Gradual replacement of wild bees by honeybees

in flowers of the Mediterranean Basin over the last 50 years

Carlos M. Herrera

Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas,

Avda. Americo Vespucio 26, E-41092 Sevilla, Spain

e-mail: herrera@ebd.csic.es

1 **Abstract**

2 Evidence for pollinator decline largely originates from mid-latitude regions in North

3 America and Europe. Geographical heterogeneity in pollinator trends combined with

4 geographical biases in pollinator studies, can produce distorted extrapolations and limit

5 understanding of pollinator responses to environmental changes. In contrast to the declines

6 experienced in some well-investigated European and North American regions, honeybees

7 seem to have increased recently in some areas of the Mediterranean Basin. Since

8 honeybees can impact negatively on wild bees, it was hypothesized that a biome-wide

9 alteration in bee pollinator assemblages may be underway in the Mediterranean Basin

10 involving a reduction in the importance of wild bees as pollinators. This hypothesis was

11 tested using data on composition of bee pollinators of wild and cultivated plants obtained

12 from studies conducted between 1963-2017 in 13 circum-Mediterranean countries.

13 Honeybee colonies increased exponentially and wild bees were gradually replaced by

14 honeybees in flowers of wild and cultivated plants. Proportion of wild bees at flowers

15 quadruplicated that of honeybees at the beginning of the period, the proportions of both

16 groups becoming roughly similar fifty years later. The Mediterranean Basin is a world

17 biodiversity hotspot for wild bees and wild bee-pollinated plants, and the ubiquitous rise

18 of honeybees to dominance as pollinators could in the long run undermine the diversity of

19 plants and wild bees, as well as their mutualistic relationships in the region.

20 **Key words:** bee pollination, honeybees, long-term trends, Mediterranean Basin, wild

21 bees.

22   *"El sur también existe"*

23   Joan Manuel Serrat, singer and songwriter

24

Introduction

25

26   The structure and dynamics of ecological communities can vary tremendously across

27   biomes and continents. Critical elements of ecological knowledge will thus be closely tied

28   to the particular location where it is attained, and attempts at extrapolations which are

29   based on limited, spatially biased ecological data may produce distorted or erroneous

30   inferences (Martin et al. 2012, Culumber et al. 2019). For instance, unawareness of

31   geographical sampling biases has been pointed out as one possible source of unsupported

32   generalizations related to the notions of "pollinator decline" and "pollination crisis"

33   (Ghazoul 2005, Archer 2014, Herrera 2019, Jamieson et al. 2019), two topics that have

34   recently elicited considerable academic and popular interest because of the importance of

35   animal pollination for the reproduction of many wild and crop plants (Ollerton et al. 2014,

36   Senapathi et al. 2015, Breeze et al. 2016, Ollerton 2017). Evidence for the widely held

37   view of a generalized pollinator decline is strongly biased geographically, as it mostly

38   originates from a few mid-latitude regions in Europe and North America (Rodger et al.

39   2004, Ghazoul 2005, Winfree et al. 2009, Archer 2014, Hung et al. 2018, Nicholson and

40   Egan 2019). Mounting evidence indicates, however, that pollinator declines are not

41   universal; that the sign and magnitude of temporal trends in pollinator abundance may

42   differ among pollinator groups, continents or regions; and that taxonomic and

43   geographical biases in pollinator studies in combination with unrecognized patterns of

44   geographical or taxonomic differences in pollinator trends are bound to limit a realistic

45   understanding of pollinator responses to environmental changes and the causal

46   mechanisms involved (Aizen and Harder 2009a,b, Potts et al. 2010, vanEngelsdorp and

47   Meixner 2010, Hofmann et al. 2018, Herrera 2019, Jamieson et al. 2019).

48   Even for well-studied social bees, data supporting a general decline of these important

49   pollinators tend to be geographically biased (Archer et al. 2014, Ollerton 2017, Hung et al.

50   2018). For example, in thoroughly studied North America and mid-western Europe the

51   number of honeybee colonies has experienced severe declines, but the trend is apparently

52   reversed in the less investigated areas of southern Europe, where honeybee colonies seem

53   to have been steadily increasing over large territories in the last decades (Aizen and

54   Harder 2009a: Fig. S1, Potts et al. 2010, vanEngelsdorp and Meixner 2010, Moritz and

55   Erler 2016). Honeybees have been repeatedly shown to have negative impacts on wild bee

56   populations in both natural and anthropogenic scenarios (Goulson and Sparrow 2009,

57   Shavit et al. 2009, Lindström et al. 2016, Torné-Noguera et al. 2016, Magrach et al. 2017,

58   Ropars et al. 2019, Valido et al. 2019). I thus formulated the hypothesis that, if the

59   abundance of managed honeybees has been actually increasing in the Mediterranean Basin

60   over the last decades, then a profound biome-wide alteration in the composition of bee

61   pollinator assemblages could be currently underway there, involving a gradual

62   replacement of wild bees by honeybees in flowers. This paper verifies this hypothesis

63   using data from a large sample of published investigations on the composition of bee

64   pollinators of wild and cultivated plants, conducted during the last 50 years throughout the

65   Mediterranean Basin. Results of this study stress the importance of broadening the

66   geographical scope of current investigations on pollinator trends, while at the same time

67   issue a warning on the perils of uncritically importing to Mediterranean ecosystems

68   honeybee conservation actions specifically designed for the contrasting situations that

69   prevail in temperate-climate European or North American countries.

70   **Material and methods**

71   *The data*

72   The literature on floral biology, pollination ecology, plant-pollinator interactions and crop

73   pollination was searched for field studies conducted during 1960-2019 in the

74   Mediterranean Basin and providing quantitative data on the relative abundance of

75   honeybees and wild bees at flowers of insect-pollinated plants, either wild-growing or

76   cultivated. Preliminary searches had shown that studies conducted before 1960 quite

77   rarely reported quantitative data on bee abundance at flowers. The literature screening

78   used searches in Web of Science, Google Scholar and my personal database of plant-

79   pollinator studies. To improve the chances of obtaining a representative, geographically

80   comprehensive coverage of all regions surrounding the Mediterranean Sea (i.e., African,

81   Asian and European shores), literature searches were conducted using terms in English,

82   French, Italian, Portuguese and Spanish. For inclusion in this study I considered

83   exclusively field investigations where (1) quantitative data were provided on relative

84   numbers of wild bees and honeybees based on direct visual counts or standardized

85   collections at flowering individuals or flowering patches of single plant species.

86   Investigations at the plant community level or providing semiquantitative or subjective

87   abundance scores of bee abundance were thus excluded; and (2) the year(s) on which bee

88   abundance data had been originally collected in the field was unambiguously stated. In a

89   few publications where information from two or more study years had been pooled into a

90   single estimate of wild bee and honeybee abundances, but the data were otherwise

91   suitable, the average year was used. A total of 336 estimates of wild bee and honeybee

92   abundance at the flowers of 200 plant species were gathered from 136 different literature

93   sources. Each data record corresponded to a unique combination of plant species x

94   sampling year x sampling location. The data had been collected in the field between 1963–

95 2017 in 13 different countries surrounding the Mediterranean Sea (Fig. 1). Information on

96 plant type (wild-growing *vs.* cultivated) and taxonomic affiliation (plant family) was also

97 incorporated into the data set.

98   The complete data set including literature sources is presented in Table S1, electronic

99 supplementary material. Most data originated from Spain, Italy, Algeria and Egypt (159,

100 59, 33 and 21 records, respectively; Fig. 1). The median of the distribution of study years

101 was 1996 (interquartile range = 1986-2008). There were 106 and 230 records for

102 cultivated and wild-growing plants, respectively. A total of 54 plant families were

103 represented in the sample, with most species belonging to Fabaceae, Lamiaceae,

104 Asteraceae, Rosaceae and Cistaceae; 51, 34, 32, 30 and 25 records, respectively).

105   Trends in honeybee abundance in the Mediterranean Basin over the period considered

106 in this study were assessed using information gathered from the Food and Agriculture

107 Organization (FAO) of the United Nations global database (FAOSTAT;

108 http://www.fao.org/faostat). This data source has been used previously in historical

109 reviews of honeybee abundance (Aizen and Harder 2009a,b, vanEngelsdorp and Meixner

110 2010, Moritz and Erler 2016). Number of honeybee colonies per country and year for the

111 period 1963-2017 was obtained from FAOSTAT (accessed 25 September 2019) for each

112 of the 13 Mediterranean countries with estimates of wild bee and honeybee relative

113 abundances in my data set (Fig. 1). Comparable abundance figures were obtained by

114 dividing the number of honeybee colonies by the land surface of the country (obtained

115 also from FAOSTAT), which provided estimates of honeybee colonies/km^2 per country

116 and year. Data on honey production per country and year were also obtained from

117 FAOSTAT to check the reliability of colony number data as a suitable proxy for honeybee

118 abundance (Aizen and Harder 2009b, Moritz and Erler 2016).

119   *Statistical analyses*

120   Original figures of bee abundance at flowers from the literature were transformed to

121   proportions of wild bees (p_{wb}) and honeybees ($p_{hb} = 1 - p_{wb}$) relative to all bees combined.

122   For the purpose of statistical analyses, the log-odds that one randomly chosen bee found at

123   flowers was a wild bee rather than a honeybee was estimated for each data record using

124   the logit transformation, logit(p_{wb}) = log(p_{wb}/p_{hb}). Since the logit function is undefined for

125    $p = 0$ or 1, proportions were remaped to the interval (0.05, 0.95) prior to the

126   transformation.

127   The null hypothesis that the relative proportions of wild and honeybees at flowers

128   were unrelated to year of data collection was tested by fitting a linear mixed effect model.

129   Logit(p_{wb}) was the response variable, and data collection year (treated as a continuous

130   numerical variable), plant type (two-level factor, wild-growing *vs.* cultivated) and their

131   interaction were included as fixed effects. Country of origin, plant family and plant

132   species were included as random effects to statistically control for, on one side, the effects

133   of likely taxonomic and geographical correlations in the data and, on the other, the

134   unbalanced distribution of data across countries and plant taxonomic groups. The

135   existence of a long-term trend in honeybee abundance in the Mediterranean Basin as a

136   whole was tested by fitting a linear mixed model to the FAOSTAT colony density data

137   (log-transformed). Year (as a numerical variable) was the single fixed effect, and country

138   was included in the model as a random effect to account for the correlated data of the

139   same country. Linear mixed models allow drawing conclusions on fixed effects with

140   reference to a broad inference space whose scope transcends the specific samples studied

141   (McLean et al. 1991, Bolker 2015). In the present instance, the universe of all countries

142   and plant species in the Mediterranean Basin that could have been sampled for this study

143   represents the broad inference space (Schabenberger and Pierce 2001). Conclusions on

144   long-term trends in honeybee abundance and logit(p_{wb}), including predicted marginal

145   effects, will thus refer to such inference space.

146   All statistical analyses were carried out using the R environment (R Core Team

147   2018). Linear mixed models were fitted with the lmer function in the lme4 package (Bates

148   et al. 2015). Statistical significance of fixed effects was assessed using analysis of

149   deviance-based, Type II Wald chi-square tests using the Anova function in the car package

150   (Fox and Weisberg 2011). The function ggpredict from the ggeffects package (Lüdecke

151   2018) was used to compute marginal effects of year on logit(p_{wb}) separately for wild-

152   growing and cultivated plants.

153   **Results**

154   Estimated density of managed honeybee colonies tended to increase steadily over the

155   1963-2017 period in most Mediterranean countries considered in this paper (Fig. 2). The

156   linear mixed model fitted to colony density data (log-transformed), with year as fixed

157   effect and country as random effect, revealed a highly significant linear effect of year on

158   colony density (Chi-squared = 412.9, $P < 10^{-16}$). The estimated linear trend for the whole

159   Mediterranean Basin obtained from this model is depicted by the blue line in Fig. 2.

160   Linearity of the estimated relationship on the logarithmic scale reveals an exponential

161   increase in the density of honeybee colonies in the region over the period considered.

162   There was a close linear relationship across years between mean per-country honey

163   production and number of honeybee colonies (Fig. S1, electronic supplementary material),

164   which supports the reliability of FAOSTAT colony number data as a proxy for honeybee

165   abundance.

166   For all years, countries and plant species combined, the logarithm of the ratio between

167   proportions of wild bees and honeybees at flowers [logit(p_{wb})] encompassed the whole

168   range of possible values, and there was extensive overlap between cultivated and wild-

169   growing plants (Fig. 3). Wild bees tended to be proportionally more abundant in flowers

170   of wild-growing plants, with mean logit(p_{wb}) differing significantly between cultivated

171   and wild-growing plants (Chi-squared = 18.96, P = 0.000013, Kruskal-Wallis rank sum

172   test). For all the data combined ("naïve" least-squares regression fitted to the data; Fig.

173   4A), there existed a statistically significant, negative relationship between logit(p_{wb}) and

174   year of study (r_s = -0.139, N = 336, P = 0.011, Spearman rank correlation), thus

175   suggesting a declining temporal trend in the importance of wild bees at flowers relative to

176   honeybees over the period considered (Fig. 4A). The reality of this trend was corroborated

177   and strenghtened after accounting statistically for correlations underlying the data and

178   unbalanced distribution across plant types, countries, plant families and plant species.

179   Results of the linear mixed model testing for the effect of year of study on logit(p_{wb})

180   are summarized in Table 1. After statistically accounting for plant type (wild-growing *vs.*

181   cultivated), country, plant family and plant species, there was a highly significant negative

182   effect of study year on logit(p_{wb}). The effect was similar for wild-growing and cultivated

183   species, as denoted by the statistical nonsignificance of the year x plant type interaction.

184   After statistically accounting for the rest of effects in the model, the effect of plant type on

185   logit(p_{wb}) was only marginally significant (Table 1). Mean predicted marginal effects of

186   year on logit(p_{wb}), computed separately for wild-growing and cultivated plants, illustrate a

187   linear decline in logit(p_{wb}) over the study period (Fig. 4B). In 1963, the data-predicted

188   proportion of wild bees at flowers roughly quadruplicated that of honeybees, while the

189   proportions of both groups had become roughly similar in 2017. This long-term

190   replacement of wild bees by honeybees at flowers occurred at similar rates in wild and

191   cultivated plants, as shown by the parallel predicted marginal effects (Fig. 4B).

192   **Discussion**

193   Previous studies that have examined long-term trends in honeybee colony numbers from a

194   wide geographical perspective have shown that (1) there is not any hint of honeybees

195   declining at a planetary scale, but instead considerable evidence that the total number of

196   colonies is increasing globally and in almost every continent; (2) well-documented

197   instances of honeybee decline are few and fairly restricted geographically, being mostly

198   circumscribed to parts of Europe and North America; and (3) in the thoroughly-

199   investigated European continent, honeybee declines have occurred in mid-latitude and

200   northern countries, while stability or increases predominate in the south (Aizen and Harder

201   2009a, Potts et al. 2010, vanEngelsdorp and Meixner 2010, Moritz and Erler 2016). As an

202   example, Fig. 5 depicts the inverse trajectories of honeybee colony density over the last

203   half century in Germany and Spain, two representative examples for mid-western Europe

204   and the Mediterranean Basin, respectively (see also vanEngelsdorp and Meixnar: Fig. 2).

205   The analyses presented in this study show that honeybee colonies have increased

206   exponentially over the last 50 years in the Mediterranean Basin, comprising areas of

207   southern Europe, the Middle East and Northern Africa. The latter two regions are

208   prominent examples of ecologically understudied areas (Martin et al. 2012) and, as far as I

209   know, have been never considered in quantitative analyses of bee population trends. The

210   empirical evidence available, therefore, supports the view that, to the extent that

211   extrapolations on "pollinator decline" or "pollination crisis" were at some time inspired by

212   honeybee declines (see, e.g., Ghazoul 2005, Potts et al. 2010, Ollerton 2017, for reviews),

213   such generalizations provide prime examples of distorted ecological knowledge arising

214   from geographically biased data (Ghazoul 2005, Martin et al. 2012, Archer et al. 2014,

215   Culumber et al. 2019).

216   Correlative and experimental evidence alike has recently shown that, at local or

217   regional scales, honeybees can have strong negative impacts on wild bee populations in

218   both natural and anthropogenic scenarios (Shavit et al. 2009, Lindström et al. 2016, Torné-

219   Noguera et al. 2016, Magrach et al. 2017, Ropars et al. 2019, Valido et al. 2019), and that

220   the absence of honeybees in well-preserved natural areas is associated with increasing

221   wild bee populations (Herrera 2019). Much of the direct or circumstantial evidence on the

222   harmful effects of honeybees on wild bees originated in the Mediterranean Basin, which

223   motivated the hypothesis formulated in this paper of a possible replacement of wild bees

224   by honeybees in the Mediterranean running parallel to the increasing abundance of

225   honeybees. This hypothesis has been tested using literature data from highly

226   heterogeneous sources, and originally collected using an enormous variety of field

227   procedures. The data were also imbalanced with regard to observation year, country of

228   origin or plant species identity, all of which combined to produce a "messy" dataset.

229   Despite these limitations, the data have verified the prediction of a gradual long-term

230   replacement of wild bees by honeybees in flowers of the Mediterranean Basin. This

231   conclusion persisted regardless of whether the hypothesis was tested "naïvely" (i.e.,

232   simple correlation on all data pooled) or by fitting a linear mixed model where major

233   sources of data "messiness" were appropriately handled by treating them as random

234   effects. Estimated marginal effects predicted from the mixed model revealed that, on

235   average, the proportion of wild bees at Mediterranean flowers roughly quadruplicated that

236   of honeybees at the beginning of the period considered ($\text{logit}(p_{\text{wb}}) \sim 1.5$) while fifty years

237   later the proportions of both groups had become roughly similar ($\text{logit}(p_{\text{wb}}) \sim 0$).

238   On average, model-predicted importance of wild bees relative to honeybees was

239   slightly lower in flowers of cultivated plants throughout the period considered, a finding

240   that seems logically related to the traditional practice of placing honeybee colonies in the

241   vicinity of orchards or cultivated land to ensure crop pollination. More difficult to

242   interpret is the close similarity between wild and cultivated plants in average replacement

243   rate of wild bees by honeybees in flowers, as denoted by parallel slopes of mean predicted

244   marginal effects of year on logit(p_{wb}) and the statistical nonsignificance of the year x plant

245   type interaction effect. A tentative interpretation of this finding is that the causal

246   mechanism behind temporal trends in bee composition at flowers was one and the same

247   for cultivated and wild plants, or in other words, that increasing honeybee colony density

248   affected in similarly negative ways to wild bees in flowers from anthropogenous and

249   natural habitats. Irrespective of the causal mechanism accounting for it, however, parallel

250   trends in the decline of wild bees relative to honeybees in wild and cultivated plants

251   corroborate in a broader geographical context previous findings at a regional scale

252   showing that natural Mediterranean habitats are not exempt from the negative impact of

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

275   2019). Large as that percent may seem, it is likely an underestimate given the imperfect

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

277   actions advocated for promoting apiculture or enhancing honeybee populations in

278   European regions where the species is actually declining (de la Rúa et al. 2009, Cayuela et

279   al. 2011) should not be transferred uncritically to the Mediterranean Basin, as Fig. 5

280   should make clear. In the Mediterranean, such actions would be aiming at the wrong

281   conservation target and, even worse, could be indirectly threatening the unique regional

282   diversity of wild bees, wild bee-pollinated plants and their mutualistic relationships.

Acknowledgements

References

Aizen, M. A., and L. D. Harder. 2009a. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Current Biology 19:915–918.

Aizen, M. A., and L. D. Harder. 2009b. Geographic variation in the growth of domesticated honey-bee stocks. Communicative & Integrative Biology 2:464–466.

Archer, C. R., C. W. W. Pirk, L. G. Carvalheiro, and S. W. Nicolson. 2014. Economic and ecological implications of geographic bias in pollinator ecology in the light of pollinator declines. Oikos 123:401–407.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Blondel, J., J. Aronson, J. Y. Bodiou, and G. Boeuf. 2010. The Mediterranean Region. Biological diversity in space and time. 2nd edition. Oxford University Press, Oxford, UK.

Bolker, B. M. 2015. Linear and generalized linear mixed models. Pages 309–333 in G. A.

308   Fox, S. Negrete-Yankelevich, and V. J. Sosa. Ecological statistics: contemporary

309   theory and application. Oxford University Press, Oxford, UK.

310   Bosch, J., and M. Blas. 1994. Foraging behaviour and pollinating efficiency of *Osmia*

311   *cornuta* and *Apis mellifera* on almond (Hymenoptera, Megachilidae and Apidae).

312   Applied Entomology and Zoology 29:1–9.

313   Breeze, T. D., N. Gallai, L. A. Garibaldi, and X. S. Li. 2016. Economic measures of

314   pollination services: shortcomings and future directions. Trends in Ecology &

315   Evolution 31:927–939.

316   Cayuela, L., S. Ruiz-Arriaga, and C. P. Ozers. 2011. Honeybees increase fruit set in native

317   plant species important for wildlife conservation. Environmental Management

318   48:910–919.

319   Culumber, Z. W., J. M. Anaya-Rojas, W. W. Booker, A. F. Hooks, E. C. Lange, B. Pluer,

320   N. Ramirez-Bullon, and J. Travis. 2019. Widespread biases in ecological and

321   evolutionary studies. BioScience 69:631–640.

322   Dafni, A., and C. O'Toole. 1994. Pollination syndromes in the Mediterranean:

323   generalizations and peculiarities. Pages 125-135 in M. Arianoutsou and R. H. Groves,

324   editors. Plant-animal interactions in Mediterranean-type ecosystems. Kluwer

325   Academic Publishers.

326   De la Rúa, P., R. Jaffé, R. Dall'Olio, I. Muñoz, and J. Serrano. 2009. Biodiversity,

327   conservation and current threats to European honeybees. Apidologie 40:263–284.

328   Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Second Edition.

329   Sage Publishing, Thousand Oaks, California.

330   Ghazoul, J. 2005. Buzziness as usual? Questioning the global pollination crisis. Trends in

331   Ecology & Evolution 20:367–373.

332   Goulson, D., and K. R. Sparrow. 2009. Evidence for competition between honeybees and

333   bumblebees; effects on bumblebee worker size. Journal of Insect Conservation

334   13:177–181.

335   Harrison, S., and R. Noss. 2017. Endemism hotspots are linked to stable climatic refugia.

336   Annals of Botany 119:207–214.

337   Herrera, C. M. 1987. Components of pollinator 'quality': comparative analysis of a diverse

338   insect assemblage. Oikos 50:79–90.

339   Herrera, C. M. 2019. Complex long-term dynamics of pollinator abundance in undisturbed

340   Mediterranean montane habitats over two decades. Ecological Monographs 89:

341   e01338.

342   Hofmann, M. M., A. Fleischmann, and S. S. Renner. 2018. Changes in the bee fauna of a

343   German botanical garden between 1997 and 2017, attributable to climate warming,

344   not other parameters. Oecologia 187:701–706.

345   Hung, K. L. J., J. M. Kingston, M. Albrecht, D. A. Holway, and J. R. Kohn. 2018. The

346   worldwide importance of honey bees as pollinators in natural habitats. Proceedings of

347   the Royal Society B 285: 20172140.

348   Jamieson, M. A., A. L. Carper, C. J. Wilson, V. L. Scott, and J. Gibbs. 2019. Geographic

349   biases in bee research limits understanding of species distribution and response to

350   anthropogenic disturbance. Frontiers in Ecology and Evolution 7:194.

351   Kuhlmann, M. 2019. Checklist of the Western Palaearctic Bees (Hymenoptera: Apoidea:

352   Anthophila). http://westpalbees.myspecies.info (accessed 1 November 2019).

353   Lindström, S. A. M., L. Herbertsson, M. Rundlöf, R. Bommarco, and H. G. Smith. 2016.

354   Experimental evidence that honeybees depress wild insect densities in a flowering

355   crop. Proceedings of the Royal Society B 283: 20161641.

356   Lüdecke, D. 2018. ggeffects: Create tidy data frames of marginal effects for 'ggplot' from

357   model outputs. R package version 0.3.1, https://CRAN.R-

358   project.org/package=ggeffects.

359   Magrach, A., J. P. González-Varo, M. Boiffier, M. Vilà, and I. Bartomeus. 2017.

360   Honeybee spillover reshuffles pollinator diets and affects plant reproductive success.

361   Nature Ecology & Evolution 1:1299–1307.

362   Martin, L. J., B. Blossey, and E. Ellis. 2012. Mapping where ecologists work: biases in the

363   global distribution of terrestrial ecological observations. Frontiers in Ecology and the

364   Environment 10:195–201.

365   McLean, R. A., W. L. Sanders, and W. W. Stroup. 1991. A unified approach to mixed

366   linear models. The American Statistician 45:54–64.

367   Michener, C. D. 2000. The bees of the World. John Hopkins, Baltimore, Maryland, USA.

368   Monzón, V. H., J. Bosch, and J. Retana. 2004. Foraging behavior and pollinating

369   effectiveness of *Osmia cornuta* (Hymenoptera: Megachilidae) and *Apis mellifera*

370   (Hymenoptera: Apidae) on "Comice" pear. Apidologie 35:575–585.

371   Moritz, R. F. A., and S. Erler. 2016. Lost colonies found in a data mine: global honey

372   trade but not pests or pesticides as a major cause of regional honeybee colony

373   declines. Agriculture, Ecosystems & Environment 216:44–50.

374   Nicholson, C. C., and P. A. Egan. 2019. Natural hazard threats to pollinators and

375   pollination. Global Change Biology. Doi: 10.1111/gcb.14840

376   Obeso, J. R. 1992. Pollination ecology and seed set in *Asphodelus albus* (Liliaceae) in

377   northern Spain. Flora 187:219–226.

378   Ollerton, J. 2017. Pollinator diversity: distribution, ecological function, and conservation.

379   Annual Review of Ecology, Evolution, and Systematics 48:353–376.

380   Ollerton, J., H. Erenler, M. Edwards, and R. Crockett. 2014. Extinctions of aculeate

381   pollinators in Britain and the role of large-scale agricultural changes. Science

382   346:1360–1362.

383   Petanidou, T., and D. Vokou. 1993. Pollination ecology of Labiatae in a phryganic (East

384   Mediterranean) ecosystem. American Journal of Botany 80:892–899.

385   Petanidou, T., and E. Lamborn. 2005. A land for flowers and bees: studying pollination

386   ecology in Mediterranean communities. Plant Biosystems 139:279–294.

387   Potts, S. G., A. Dafni, and G. Ne'eman. 2001. Pollination of a core flowering shrub species

388   in Mediterranean phrygana: variation in pollinator diversity, abundance and

389   effectiveness in response to fire. Oikos 92:71–80.

390   Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin.

391   2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology &

392   Evolution 25:345–353.

393   Potts, S. G., S. P. M. Roberts, R. Dean, G. Marris, M. A. Brown, R. Jones, P. Neumann,

394   and J. Settele. 2010. Declines of managed honey bees and beekeepers in Europe.

395   Journal of Apicultural Research 49:15–22.

396   R Core team. 2018. R: a language and environment for statistical computing. R

397   Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

398   Rodger, J. G., K. Balkwill, and B. Gemmill. 2004. African pollination studies: where are

399   the gaps? International Journal of Tropical Insect Science 24:5–28.

400   Ropars, L., I. Dajoz, C. Fontaine, A. Muratet, and B. Geslin. 2019. Wild pollinator activity

401   negatively related to honey bee colony densities in urban context. PLoS One

402   14:e0222316.

403   Schabenberger, O., and F. J. Pierce. 2001. Contemporary statistical models for the plant

404   and soil sciences. CRC Press, Boca Raton, Florida, USA.

405   Senapathi, D., L. G. Carvalheiro, J. C. Biesmeijer, C. A. Dodson, R. L. Evans, M.

406   McKerchar, R. D. Morton, E. D. Moss, S. P. M. Roberts, W. E. Kunin, and S. G.

407   Potts. 2015. The impact of over 80 years of land cover changes on bee and wasp

408   pollinator communities in England. Proceedings of the Royal Society B

409   282:20150294.

410 Shavit, O., A. Dafni, and G. Ne'eman. 2009. Competition between honeybees (*Apis*

411   *mellifera*) and native solitary bees in the Mediterranean region of Israel–Implications

412   for conservation. Israel Journal of Plant Sciences 57:171–183.

413 Torné-Noguera, A., A. Rodrigo, S. Osorio, and J. Bosch. 2016. Collateral effects of

414   beekeeping: impacts on pollen-nectar resources and wild bee communities. Basic and

415   Applied Ecology 17:199–209.

416 Valido, A., M. C. Rodríguez-Rodríguez, and P. Jordano. 2019. Honeybees disrupt the

417   structure and functionality of plant-pollinator networks. Scientific Reports 9:4711.

418 vanEngelsdorp, D., and M. D. Meixner. 2010. A historical review of managed honey bee

419   populations in Europe and the United States and the factors that may affect them.

420   Journal of Invertebrate Pathology 103:S80–S95.

421 Vicens, N., and J. Bosch. 2000. Pollinating efficacy of *Osmia cornuta* and *Apis mellifera*

422   (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' apple. Environmental

423   Entomology 29:235–240.

424 Winfree, R., R. Aguilar, D. P. Vázquez, G. LeBuhn, and M. A. Aizen. 2009. A meta-

425   analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068–2076.

426

427   Table 1. Summary of results of the linear mixed model testing for the significance of

428   supra-annual variation in logit(p_{wb}), the log of the quotient between proportions of

429   wild bees and honeybees, in flowers of wild-growing and cultivated plants of the

430   Mediterranean Basin.

	Standardized parameter estimate (standard error)	Chi-squared	*P* 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)

431

432

Legends to figures

433

434   Fig. 1. Distribution among 13 circum-Mediterranean countries of the $N = 336$

435   published estimates of wild bee and honeybee abundance in flowers of cultivated and

436   wild-growing plants for the period 1963-2017 considered in this study (Table S1,
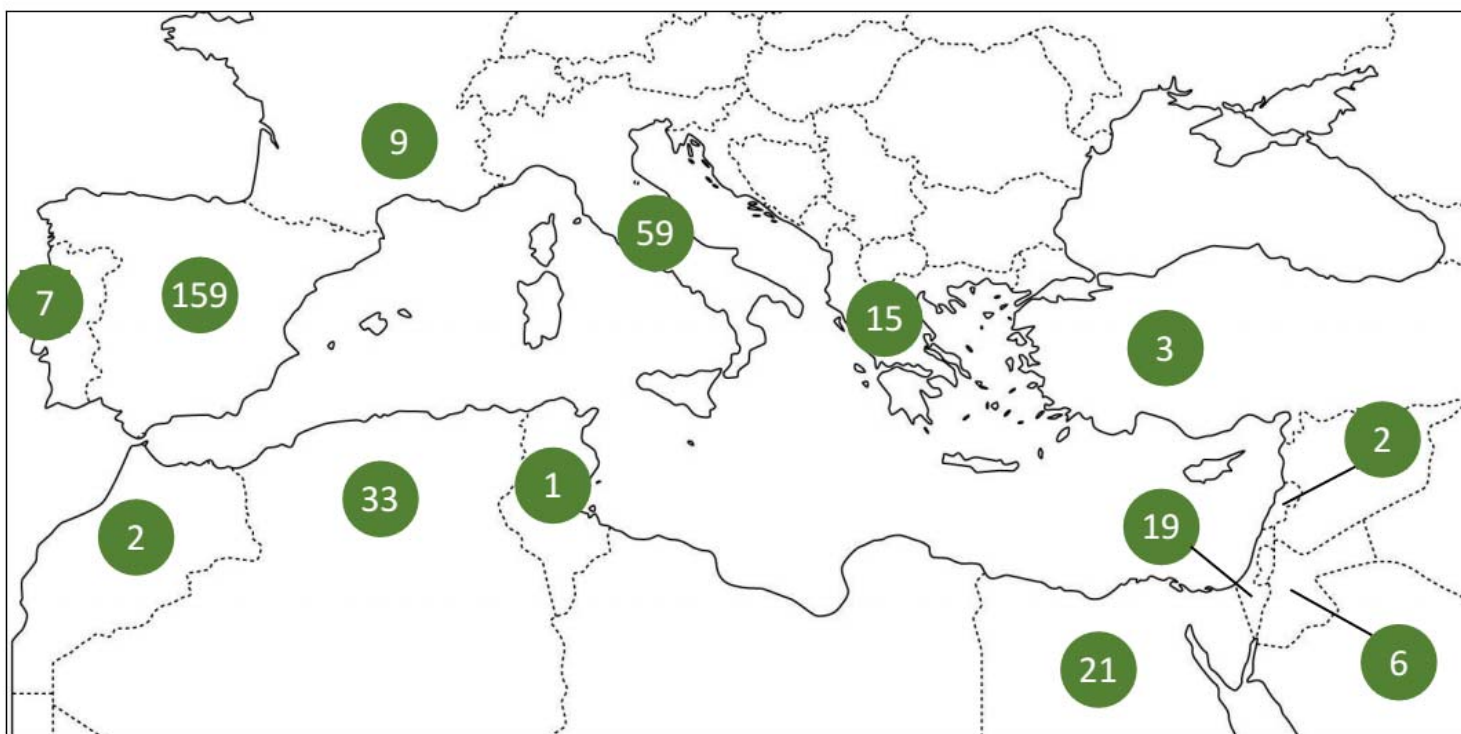
437   electronic supplementary material).

438   Fig. 2. Variation over 1963-2017 in density of honeybee colonies in the 13 circum-

439   Mediterranean countries considered in this study (gray lines), and overall relationship

440   for the Mediterranean Basin as a whole (blue line; estimated from parameters obtained

441   by fitting a linear mixed model to the data with country as a random effect). Note the

442   logarithmic scale on vertical axis.

443   Fig. 3. Frequency distribution of logit(p_{wb}), the logarithm of the ratio between

444   proportions of wild bees and honeybees at flowers, in the $N = 336$ unique combinations

445   of plant species x sampling year x sampling location considered in this study. Bars to

446   the left and right of the vertical dashed line [logit(p_{wb}) = 0] correspond to situations of

447   numerical dominance at flowers of honeybees and wild bees, respectively.

448   Fig. 4. A. Relationship between logit(p_{wb}), the logarithm of the ratio between

449   proportions of wild bees and honeybees at flowers, and year of study. Each dot

450   corresponds to a unique combinations of plant species x sampling year x sampling

451   location ($N = 336$). The black line is the "naïve" least-squares regression fitted to the

452   data, all countries, plant species and plant types (cultivated and wild-growing)

453   combined. B. Mean marginal effects of year on logit(p_{wb}) for cultivated and wild-

454   growing plants, as predicted from the linear mixed model with country, plant family,

455   and plant species as random effects (Table 1).

456   Fig. 5. Variation over 1963-2017 in density of honeybee colonies in Germany an

457   Spain (gray lines), based on FAOSTAT data (see text). These two countries were

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

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

460   The blue line depict least-squares fitted linear regressions.
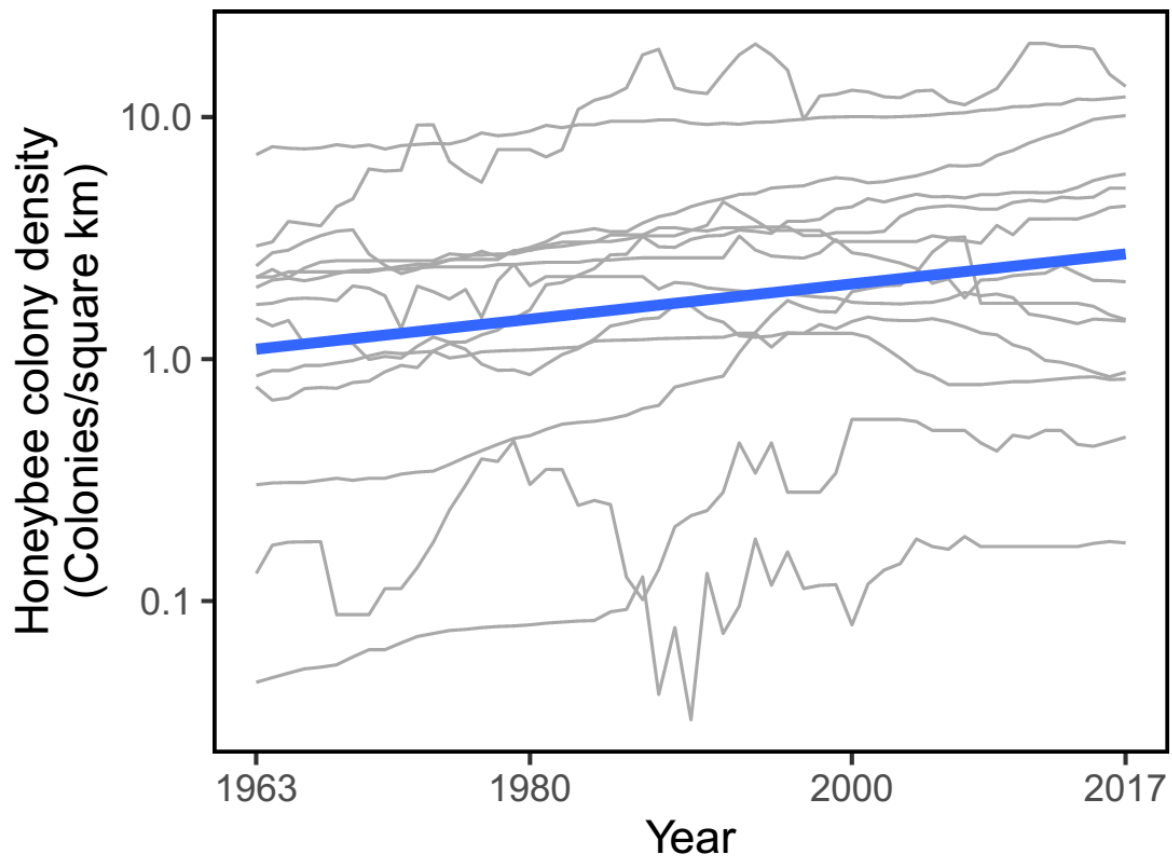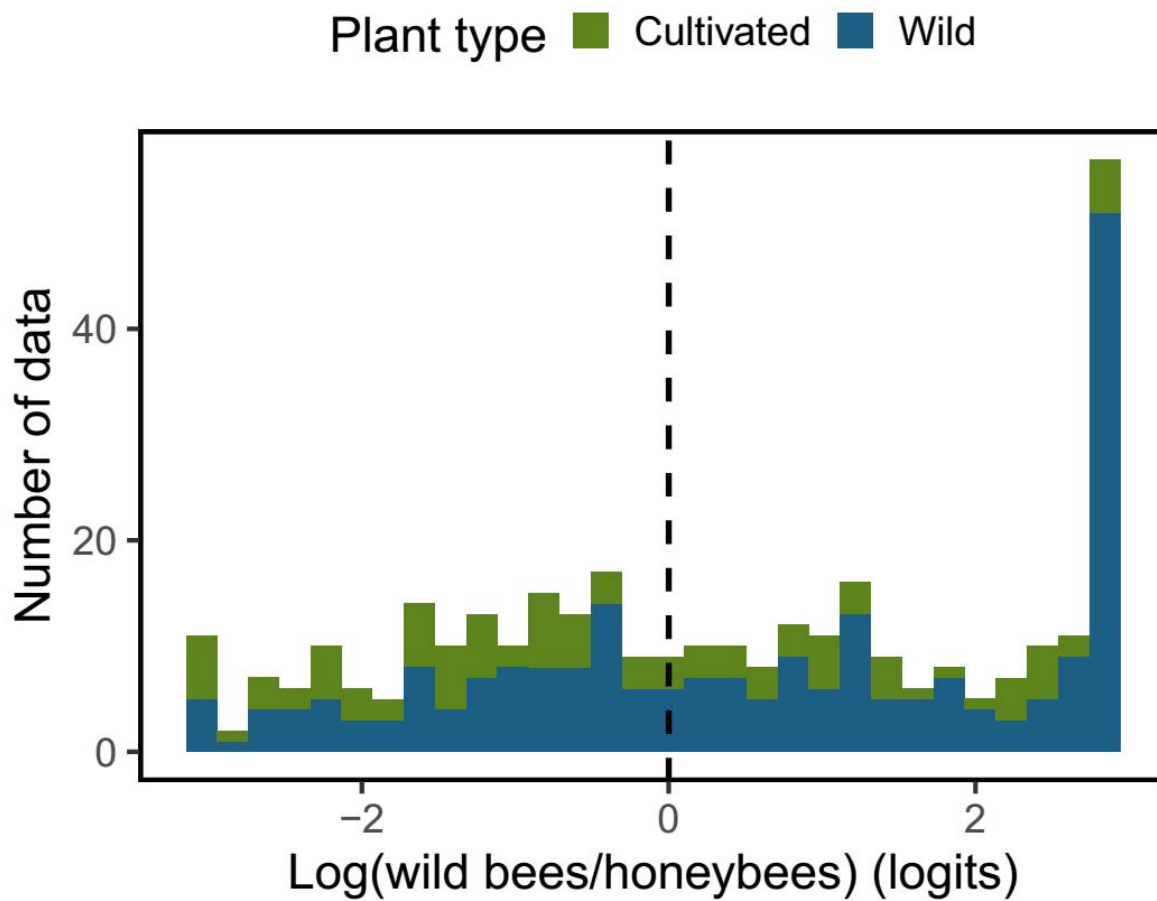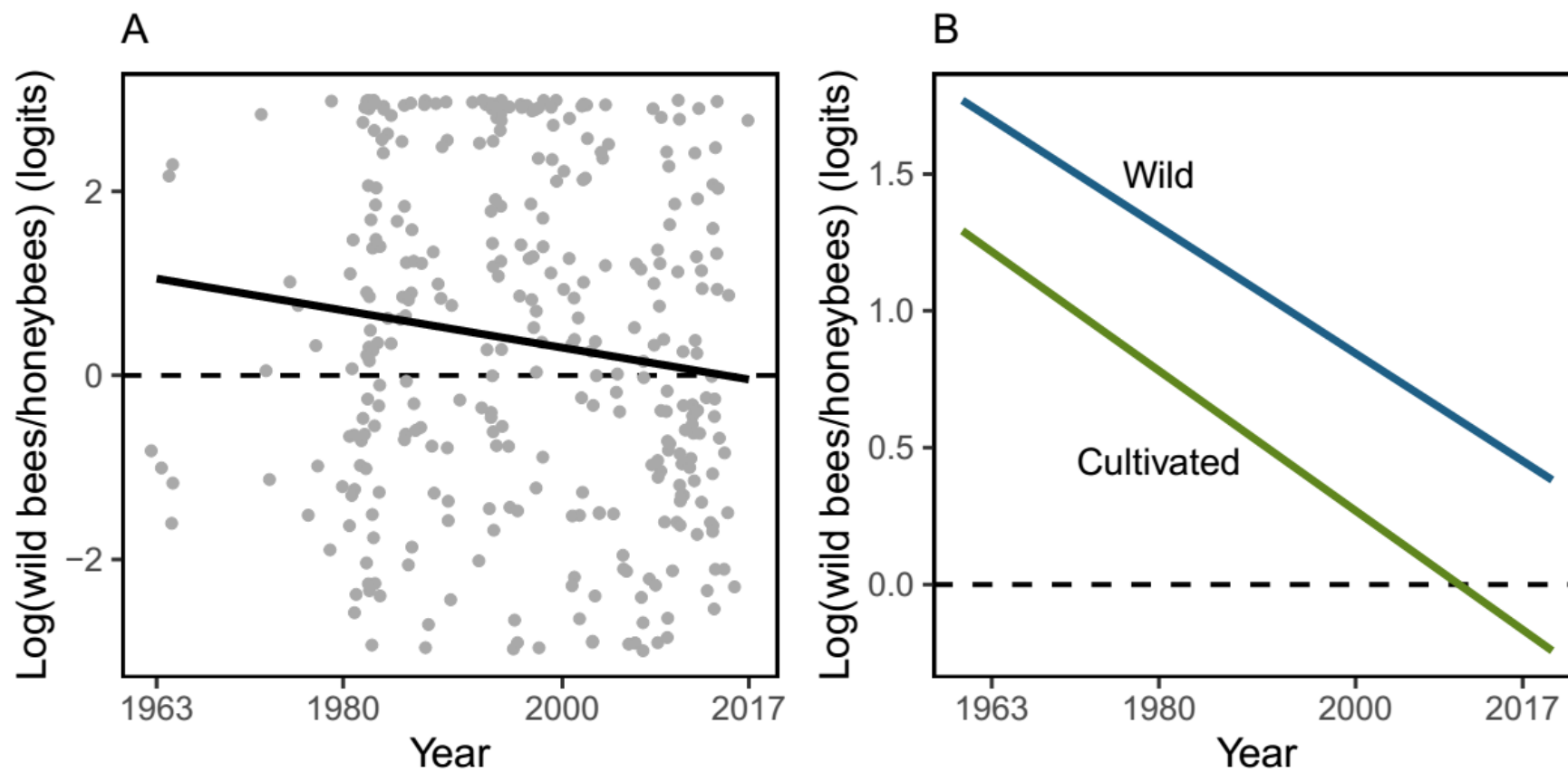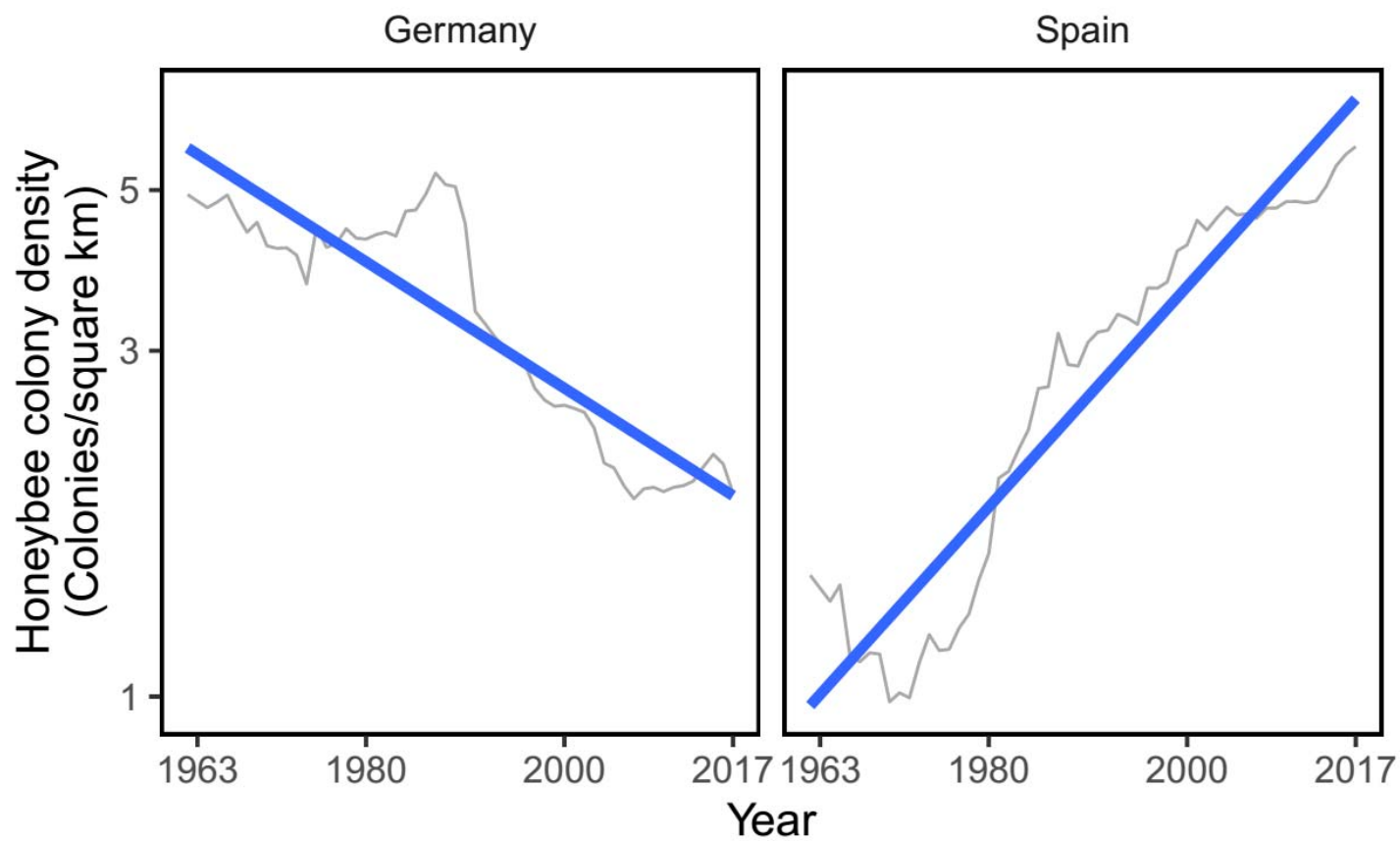
461

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5