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3 Pollination of exotic fruit crops depends more on extant pollinators and

4 landscape structure than on local management of domestic bees

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18 **Highlights**

- 19 • Kiwifruit and blueberry crops deal with different pollinator assemblages in Europe
- 20 • These exotic crops differed in their assemblage of floral visitors
- 21 • Their pollinator assemblages mostly depended on landscape structure
- 22 • Assemblages depended to only a small degree on management of domestic pollinators
- 23 • Kiwifruit, but not blueberry, crops suffered from pollination limitation

24

25

26 **Abstract**

27 Agricultural globalisation has driven the expansion of exotic crops into new agricultural areas.  
28 Pollinator-dependent exotic crops not only have to face the abiotic constraints of the new  
29 cultivation regions but also deal with local pollinator assemblages, which may or may not fulfil  
30 pollination requirements. Here, we studied how three entomophilous exotic crops (kiwifruit,  
31 northern highbush blueberry and rabbiteye blueberry) adapt to a common pollination  
32 environment in new cultivation areas in Spain. For this, we assessed the pollination limitation of  
33 those crops, the contribution of insect assemblages to the pollination service, and the effect of  
34 landscape structure and the management of domestic pollinators on these assemblages. The  
35 three exotic crops showed large and diverse pollinator assemblages but differed in the  
36 assemblage composition and in the identity of the main pollinator species. Honeybee clearly  
37 dominated kiwifruit assemblages, representing almost 70% of visits to flowers. Bumblebees and  
38 honeybee fairly equally dominated floral visits in highbush blueberry, and bumblebees  
39 accounted for more than 90% of visits in rabbiteye blueberry. Floral morphology partially  
40 explained interspecific differences in pollinator assemblages and led to the distinct contributions  
41 of the different insects to the different crops. Kiwifruit (but not blueberry) crops experienced  
42 pollination limitation that led to, on average, a 7.2% reduction in fruit weight. This pollination  
43 limitation decreased when honeybee abundance rose. In all three crops, the local pollinator  
44 assemblages mostly depended on the landscape structure around orchards but were only  
45 affected by the management of domestic pollinators in rabbiteye blueberry crops. Our results  
46 highlight the importance of understanding the interspecific differences in the pollination ecology  
47 of new exotic crops before designing general management recommendations, and also

48 question the use of managed pollinators before making an assessment of the contribution of  
49 extant insects to the pollination service.

50

51 **Keywords:** blueberry, bumblebees, hive management, honeybee, kiwifruit, landscape effects,  
52 pollination limitation

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## 55 **1. Introduction**

56 The expansion of exotic crops into farming areas far from a crop-plant's origins is a main  
57 exponent of the agricultural globalisation, which has been boosted not only by growing human  
58 food demands but also by global changes in diets (Lambin and Meyfroidt, 2011; Kastner et al.,  
59 2012). From an agronomic perspective, the success of exotic crops firstly depends on the  
60 degree of physiological pre-adaptation to the somewhat different edaphic and climatic  
61 conditions of the new farming environments. When pre-adaptation is low, agricultural  
62 management (irrigation, fertilization, climatic protection through greenhouses or hail nets, etc)  
63 becomes essential to establish productive crops in new areas (e.g. Middleton and McWaters,  
64 2002; Heuvelink et al., 2005). Besides adapting to abiotic constraints, exotic crops must also  
65 deal with new biotic environments and cope with, for example, different pollinator assemblages  
66 that may, or may not, fulfil crop pollination requirements. In this sense, it is known that crop  
67 plants usually suffer a decrease in the diversity of flower visitors when cultivated far from their  
68 region of origin (Brown and Cunningham, 2019). Considering that the recent increase in  
69 agricultural production primarily involves the cultivation of pollinator-dependent crops (which  
70 increased by 150% between 1961 and 2018 compared to just 20% for pollinator-independent  
71 crops, Aizen et al. 2022), it would appear to be crucial to better understand the magnitude and  
72 the mechanisms of pollinator-related constraints in exotic crops.

73 The adaptation of displaced crops to the resident pollinators of new cultivation areas  
74 may be conditioned by species-specific filters related to crop floral traits that modulate their  
75 attractiveness for and reward to local pollinator communities (Krishna and Keasar, 2018;  
76 Dellinger, 2020). In this sense, generalist floral morphologies, i.e. those enabling easy access to  
77 nectar or pollen resources for a wide range of pollinators (e.g. big flower sizes, short corollas,  
78 open flower receptacles, numerous and accessible stamens, etc, Olesen et al., 2007), should

79 promote adaptation to local pollinators assemblages of variable size and composition.  
80 Conversely, exotic crops with specialist traits (e.g. small flower sizes, long tubular corollas,  
81 tubular closed anthers, etc.) that restrict pollen or nectar gathering to few specific pollinator  
82 types (e.g. long-tongued insects, buzz-pollinating bees; Olesen et al., 2007) are expected to be  
83 more prone to pollination limitation. Thus it becomes necessary to evaluate how crop species  
84 that differ in flower morphology and their expected degree of generalism in pollinator  
85 assemblages, develop their pollination niches when expanding across the same farming region.

86 Irrespective of floral traits, the magnitude of the pollination service in entomophilous  
87 crops depends greatly on the abundance and the diversity of the visiting wild insects (Garibaldi  
88 et al., 2013; Pérez-Méndez et al., 2020). Thus, farms with more diverse pollinator communities  
89 receive a better service, frequently because the different insect species complement each other  
90 and generate an additive effect (Winfree, 2013; Miñarro and García, 2018). Sometimes,  
91 however, differences between farms in the overall pollination function depend more on  
92 variations in the abundance of a few dominant and effective species than on changes in  
93 richness per se (Kleijn et al., 2015; Winfree et al., 2015). Nevertheless, many entomophilous  
94 crops suffer reduced production as a result of pollination limitations, failing to achieve maximum  
95 production because they do not receive the maximum possible pollen supply, both in quantity  
96 and quality, from wild insects that spontaneously occur within farms (Garibaldi et al., 2016;  
97 Garratt et al., 2021). This is well known to farmers, who traditionally encourage insect pollination  
98 by managing domestic pollinators, like honeybee or a few bumblebee and solitary bee species,  
99 through livestock practices (Garibaldi et al., 2013; Osterman et al., 2021). Therefore, a thorough  
100 understanding of the relative relevance of extant pollinator, i.e. those spontaneously occurring in  
101 farms, and those that are domestic, i.e. locally introduced by farmers, in exotic crops seems  
102 indispensable.

103 Insect pollinators are highly mobile animals, often arriving on farms from surrounding  
104 habitats hundreds of metres away (e.g. Greenleaf et al., 2007). The capacity of an insect  
105 species to extend its foraging area depends on specific traits, such as body size (Greenleaf et  
106 al., 2007; Benjamin et al., 2014), and thus different species may respond in their own particular  
107 way to the gradients imposed by agriculture on the landscape, such as habitat loss or  
108 fragmentation (Brosi et al., 2008; Bommarco et al., 2010). In this sense, the structure of the

109 landscape surrounding farms determines the abundance, richness and composition of pollinator  
110 assemblages in crops (e.g. Saturni et al., 2016; Senapathi et al., 2017; Roquer-Beni et al.,  
111 2021) by conditioning the type and the extent of source habitats as well as the flow from these  
112 sources to crops (Tscharntke et al., 2005). Addressing the modulating effects of surrounding  
113 habitats on pollinator assemblages is thus a requisite to ultimately understanding the  
114 characteristics of the pollination service to exotic crops (e.g. Greenleaf and Kremen, 2006;  
115 Blaauw and Isaacs, 2014).

116         Here, we study the pollination of kiwifruit (*Actinidia deliciosa*; native to China), northern  
117 highbush blueberry (*Vaccinium corymbosum*) and rabbiteye blueberry (*Vaccinium ashei*) (both  
118 native to North America)—three of the fruit crops that are increasing most rapidly in the world  
119 (Ward and Courtney, 2013; Rodríguez-Saona et al., 2019)—in new cultivation areas in NW  
120 Spain. All these crops depend on insects for pollination (Klein et al., 2007) and can suffer  
121 pollination limitations (Campbell et al., 2018; Castro et al., 2021; Martin et al., 2021). Kiwifruit is  
122 a dioecious species with large, open and stamen-abundant male and female flowers on different  
123 trees (Fig. S1). Both sexes produce pollen but no nectar (Hopping, 1990). Thus, although highly  
124 accessible and pollen rich, kiwifruit flowers can be unattractive for nectar-feeders (Clinch, 1984;  
125 Pomeroy and Fisher, 2002). Blueberry shows specialized flower traits (narrow-opening bell-  
126 shaped corolla, protected poricidal anthers, protruding stigma, nectaries at the bottom of the  
127 flower; Fig. S1) that may restrict pollinator assemblages to species with buzzing behaviour and  
128 long tongues and some very small insects that can enter the corolla completely (Sampson et al.,  
129 2013; Blaauw and Isaacs, 2014; Cortés-Rivas et al., 2022). Bearing these between-crop  
130 differences in mind, we evaluate how these exotic crops adapt to the common pollination  
131 environment of a new cultivation region, by estimating the contribution of insect assemblages to  
132 the pollination service and the landscape and management factors regulating these same  
133 assemblages. To do this, we address the following questions: 1) How diverse are pollinator  
134 assemblages of introduced kiwifruit and blueberry crops? 2) Do crop yields suffer from  
135 pollination limitation? 3) Do pollinator abundance and richness affect crop yields? and 4) Are  
136 pollinator abundance and richness affected by landscape structure and the management of  
137 domestic pollinators?

138

## 139 **2. Materials and Methods**

### 140 **2.1. Study sites**

141 The study was carried out in commercial orchards located in Asturias, Northern Spain (43°20N,  
142 6°00W; Fig. S2A and B). Asturias has a temperate oceanic climate with rainfall usually  
143 exceeding 1100 mm that is fairly evenly spread out over the year. The orography is very  
144 variable from the narrow coastline inland, where mountainous terrain dominates, and altitudes  
145 range from 0 to 2500 m a.s.l. Kiwifruit orchards are usually located in the lowlands, next to  
146 rivers (due to the high water demand of this crop) and on flat or low-slope land (as they require  
147 relatively complex infrastructures to support trees). Meanwhile, blueberry crops are not as  
148 demanding in terms of water and infrastructure, and thus orchards can be found typically on  
149 terrain with variable slopes and from sea level to 800 m a.s.l. Asturias has a highly  
150 heterogeneous landscape, with fruit crops embedded in a fine-grain mosaic of pastures, crops,  
151 eucalyptus plantations and varying-sized patches of natural woody vegetation, from hedgerows  
152 separating fields to forests or shrublands surrounding orchards (Fig. S2C-H).

153 For kiwifruit, the study was conducted in 2015 and 2016 in the same 15 commercial  
154 orchards both years (14 in 2016). All the female trees in all orchards were from the cultivar  
155 'Hayward', whereas male trees were of various cultivars (even within each site). Details on  
156 orchard features (size, tree age, tree density) are given in Table S1. No serious pests attack  
157 kiwifruit in this region so typically no pesticides are applied. The study on northern highbush and  
158 rabbiteye blueberry crops was conducted in 2019 and 2021 in the same 20 commercial  
159 orchards each year, as all orchards grew both blueberry species (see Table S1 for orchard  
160 details). Some blueberry growers applied pesticides against spotted wing drosophila  
161 (*Drosophila suzukii*) pest attack in summer, some months after the pollinator samplings.

162

### 163 **2.2. Pollinator assemblages**

164 We aimed to identify the insect groups and species that comprised the pollinator assemblages  
165 in kiwifruit and blueberry orchards, as well as to assess their visit rates to crop flowers.

166 All kiwifruit orchards were sampled when they were in full bloom, what occurred from 2<sup>nd</sup>  
167 to 8<sup>th</sup> June in 2015 and from 9<sup>th</sup> to 27<sup>th</sup> June in 2016, depending on the orchard. As full bloom in  
168 kiwifruit last just a few days, each orchard was visited just once in each year and during the day

169 of the visit was surveyed at three different times (1200h, 1400h and 1600h) in order to cover the  
170 maximum range of pollinator activity and to limit temporal biases. Samplings were conducted  
171 under standard climatic conditions: dry vegetation, clear to lightly overcast skies, temperatures  
172 >13°C and wind speed <2.5 m.s-1. At each site and for each year, five female trees (at least 15  
173 m from the edge to avoid potential edge effects) were randomly selected for pollinator  
174 observations. In each census we observed a 1-m diameter area of the canopy of each tree for a  
175 period of 5 min, recording the number of insect visits and the number of flowers in the selected  
176 area. In total, therefore, each orchard accounted for 75 minutes of observation (3 censuses \* 5  
177 trees \* 5 min) per year. To avoid disrupting floral visits, no insects were collected during the  
178 surveys and, therefore, we were only able to reliably identify certain easily recognised species  
179 (e.g. *Apis mellifera*, *Bombus* species, *Episyrphus balteatus*, etc.). Most visitors were, thus,  
180 assigned to one of the following groups: bumblebees, wild bees, hoverflies (predatory hoverflies  
181 with aphidophagous larvae or *Eristalis* hoverflies) or flies (Diptera other than hoverflies). In order  
182 to better assess species richness, and just after each visitation survey, we also made separate  
183 assessments of kiwifruit pollinators by walking slowly along tree rows and catching all floral  
184 visitors observed over a 10 min period for each survey event (i.e. a sum of 30 min per orchard  
185 per year). Captured specimens were identified in the laboratory.

186         The sampling in blueberry orchards was conducted on the cultivar ‘Duke’ (at one site it  
187 was substituted by ‘Chandler’) for highbush type and on ‘Ochlockonee’ (‘Centrablue’ at one site)  
188 for the rabbiteye type. All orchards had at least two highbush cultivars and plants of another  
189 rabbiteye cultivar (typically Powderblue) interspersed in the rows of Ochlockonee plants, what  
190 ensures cross-pollination. Blueberry bloom period can last for one month so, to cover any  
191 temporal variability in the pollinator assemblage, two censuses (with 5 to 12 days between  
192 censuses) per year were performed for each blueberry type. Surveys were conducted between  
193 1100 h and 1600 h and under standard climatic conditions (see above). Orchards were visited  
194 at different times of the day and in a different order for each census in order to limit temporal  
195 biases. All orchards were sampled from 12<sup>th</sup> to 30<sup>th</sup> April in 2019 and from 29<sup>th</sup> of March to 22<sup>nd</sup>  
196 April in 2021.

197         For each blueberry type, a group of 30 consecutive plants 15 m away from the edge  
198 were randomly selected and marked at the beginning of the bloom. Before each survey we

199 counted the total number of open flowers in five randomly selected plants (in the group of 30)  
200 and used such information to estimate the total number of flowers observed. In each survey we  
201 walked slowly along the 30 plants recording all visits to blueberry flowers and catching floral  
202 visitors non-identified by sight, during a 10 min period at each survey event (i.e. a sum of 20 min  
203 per blueberry type per orchard and per year). Captured specimens were identified in the  
204 laboratory.

205 Insect visitation data were used to estimate the richness (number of species) of  
206 pollinators, as well as the abundances of honeybees and wild pollinators as the number of  
207 individuals visiting flowers per 100 flowers per 5 minutes, on a plant, census or orchard basis.  
208

## 209 **2.2. Pollination effect on crop yield**

210 In order to understand the effects of pollination on crop yields, we measured fruit set (number of  
211 flowers to set fruits) and fruit weight for all crops, both in flowers open to pollinators and in  
212 flowers that received a hand-made supplementation of pollen.

213 In kiwifruit, in the visit to sample pollinators (see above), 3 similar target female trees  
214 per orchard and 40 recently opened flowers per tree were selected each year. Twenty of the  
215 flowers were randomly selected, marked with blue wires and left unmanipulated, potentially  
216 allowing for pollination through insect and wind vectors (open-pollination treatment). The other  
217 20 flowers were marked with red wires and supplemented with pollen by brushing each of them  
218 with three different flowers previously collected from different male trees from the same orchard  
219 (supplementary-pollination treatment). These flowers were saturated with pollen, meaning that  
220 fruit set and fruit weight in the supplementary-pollination treatment would be the maximum  
221 possible for the corresponding tree. In early November, when fruits were ripe, we counted the  
222 number of fruits that had developed from all marked flowers in each treatment. Those fruits  
223 were harvested and weighed individually. Then we averaged the weight of all the fruits of each  
224 tree and treatment.

225 In blueberry, on the first visit to sample pollinators (see above), five target plants  
226 (included in the 30 for pollinator surveys) per type (highbush and rabbiteye) and orchard were  
227 selected each year. Then, two distal clusters of buds with open flowers were selected on each  
228 plant and marked with coloured flagging and numbered. The total number of flowers (open and



229 closed) of each cluster were counted. One randomly selected cluster was left unmanipulated,  
230 potentially allowing for self-pollination and cross-pollination through insect and wind vectors  
231 (open-pollination treatment). The other cluster was supplemented with pollen collected  
232 previously from the same and different blueberry cultivars from the same orchard and randomly  
233 mixed (supplementary-pollination treatment). An electric toothbrush (Oral-B, Procter & Gamble,  
234 USA) was placed on the corolla of flowers to vibrate pollen out of donor flowers into a Petri dish,  
235 and then a small paint brush was used to immediately apply pollen directly on the stigma of the  
236 hand-pollinated flowers (Gibbs et al., 2016). As flowers open sequentially and not all flowers  
237 could be pollinated in a single visit, the pollen supplementation was performed twice, once  
238 during each visit to sampling pollinators, in order to pollinate as many flowers as possible  
239 (average 92.8%, min-max 71-100% of flowers per cluster were pollinated). Flowers were  
240 allowed to develop normally throughout the bloom and fruit development periods. When at least  
241 50% of the fruits in the clusters had ripened, and just before the first harvest by growers, all  
242 those experimental fruits (the ripe and unripe fruits) were harvested and brought into the  
243 laboratory. We counted the number of fruits in each cluster and obtained fruit set by dividing the  
244 total number of fruits by the number of flowers counted earlier in the season. Then we weighed  
245 all the ripe fruits of each cluster together and obtained the average fruit weight by dividing the  
246 total weight of the ripe fruits by the number of ripe fruits in that cluster.

247

#### 248 **2.4. Landscape structure**

249 Landscape structure for kiwifruit and blueberry crops was quantified by means of a Geographic  
250 Information System (GIS, ArcGIS9.3) based on 1:5000- scale orthophotographs (2017). We  
251 delimited a circular plot of 1000-m radius (R1000 plot, hereafter), centred on the sampled  
252 trees/plants of each orchard, within which we distinguished, by carefully digitizing landscape  
253 patches, six general types of land cover: 1) semi-natural woody habitats (including forest,  
254 heathland, hedgerows and isolated trees); 2) exotic tree plantations (mainly eucalyptus); 3) fruit  
255 tree plantations (apple, kiwi and blueberry); 4) pastures (meadows, gardens and crops), 5) other  
256 habitats (mainly water courses) and 6) urbanized land (roads and buildings; see examples in  
257 Fig. S2). We estimated the availability of each land cover type around each orchard from the  
258 percentage of cover in each R1000 plot.

259           The landscape surrounding kiwifruit orchards was dominated by pastures (mean  
260 percentage 46.0, min-max percentage 20.5-68.9), followed by semi-natural woody habitats  
261 (26.2, 11.3-58.1), eucalyptus tree plantations (10.0, 0.00-33.2), urbanized land (7.5, 1.6-19.4),  
262 fruit plantations (7.2, 1.0-11.9) and other (3.2, 0-13.1). Around blueberry orchards the landscape  
263 was dominated by semi-natural woody habitats (mean percentage 37.7, min-max percentage  
264 16.9-74.2) and pastures (37.2, 20.5-54.9), followed by exotic tree plantations (12.9, 0.2-46.9),  
265 urbanized land (6.4, 2.3-25.1), fruit plantations (4.6, 0.4-11.8) and other habitats (1.2, 0-7.1).

266           In the studied region, the main trends of landscape change across space are shaped by  
267 the complex and interrelated variation of different land cover types, rather than by major  
268 changes in single cover types (e.g. Martínez-Sastre et al., 2020). Thus, for an accurate  
269 representation of the general landscape gradients surrounding orchards, we used a Principal  
270 Component Analysis (PCA, performed with the princomp function in the R Stats package, R  
271 Core Team (2022)) applied to the six general cover types in the R1000 plots around orchards  
272 (Table S2). For kiwifruit, the first three principal components accounted for 81.3% of the  
273 variation in our landscape data: PC1 (42.0% of variance explained) described a gradient  
274 ranging from landscapes dominated by other habitats to pasture-dominated landscapes; PC2  
275 (23.7%) represented a gradient of increased proportions of exotic (eucalyptus) plantations  
276 around the orchards; and PC3 (15.6%) a gradient from semi-natural woody habitats to  
277 urbanized landscapes. In the case of blueberry orchards, the first three principal components  
278 accounted for 79.8% of the variation in our landscape data: PC1 (36.8% of variance explained)  
279 described a gradient that ranged from landscapes dominated by semi-natural woody habitats to  
280 pasture-dominated landscapes; PC2 (22.6%) a gradient of increased proportions of exotic  
281 (eucalyptus) plantations around the orchards; and PC3 (20.3%) a gradient from landscapes  
282 dominated by fruit tree plantations to urbanized landscapes. In both crop types, these three  
283 principal components were used as non-correlated parameters of landscape structure.

284

## 285 **2.5. Pollinator management within orchards**

286 In order to account for within-orchard features affecting pollinator occurrence and availability,  
287 we asked the growers about the occurrence/absence and the density of honeybee hives and  
288 commercial bumblebee colonies (number per ha). Both occurrence and density of honeybee

289 hives and commercial bumblebee colonies varied greatly across kiwifruit and blueberry  
290 orchards (Table S1). For kiwifruit, 73% (year 1) and 64% (year 2) of the orchards had honeybee  
291 hives and/or commercial bumblebee colonies for pollination, with up to 10-fold differences in  
292 colony density. In blueberry orchards, around half of the growers had introduced honeybee  
293 hives and/or bumblebee colonies for pollination, and differences in colony density were up to  
294 20-fold.

295 We did not consider other orchard features typically targeted as drivers of pollinator  
296 assemblages, such as flowering groundcover or organic management (e.g. Samnegard et al.,  
297 2020), as they did not represent large enough environmental gradients in our study cases.  
298 Concerning flowering groundcover, both kiwifruit and blueberry producers typically remove  
299 flowers from the ground by shredding during crop bloom to avoid expected competition with the  
300 crop flowers. In addition, a comparison between organic and conventional management types  
301 was not possible in kiwifruit (just one orchard was organic, see above) and it was discarded in  
302 blueberry because management is very similar in both certified-organic and non-certified  
303 orchards due to the low level of intensification of these crops.

304

## 305 **2.6. Statistical analysis**

306 We evaluated whether crop yields suffered pollination limitation by means of Generalized Linear  
307 Mixed Models (GLMMs; Bolker et al., 2009) through the comparison of the effects of the  
308 pollination treatments (open vs. supplementary pollination; predictor) on fruit set and fruit weight  
309 per tree (response variables), for each crop type. Binomial (logit link) and Gaussian (identity  
310 link) family distributions were considered for fruit set and fruit weight, respectively. All models  
311 contained a random structure where plant identity was nested within orchard.

312 For all crop types, we evaluated whether pollinator abundance and richness affected  
313 crop yields by means of GLMMs using, as response variables, fruit set and fruit weight in  
314 flowers open to pollinators. Binomial (logit link) and Gaussian (identity link) family distributions  
315 were considered for fruit set and fruit weight, respectively. In those crops where pollination  
316 limitation had been previously demonstrated, we used, as a response variable (Gaussian error  
317 distribution, identity link), an explicit estimation of per-tree/plant pollen limitation effect on fruit  
318 set or fruit weight, estimated as the natural logarithm of the response ratio,  $\ln(X_{\text{supplemented}}/X_{\text{open}})$ ,

319 where  $X_{\text{supplemented}}$  and  $X_{\text{open}}$  are the crop yields (fruit set or fruit weight) observed after  
320 supplemental and open pollination, respectively (Sáez et al., 2022). As fixed-effect predictors,  
321 we considered the abundance of honeybee, the abundance of wild pollinators and pollinator  
322 richness (orchard-level estimates). In kiwifruit models, we also considered as fixed predictor the  
323 proportion of male trees with respect to female trees per orchard, given that kiwifruit is a  
324 dioecious plant and the density of male plants could condition the quantity of fertile pollen  
325 available to pollinate female flowers. All models included orchard identity as random factor.  
326 Correlation between fixed-effect predictors was low (Pearson correlation coefficient:  $|r| < 0.450$ ,  
327  $N = 89$ ) except in the case between the abundance of honeybee and the abundance of wild  
328 pollinators ( $r = -0.610$ ,  $p < 0.001$ ,  $n = 89$ ). Thus, values of Variance Inflation Factor (VIF) were  
329 estimated for fixed effects in all models, in order to interpret potential effects of collinearity (all  
330 VIF values were lower than 2, what is considered indicative of low collinearity; Quinn & Keough  
331 2002).

332         In order to evaluate the effects of landscape structure and the management of domestic  
333 pollinators in the orchards on pollinator abundances and richness, we used GLMMs,  
334 considering honeybee abundance, wild pollinator abundance and pollinator richness per census  
335 and orchard as three different response variables for each crop type. Gaussian (identity link)  
336 and Gamma (log link) family distributions were considered for abundance measures, and  
337 Gaussian (identity link), Gamma (log link) and Poisson (log link) family distributions for richness.  
338 Different models with the different family distributions were checked for a given response  
339 variable, choosing that with the lowest AICc value. For each crop type and response variable,  
340 we considered a whole model incorporating as fixed predictors the three landscape PCA  
341 vectors, the occurrence of honeybee hives, the occurrence of bumblebee colonies, and the  
342 interaction between occurrence of honeybee hives and that of bumblebee colonies (this  
343 interaction proved not significant [ $p > 0.1$ ] in all models and it was subsequently removed in final  
344 models). Orchard identity was included as a random factor. Given the high between-site  
345 variability in the density of pollinator hives, we compared this model with a second whole model,  
346 substituting the occurrences with the densities of honeybee hives and bumblebee colonies (and  
347 their interaction), choosing that with the lowest AICc value. Values of PCA vectors and densities  
348 of honeybee hives or bumblebee colonies were uncorrelated across orchards, as were densities

349 of honeybee hives and bumblebee colonies (Pearson correlation coefficients, kiwifruit:  $|r| <$   
350  $0.274$ ,  $p > 0.05$ ,  $N = 29$ ; blueberry:  $|r| < 0.286$ ,  $p > 0.05$ ,  $N = 40$ ). In any case, VIF was estimated  
351 for all fixed predictors in all models, resulting lower than 2 in all cases.

352 All models were fitted using the lme4 R package (Bates et al., 2015), and model  
353 adequacy was checked by visual diagnosis (residuals vs fitted values plot, and quantile-quantile  
354 plot). Model  $R^2_{\text{GLMM}(m)}$  values (marginal  $R^2$ , that is, the variance explained by the fixed effects  
355 only, Nakagawa and Schielzeth, 2013) were obtained with the MuMIn R package (Barton,  
356 2022).

357

### 358 **3. Results**

#### 359 **3.1. How diverse are pollinator assemblages of introduced kiwifruit and blueberry crops?**

360 In kiwifruit, we recorded 2,273 insects visiting flowers (mean number of visits per 100 flowers  
361 per 5 minutes:  $10.97 \pm 0.53$  SE,  $N = 435$  censuses). As pollinator assemblages were almost  
362 identical in the two years (Fig. S3A), data were pooled for the description of the pollinator  
363 community, that was composed by 51 species, mainly hoverflies (21 species) and wild bees  
364 from the family Halictidae (17 species; Table S3). Considering all orchards, honeybee, with  
365 69.0% of the visits, was the dominant pollinator (Fig. 1A), followed by hoverflies (17.1%; mainly  
366 predatory hoverflies) and other dipterans (9.1%). Wild bees (2.5%) and bumblebees (2.3%;  
367 mostly *Bombus terrestris*) completed the assemblage. Honeybee was the most numerous flower  
368 visitor in all sites but one (Fig. S4A).

369 We recorded 2,290 insects visiting highbush blueberry flowers ( $0.285 \pm 0.022$  SE  
370 visits/100 flowers/5 minutes,  $N = 80$  censuses). Pollinator assemblages were similar between  
371 years (Fig. S3B) and composed of 28 species, mainly wild bees (13 species) and bumblebees  
372 (6 species; Table S4). Globally, bumblebees (51.5%), followed closely by honeybee (43.9%),  
373 were the dominant pollinators (Fig. 1B). Wild bees (2.7%) and dipterans and butterflies (1.9% in  
374 total) completed the assemblage. *Bombus terrestris* (85%) was the most numerous bumblebee  
375 species, followed by *B. pascuorum* (10%) and *B. pratorum* (4%). Bumblebees dominated the  
376 assemblage in 11 orchards and honeybee in 9 (Fig. S4B).

377 In rabbiteye blueberry, we recorded 2,546 insects visiting flowers ( $0.178 \pm 0.011$  SE  
378 visits/100 flowers/5 minutes,  $N = 80$  censuses). Again, pollinator assemblages were very similar

379 between years (Fig. S3C). Bumblebees (12 species) and wild bees (11 species) dominated the  
380 assemblage of floral visitors (28 species in total; Table S5). Considering all orchards,  
381 bumblebees (90.6%) clearly dominated the assemblage, with honeybee representing only 5.8%  
382 of total visits, wild bees 2.3% and others 1.3%. *B. terrestris* (77%) was the most numerous  
383 bumblebee species, followed by *B. pascuorum* (9%), *B. pratorum* (8%) and *B. hortorum* (5%).  
384 Bumblebees were the dominant pollinator in all orchards, whereas honeybee accounted for less  
385 than 20% in all sites but one (Fig. S4C).

386

### 387 **3.2. Do crop yields suffer from pollination limitation?**

388 In kiwifruit, fruit set was very high (95.5%) and did not differ between open and supplementary  
389 pollination treatments (Tables S6 and S7). Nevertheless, we found evidence of pollination  
390 limitation in fruit weight (effect estimate:  $0.11 \pm 0.02$  (SE);  $t = 5.74$ ;  $P < 0.001$ ), which increased  
391 7.2% in the supplementary pollination treatment relative to the open pollination treatment (on  
392 average, 100.9 g and 94.1 g, respectively; Fig. 2 and Tables S6 and S7). Pollen limitation was  
393 inconsistent across sites, with some orchards showing similar fruit weights across treatments  
394 but others where trees bore fruits up to 40% heavier with supplementary pollination (Fig. S5).

395 No signs of pollination limitation were found in highbush blueberry, neither in terms of  
396 fruit set (open pollination: 82.1%, supplementary pollination: 82.2%) nor in terms of fruit weight  
397 (open pollination: 1.47 g, supplementary pollination: 1.52 g; Tables S6 and S7). A similar  
398 pattern was found in rabbiteye blueberry, with fruit set of 84.8% and 84.9%, and fruit weight of  
399 0.83 g and 0.85 g, in open- and in supplementary pollination, respectively (Tables S6 and S7).

400

### 401 **3.3. Do pollinator abundance and richness affect crop yields?**

402 Kiwifruit crop yield was affected by the local abundance of pollinators (Table S8). On the one  
403 hand, fruit set was significantly lower in those orchards with higher abundance of wild pollinators  
404 ( $-0.32 \pm 0.09$ ;  $z = -3.69$ ;  $P < 0.001$ ; Fig. 3A). On the other hand, pollination limitation in fruit  
405 weight decreased significantly when the abundance of honeybee rose ( $-0.07 \pm 0.02$ ,  $t = -3.61$ ;  $P$   
406  $< 0.001$ ; Fig. 3B) and when wild pollinator abundance declined ( $0.02 \pm 0.01$ ,  $t = 2.43$ ;  $P =$   
407  $0.021$ ). Finally, kiwifruit crop yield was independent of the proportion of male:female trees in the  
408 orchard (Table S8).

409 In highbush blueberry, fruit set responded positively to the abundance of wild pollinators  
410 ( $5.92 \pm 0.99$ ;  $z = 5.98$ ;  $P < 0.001$ ; Fig. 3C and Table S8), but fruit weight was negatively related  
411 to the abundance of honeybee ( $-0.95 \pm 0.27$ ;  $t = -3.47$ ;  $P < 0.001$ ; Fig. 3D and Table S8). In  
412 rabbiteye blueberry, fruit set was negatively affected by the abundance of honeybee ( $-36.82 \pm$   
413  $7.69$ ;  $z = -4.78$ ;  $P < 0.001$ ; Fig. 3E and Table S8), whereas fruit weight was positively predicted  
414 by the abundance of wild pollinators ( $0.78 \pm 0.38$ ;  $t = 2.06$ ;  $P = 0.042$ ; Fig. 3F and Table S8).

415

#### 416 **3.4. Are pollinator abundance and richness affected by landscape structure and the** 417 **management of domestic pollinators?**

418 In kiwifruit orchards, pollinator abundance and richness showed significant responses to  
419 landscape structure (represented by landscape cover type PCA vectors) but was not affected by  
420 the management of honeybee hives or commercial bumblebee colonies (Table S9). The model  
421 for honeybee abundance accounted for a third of the variability of this response variable  
422 (marginal  $R^2 = 0.351$ ). Specifically, honeybee abundance was only and negatively affected by  
423 PC1 (gradient from other habitats to pastures;  $-0.67 \pm 0.15$ ,  $t = -4.49$ ;  $P = 0.001$ ; Fig. 4A). The  
424 abundance of wild pollinators was negatively affected by PC3 (gradient from semi-natural  
425 habitat to urbanized land;  $-0.37 \pm 0.15$ ;  $t = -2.37$ ;  $P = 0.041$ ; Fig. 4B). Finally, none of the tested  
426 variables affected significantly the richness of pollinators (Table S9).

427 Abundance and richness of pollinators in highbush blueberry also showed significant  
428 responses to landscape structure, but not to the management of pollinator hives (Table S10).  
429 That is, honeybee abundance was negatively affected by PC1 (gradient from semi-natural  
430 woody habitat to pasture cover;  $-0.06 \pm 0.03$ ;  $t = -2.40$ ;  $P = 0.016$ ; Fig. 4C) and PC3 (gradient  
431 from fruit tree plantation to urbanized land;  $-0.05 \pm 0.03$ ;  $t = -1.99$ ;  $P = 0.046$ ). In contrast, PC1  
432 and PC2 (gradient of intensity of exotic tree plantation cover) had positive effects on wild  
433 pollinator abundance ( $0.27 \pm 0.12$ ;  $t = 2.34$ ;  $P = 0.019$  (Fig. 4D) and  $0.27 \pm 0.11$ ;  $t = 2.55$ ;  $P =$   
434  $0.011$ , respectively). In rabbiteye blueberry, landscape structure and domestic pollinators never  
435 accounted for more than 13% of the variability of the abundance and richness of pollinators  
436 (marginal  $R^2 < 0.134$  in all cases; Table S11). The role of landscape was limited to a negative  
437 effect of PC1 (gradient from semi-natural woody habitat to pasture cover) on pollinator richness

438 (-0.15 ± 0.05; t = -2.65; P = 0.008; Fig. 4E). The density of bumblebee colonies negatively  
439 affected honeybee abundance (-0.00 ± 0.00; t = -2.04; P = 0.041; Fig. 4F).

440

#### 441 **4. Discussion**

442 The three exotic crops studied here showed large and diverse pollinator assemblages in the  
443 new cultivation areas of NW Spain and differed in the composition of their insect assemblages  
444 and the identity of their main pollinator species. Despite these differences, the local  
445 assemblages of pollinators of the three crops mostly depended on landscape structure around  
446 orchards and, at the same time, were scarcely affected by the introduction of domestic  
447 pollinators. Our results highlight the importance of understanding the specific differences in the  
448 pollination ecology of new exotic crops before designing general management  
449 recommendations, and they question the use of managed pollinators in advance of assessing  
450 the contribution of extant insects to the pollination service.

451

##### 452 **4.1. How diverse are pollinator assemblages of introduced fruit crops?**

453 The three study crops had diverse assemblages of insect pollinators that were each numerically  
454 dominated by bees. Honeybee clearly dominated kiwifruit assemblages, representing almost  
455 70% of visits to flowers. Bumblebees and honeybee dominated more or less equally floral visits  
456 in highbush blueberry, and, finally, bumblebees accounted for more than 90% of visits in  
457 rabbiteye blueberry. Floral morphology of the different crops partially explains interspecific  
458 differences in pollinator assemblages. In this sense, the large open flowers of kiwifruit, and the  
459 accessibility to different pollinator types derived from this floral morphology, would explain the  
460 generalism (i.e. the richest assemblage of visitors, with 51 species) of this crop species. Many  
461 of these floral visitors can also be considered highly generalist themselves, like honeybee and  
462 many halictid bees and dipterans (see also Howlett et al., 2017; Gaspar et al., 2022). As  
463 expected from their floral traits, blueberry crops were more specialized and, compared to  
464 kiwifruit, were visited by a smaller array of pollinator species (28 for both blueberry types) which  
465 showed either buzzing behaviour to release pollen, long tongues or small size (Sampson et al.,  
466 2013; Cortés-Rivas et al., 2022). Specialization degree differed even between blueberry types  
467 (and even between highbush cultivars; Courcelles et al. 2013; Cortés-Rivas et al., 2022), being



468 higher in the rabbiteye type, likely due to its longer corolla and narrower flower opening,  
469 compared to the highbush type (Sampson et al., 2013; Fig. S1). This would explain why  
470 honeybee, despite being abundant in the blueberry orchards (44% of visits in highbush  
471 blueberry) accounted for only 6% of visits in the rabbiteye type: this insect had poor access to  
472 nectaries due the narrow flower and its short tongue. The specialization of the rabbiteye was  
473 also reflected in the characteristics of the assemblage of bumblebees, with more species and a  
474 higher occurrence of those with longer tongues (e.g. *B. hortorum*), and those of wild solitary  
475 bees (the long-tongued *Anthophora* bees accounted for 64% of wild bee visits in rabbiteye and  
476 only 38% in highbush). Interestingly, honeybee made a significant numerical contribution to the  
477 pollination assemblages of other rabbiteye blueberry cultivars (Sampson and Cane, 2000;  
478 Kendall et al., 2020), whereas their contribution to assemblages of other highbush cultivars is  
479 lower than that to Duke (Courcelles et al. 2013; Cortés-Rivas et al., 2022). Such intraspecific  
480 variability reflects the need of evaluating cultivar differences in pollination considering the  
481 relation between pollinators and flower traits.

482

#### 483 **4.2. Do crop yields suffer from pollination limitation?**

484 Despite its large and diverse pollinator assemblages, kiwifruit crops experienced pollination  
485 limitation in the region studied (see Castro et al., 2021 for a similar case in kiwifruit non-native  
486 areas). Pollination limitation led to, on average, 7.2% reductions in fruit weight (40% in some  
487 orchards). In other words, the proper management of pollination could increase fruit weight (and  
488 associated yield and economic value) up to 40%. Fruit weight in kiwifruit is strongly dependent  
489 on the number of seeds, which in turn depends on the number of pollen grains fertilizing ovules.  
490 A flower contains up to 1500 ovules and a marketable kiwifruit of 100 g has around 1200 seeds  
491 (Hopping, 1990; Testolin et al., 1991), which means that the flower received at least 1200 grains  
492 of compatible pollen. Therefore, the fruit weight difference is reflecting insufficient quantity of  
493 male compatible pollen reaching the female flowers. This could result from 1) scarcity of  
494 pollinators to transfer pollen from male to female flowers (e.g. Abbate et al., 2021; see  
495 discussion below, point 4.3), 2) low pollen availability in the orchard due to low male-female tree  
496 ratios (Greatti and Barbattini, 1997; García et al., 2015), or 3) lack of compatibility or bloom  
497 synchronization between male and female flowers (Hopping, 1990; García et al., 2015). Our

498 results evidence no effect of male pollen availability on pollination service, suggesting an  
499 adequate proportion of male and female trees in the orchards. However, the compatibility  
500 between male and female trees remains unexplored.

501 Even with their specialized flower morphology, there was no pollination limitation in any  
502 of the blueberry types. This suggests that flowers are receiving enough quantities of compatible  
503 pollen, basically from insect vectors, since self-pollination and wind-pollination in blueberry  
504 flowers is limited (Klein et al., 2007). This also suggest that the current cultivar layout in the  
505 studied blueberry orchards favours cross-pollination in the rabbiteye type, which is known to be  
506 partially self-incompatible (Kendall et al., 2020). These results contrast with those found in other  
507 regions outside of the native range, where, at least for the highbush type, the crop frequently  
508 suffers pollination limitation that are most likely the result of a scarcity of native pollinators (e.g.  
509 Gibbs et al., 2016; Campbell et al., 2018; Martin et al., 2021 but see Kendall et al., 2020).

510

#### 511 **4.3. Do pollinator abundance and richness affect crop yields?**

512 We found marked effects of pollinator abundances on the yields of the exotic crops examined,  
513 although both effect type (derived from abundances of honeybees or wild pollinators, and  
514 affecting fruit set or fruit weight) and sign (positive or negative) varied considerably across crop  
515 types. In kiwifruit, the higher the abundance of honeybees visiting flowers, the lower the  
516 limitation of fruit weight (see also Castro et al., 2021), which suggests that abundance can  
517 compensate for the low efficiency of honeybee as pollinator in terms of legitimate visits or  
518 productivity per single visit (Miñarro and Twizell, 2015). Contrary to previous evidence in other  
519 crops (e.g. Garibaldi et al., 2013; Martínez-Sastre et al., 2020; Pérez-Méndez et al., 2020),  
520 higher abundance of wild pollinators in kiwifruit led to pollination-derived yield constraints, in this  
521 case on fruit-set. Fifty-seven percent of the pollinator species in the present study were  
522 dipterans and beetles, which accounted for more than 26% of visits (Fig. 1; Table S3). These  
523 species notably increased wild pollinator abundance locally (Fig. S4A) but probably contributed  
524 little to kiwifruit pollination due to their very passive foraging behaviour and low rates of  
525 legitimate visit (Testolin et al., 1991; Miñarro and Twizell, 2015). However, it remains unknown  
526 for us whether the negative relationship between wild pollinator abundance and kiwifruit  
527 productivity is direct (due to pollen losses, higher pollen loads of incompatible pollen, damages

528 in stigmas) or mediated by effects of other factors not considered in this study, such as negative  
529 interactions between the dominant pollinator and those less efficient wild pollinators (Perfectti et  
530 al. 2009).

531 In both blueberry types, wild pollinator (basically bumblebee) abundance had positive  
532 effects on crop yields, whereas that of honeybee affected yield negatively. Bumblebees are  
533 known to be better pollinators for blueberry than honeybee, in terms of number of flowers visited  
534 per time, pollen transfer, buzzing behaviour and resulting yield (Estravis-Barcala et al., 2021;  
535 Miñarro and García, 2021; Sun et al., 2021; Cortés-Rivas et al., 2022). Consequently, the  
536 negative relationship between honeybee abundance and blueberry yields could be more a  
537 consequence of a negative covariation between honeybee and bumblebees rather than a direct  
538 detrimental effect of honeybee on pollination. In fact, bumblebees and honeybee clearly have  
539 different peaks of activity throughout the blueberry bloom season as well as along gradients of  
540 daily temperature and relative humidity (Miñarro and García, 2021). Interestingly, honeybee  
541 may accomplish the pollination needs of highbush blueberry in other situations when local  
542 pollinator populations are scarce or absent (Cavigliasso et al., 2021; Martin et al., 2021).

543

#### 544 **4.4. Are pollinator abundance and richness affected by landscape structure and the** 545 **management of domestic pollinators?**

546 We show here that the management of domestic pollinators, at least in terms of the frequencies  
547 of occurrence and densities of hives and colonies used currently, had practically no effect on  
548 the pollinator assemblages of any of the studied crops. This suggests that extant insect  
549 assemblages, spontaneously occurring within orchards, are responsible for the pollination of the  
550 exotic crops under study. These extant populations almost certainly combine local wild  
551 pollinators with domestic honeybee individuals that spill-over into the orchards from surrounding  
552 areas attracted by the mass bloom of fruit crops, thus masking the expected effect of the  
553 intentionally introduced colonies. Both this study and previous research in other crops in this  
554 region evidence that honeybee and bumblebees occurred spontaneously in the crops in the  
555 absence of managed colonies (Miñarro and Twizell, 2015; Martínez-Sastre et al., 2020; Miñarro  
556 and García, 2021). Honeybees could originate from the small and profuse domestic apiaries in  
557 the surrounding landscape and/or feral populations, whereas *B. terrestris* is an abundant and

558 widely-distributed native pollinator in this region (this study, Miñarro and Twizell, 2015; Miñarro  
559 and García, 2018; Martínez-Sastre et al., 2020; Miñarro and García, 2021). During the surveys,  
560 we confirmed that commercial bumblebees stayed in the orchards and visited crop flowers (the  
561 commercial subspecies had black hairs whereas they are blond in local subspecies), although  
562 they accounted for a very low fraction of pollinator visits.

563         Local variability in pollinator assemblages of all exotic crops under study was controlled  
564 by the structure of the landscape surrounding orchards. The landscape may affect the local  
565 pollinator assemblages by providing source, or even sink, habitat patches rich in nesting,  
566 feeding, and refuge resources (Senapathi et al., 2017). In our case, honeybee abundance in  
567 kiwifruit crops decreased in landscapes with high cover of pastures around the crop, suggesting  
568 that honeybee most likely prefer pasture flowers over the nectar-less flowers of kiwifruit (Clinch,  
569 1984; Pomeroy and Fisher, 2002). For instance, less than 5% of the pollen collected in  
570 honeybee hives within kiwifruit plantations in Argentina was kiwifruit pollen (De Piano et al.,  
571 2021).

572         The pollinator assemblages of highbush blueberry were also partially driven by  
573 landscape structure. Honeybees were favoured by semi-natural habitats but hindered by  
574 pastures. The presence of fruit-tree plantations (mostly other blueberry crops) also benefited  
575 honeybee abundance, likely because of the higher availability of trophic resources from this  
576 type of land cover (see Marini et al., 2012 for a similar case in apple crops). Wild pollinator (i.e.  
577 bumblebees) abundances responded positively to the coverage of pastures and eucalyptus and  
578 negatively to that of semi-natural woody habitats, that is, rather the opposite pattern to that of  
579 honeybee (Gibbs et al., 2016; Bobiwash et al., 2017; Mallinger et al., 2021). We should not  
580 discard that these opposing patterns could be mediated by the previously mentioned negative  
581 interaction between honeybee and bumblebees (Miñarro and García, 2021). The negative effect  
582 of the density of bumblebee colonies on honeybee abundance observed in rabbiteye blueberry  
583 is consistent with the negative interaction hypothesis. Also in rabbiteye blueberry, pollinator  
584 richness was lower in habitats with higher pasture cover than in those with more semi-natural  
585 woody habitats. Pollinator richness is probably shaped by the variation in the number of  
586 *Bombus* species (the main pollinators of this blueberry type), which find in hedgerows and forest  
587 a high quality habitat (Proesmans et al., 2019; Timberlake et al., 2019).

588

589 **4.5. Management recommendations**

590 The two main pollinator types, honeybee and bumblebees (especially *B. terrestris*), of the exotic  
591 crops studied are ubiquitous in the study region and occur spontaneously in the orchards. Both  
592 pollinator types are largely influenced by landscape structure around orchards, but scarcely  
593 affected by the installation of hives or commercial colonies. Thus, general management actions  
594 should be recommended at the landscape scale (Tschartke et al., 2021). We have shown that  
595 kiwifruit pollen limitation decreases in orchards with higher honeybee visits. Accordingly, kiwifruit  
596 growers should promote actions to increase honeybee abundance in and around fields and, at  
597 the same time, reduce trophic competition with crop bloom. New approaches in hive  
598 management, such as sprinkling flowers with attractant substances to increase the permanence  
599 of honeybee inside the orchards should be explored (Meroi Arcerito et al., 2021). For blueberry  
600 crops, we recommend any strategy to promote bumblebee communities both in the fields and  
601 around them, like increasing nesting habitats as well as the quantity, diversity and temporal  
602 availability of floral resources (Lye et al., 2009; Senapathi et al., 2017; Timberlake et al., 2021).  
603 The use of bumblebee colonies should be questioned in all three crops, also bearing in mind  
604 that the introduction of commercial non-local subspecies is an unnecessary health risk for local  
605 insect populations (Goka et al., 2006; Trillo et al., 2019). In conclusion, the present work  
606 highlights that the pollination of exotic crops depend on the crop type, the regional landscape  
607 characteristics and the local pollinator assemblages. This sort of contingencies may hamper to  
608 generalize our specific findings to other crops or regions. However, in any case, what is fully  
609 generalizable is the idea that studying the local pollination ecology of exotic crops is a  
610 prerequisite to optimize agricultural practices depending on the crop and the local pollination  
611 environment.

612

613 **Author contributions**

614 MM and DG designed the study. All authors contributed to data collection. MM curated the data.  
615 DG performed the analyses. MM drafted the manuscript and all authors contributed to  
616 interpretation and writing.

617

618 **Declaration of Competing Interest**

619 The authors declare that they have no known competing financial interests or personal  
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821

822 Figure legends

823 Figure 1. Pollinator community in kiwifruit (A), highbush blueberry (B) and rabbiteye blueberry  
824 (C) crops. N is the number of insect visits recorded for each crop.

825

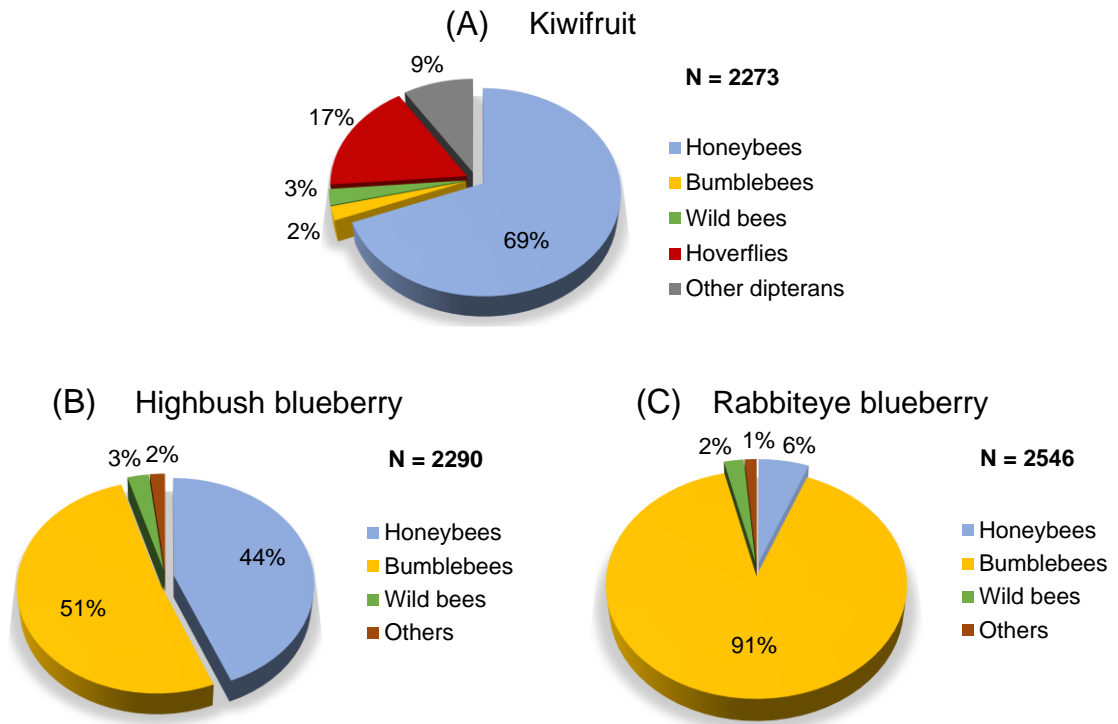
826 Figure 2. Distributions of fruit weight in kiwifruit according to pollination treatment (open or  
827 supplementary). The difference between treatments reflects pollination limitation. Boxplots are  
828 based on per-tree average values and indicate 25–75% quartiles (box boundaries), median  
829 (thick horizontal bar), largest and smallest observed values (whiskers), outliers (small circles)  
830 and extreme values (asterisks).

831

832 Figure 3. Examples of significant effects predicted by Generalized Linear Mixed Models of  
833 pollinator abundances on pollination effect on crop yields: (A) abundance of wild pollinators on  
834 fruit set in kiwifruit; (B) abundance of honeybee on fruit weight limitation (log of the ratio  
835 between fruit weight in supplementary-pollination treatment and in open-pollination treatment) in  
836 kiwifruit; (C) abundance of wild pollinators on fruit set in highbush blueberry; (D) abundance of  
837 honeybee on fruit weight (in open pollination treatment) in highbush blueberry; (E) abundance of  
838 honeybee on fruit set in rabbiteye blueberry; and (F) abundance of wild pollinators on fruit  
839 weight in rabbiteye blueberry. Confidence bounds and fitted values of partial effects predicted  
840 by models are shown.

841

842 Figure 4. Examples of significant effects predicted by Generalized Linear Mixed Models of  
843 landscape features on pollinator abundances: effect of PC1 on abundance of honeybees (A)  
844 and of PC3 on abundance of wild pollinators in kiwifruit (B), effect of PC1 on abundance of  
845 honeybees (C) and wild pollinators (D; note the logarithmic scale for representation purposes) in  
846 highbush blueberry, and effect of PC1 on pollinator richness (E) and of density of bumblebee  
847 colonies on honeybee abundance (F) in rabbiteye blueberry. Landscape gradients represented  
848 by PCA axes are quoted. Confidence bounds and fitted values of partial effects predicted by  
849 models are shown.

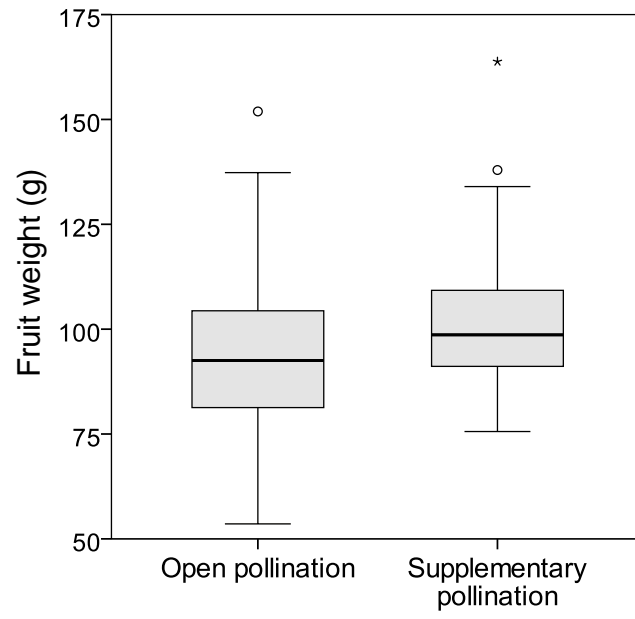


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851 Figure 1.

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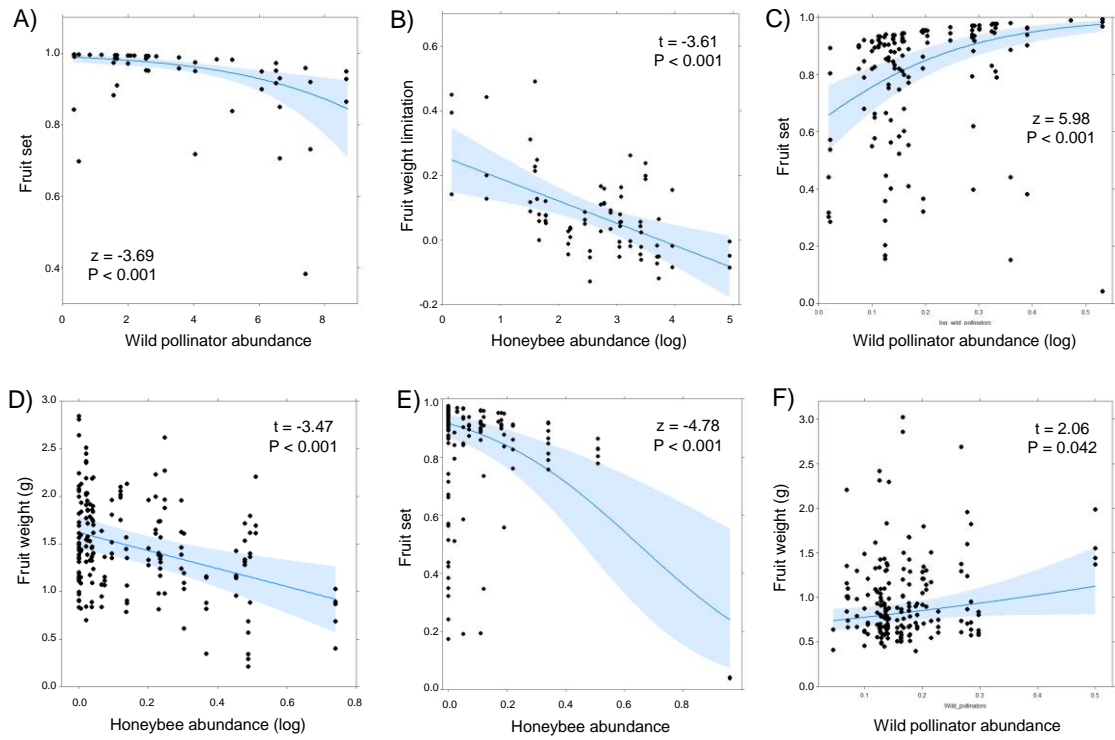
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864 Figure 3.

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