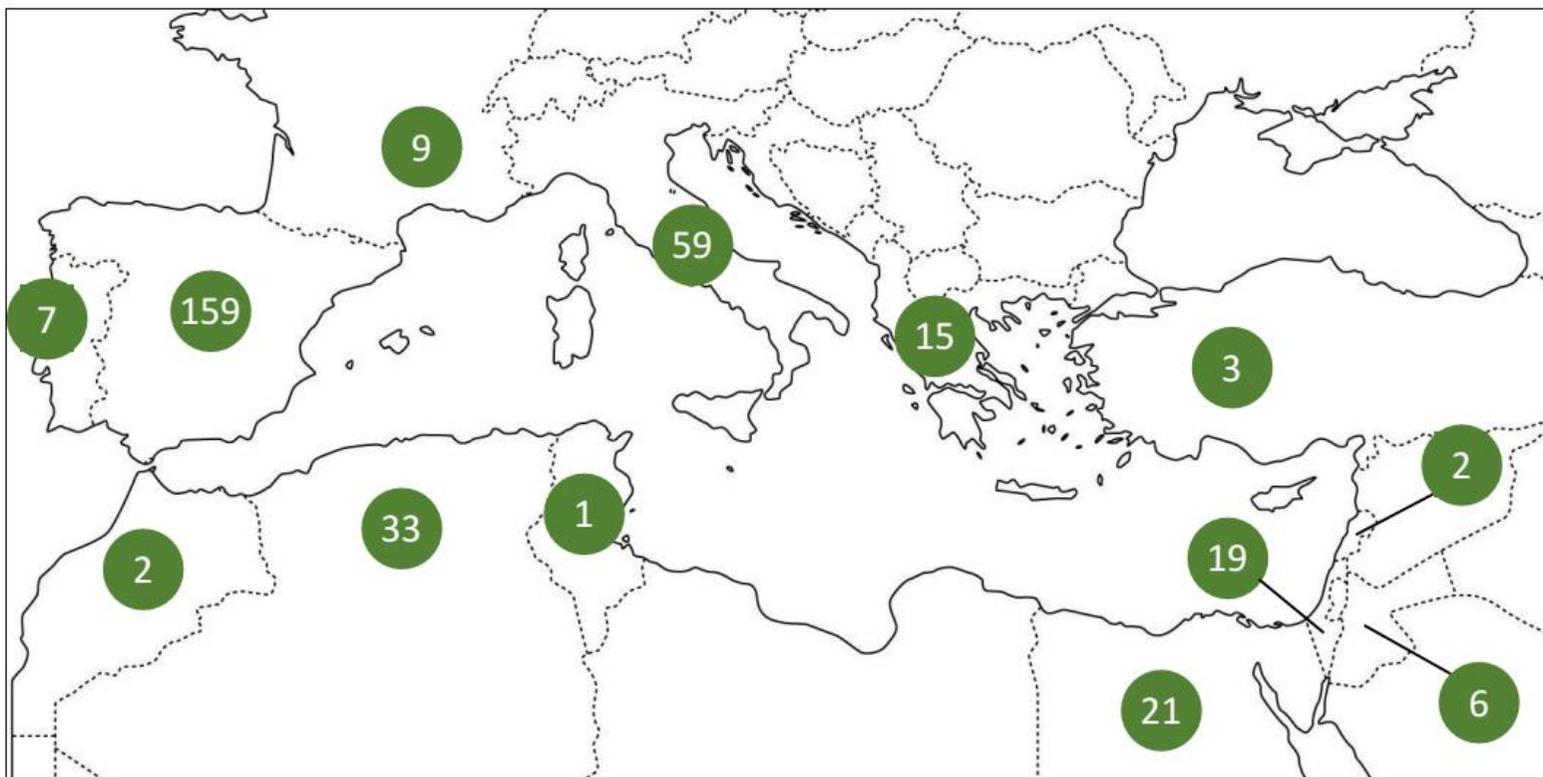


Fig. 1

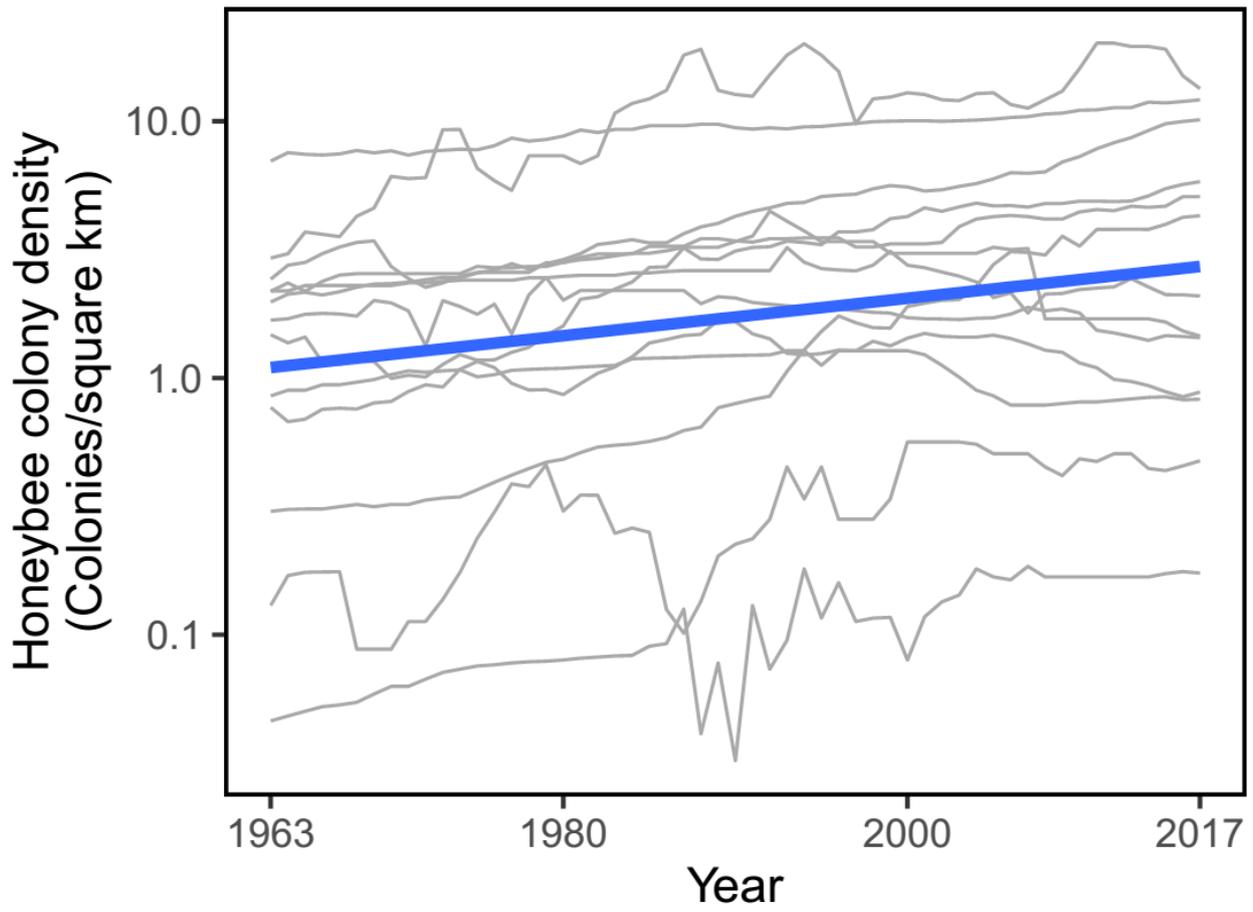


Fig. 2

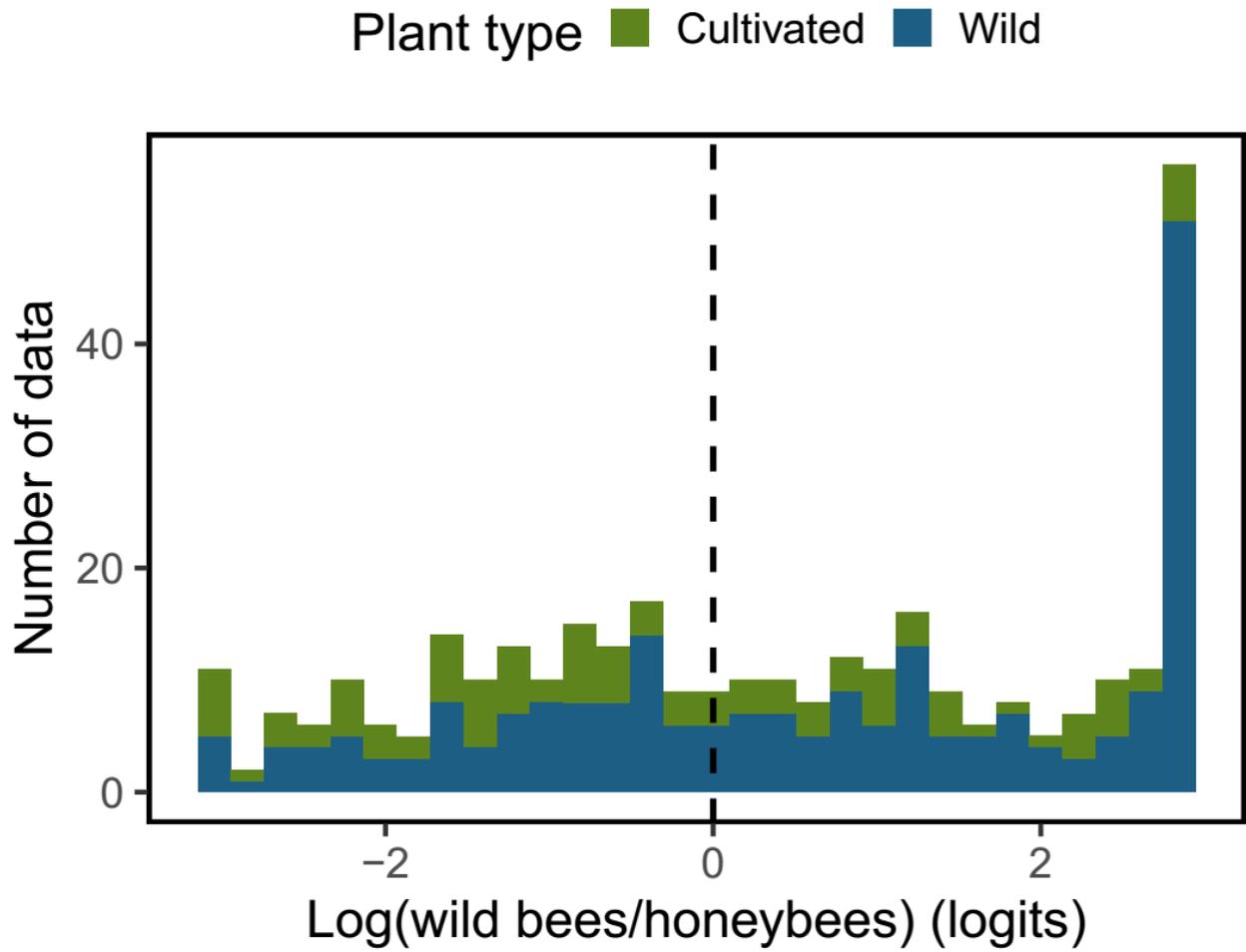


Fig. 3

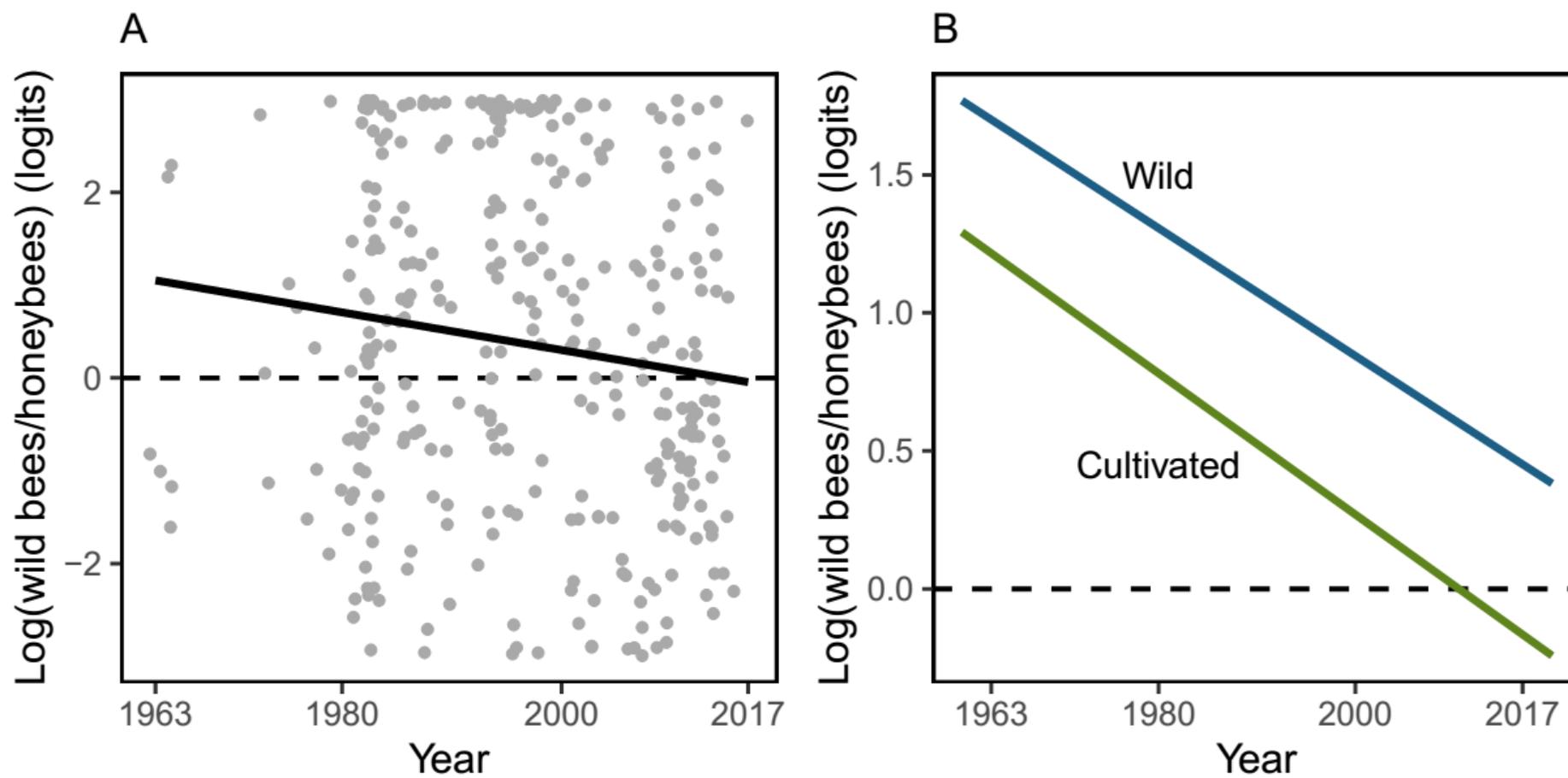


Fig. 4

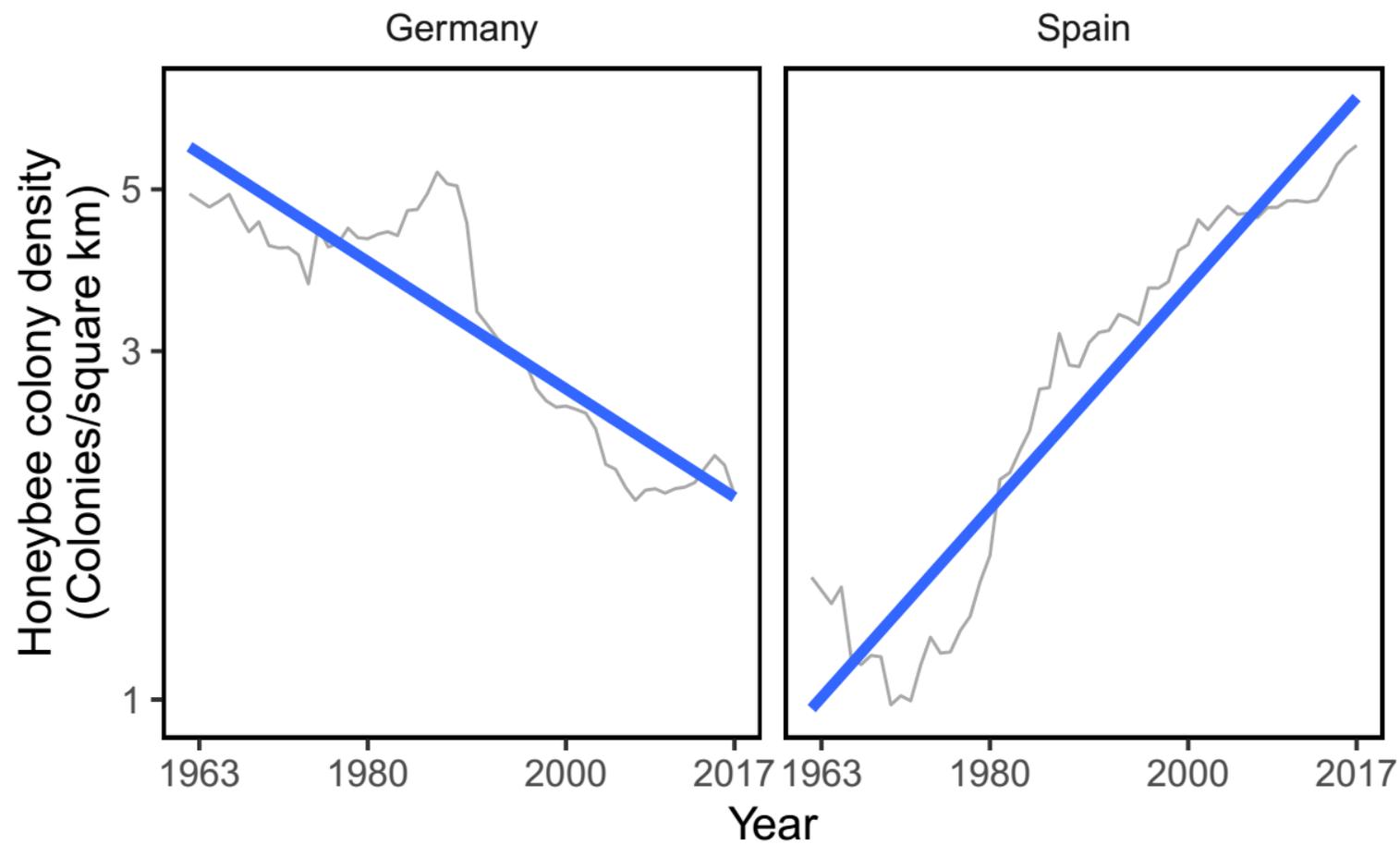


Fig. 5