



Pollination of exotic fruit crops depends more on extant pollinators and landscape structure than on local management of domestic bees

Marcos Miñarro^{a,*}, Daniel García^b, Rocío Rosa-García^a

^a Servicio Regional de Investigación y Desarrollo Agroalimentario (SERIDA), Ctra. AS-267, PK 19, E-33300 Villaviciosa, Asturias, Spain

^b Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo and Instituto Mixto de Investigación en Biodiversidad (CSIC-Uo-PA), C/Catedrático Rodrigo Uría s/n, E-33006 Oviedo, Asturias, Spain

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ABSTRACT

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

1. Introduction

The expansion of exotic crops into farming areas far from a crop's origins is a main exponent of the agricultural globalization, which has been boosted not only by growing human food demands but also by global changes in diets (Lambin and Meyfroidt, 2011; Kastner et al., 2012). From an agronomic perspective, the success of exotic crops firstly depends on the degree of physiological pre-adaptation to the somewhat different edaphic and climatic conditions of the new farming environments. When pre-adaptation is low, agricultural management (irrigation, fertilization, climatic protection through greenhouses or hail nets, etc) becomes essential to establish productive crops in new areas (e.g. Middleton and McWaters, 2002; Heuvelink et al., 2005). Besides

adapting to abiotic constraints, exotic crops must also deal with new biotic environments and cope with, for example, different pollinator assemblages that may, or may not, fulfill crop pollination requirements. In this sense, it is known that crop plants usually suffer a decrease in the diversity of flower visitors when cultivated far from their region of origin (Brown and Cunningham, 2019). Considering that the recent increase in agricultural production primarily involves the cultivation of pollinator-dependent crops (which increased by 150 % between 1961 and 2018 compared to just 20 % for pollinator-independent crops, Aizen et al., 2022), it would appear to be crucial to better understand the magnitude and the mechanisms of pollinator-related constraints in exotic crops.

The adaptation of displaced crops to the resident pollinators of new

* Corresponding author.

E-mail address: mminarro@serida.org (M. Miñarro).

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cultivation areas may be conditioned by species-specific filters related to crop floral traits that modulate their attractiveness for and reward to local pollinator communities (Krishna and Keasar, 2018; Dellinger, 2020). In this sense, generalist floral morphologies, i.e. those enabling easy access to nectar or pollen resources for a wide range of pollinators (e.g. big flower sizes, short corollas, open flower receptacles, numerous and accessible stamens, etc. Olesen et al., 2007), should promote adaptation to local pollinators assemblages of variable size and composition. Conversely, exotic crops with specialist traits (e.g. small flower sizes, long tubular corollas, tubular closed anthers, etc.) that restrict pollen or nectar gathering to few specific pollinator types (e.g. long-tongued insects, buzz-pollinating bees; Olesen et al., 2007) are expected to be more prone to pollination limitation. Thus it becomes necessary to evaluate how crop species that differ in flower morphology and their expected degree of generalism in pollinator assemblages, develop their pollination niches when expanding across the same farming region.

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

Insect pollinators are highly mobile animals, often arriving on farms from surrounding habitats hundreds of meters away (e.g. Greenleaf et al., 2007). The capacity of an insect species to extend its foraging area depends on specific traits, such as body size (Greenleaf et al., 2007; Benjamin et al., 2014), and thus different species may respond in their own particular way to the gradients imposed by agriculture on the landscape, such as habitat loss or fragmentation (Brosi et al., 2008; Bommarco et al., 2010). In this sense, the structure of the landscape surrounding farms determines the abundance, richness and composition of pollinator assemblages in crops (e.g. Saturni et al., 2016; Senapathi et al., 2017; Roquer-Beni et al., 2021) by conditioning the type and the extent of source habitats as well as the flow from these sources to crops (Tscharntke et al., 2005). Addressing the modulating effects of surrounding habitats on pollinator assemblages is thus a requisite to ultimately understanding the characteristics of the pollination service to exotic crops (e.g. Greenleaf and Kremen, 2006; Blaauw and Isaacs, 2014).

Here, we study the pollination of kiwifruit (*Actinidia deliciosa*; native to China), northern highbush blueberry (*Vaccinium corymbosum*) and rabbiteye blueberry (*Vaccinium ashei*) (both native to North America)—three of the fruit crops that are increasing most rapidly in the world (Ward and Courtney, 2013; Rodríguez-Saona et al., 2019)—in new cultivation areas in NW Spain. All these crops depend on insects for pollination (Klein et al., 2007) and can suffer pollination limitations (Campbell et al., 2018; Castro et al., 2021; Martin et al., 2021). Kiwifruit is a dieocious species with large, open and stamen-abundant male and female flowers on different trees (Fig. S1). Both sexes produce pollen but

no nectar (Hopping, 1990). Thus, although highly accessible and pollen rich, kiwifruit flowers can be unattractive for nectar-feeders (Clinch, 1984; Pomeroy and Fisher, 2002). Blueberry shows specialized flower traits (narrow-opening bell-shaped corolla, protected poricidal anthers, protruding stigma, nectaries at the bottom of the flower; Fig. S1) that may restrict pollinator assemblages to species with buzzing behavior and long tongues and some very small insects that can enter the corolla completely (Sampson et al., 2013; Blaauw and Isaacs, 2014; Cortés-Rivas et al., 2022). Bearing these between-crop differences in mind, we evaluate how these exotic crops adapt to the common pollination environment of a new cultivation region, by estimating the contribution of insect assemblages to the pollination service and the landscape and management factors regulating these same assemblages. To do this, we address the following questions: 1) How diverse are pollinator assemblages of introduced kiwifruit and blueberry crops? 2) Do crop yields suffer from pollination limitation? 3) Do pollinator abundance and richness affect crop yields? and 4) Are pollinator abundance and richness affected by landscape structure and the management of domestic pollinators?

2. Materials and methods

2.1. Study sites

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

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

2.2. Pollinator assemblages

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

All kiwifruit orchards were sampled when they were in full bloom, what occurred from 2nd to 8th June in 2015 and from 9th to 27th June in 2016, depending on the orchard. As full bloom in kiwifruit last just a few days, each orchard was visited just once in each year and during the day of the visit was surveyed at three different times (1200 h, 1400 h and 1600 h) in order to cover the maximum range of pollinator activity and to limit temporal biases. Samplings were conducted under standard climatic conditions: dry vegetation, clear to lightly overcast skies,

temperatures $> 13\text{ }^{\circ}\text{C}$ and wind speed $< 2.5\text{ m s}^{-1}$. At each site and for each year, five female trees (at least 15 m from the edge to avoid potential edge effects) were randomly selected for pollinator observations. In each census we observed a 1-m diameter area of the canopy of each tree for a period of 5 min, recording the number of insect visits and the number of flowers in the selected area. In total, therefore, each orchard accounted for 75 min of observation (3 censuses \times 5 trees \times 5 min) per year. To avoid disrupting floral visits, no insects were collected during the surveys and, therefore, we were only able to reliably identify certain easily recognized species (e.g. *Apis mellifera*, *Bombus* species, *Episyrphus balteatus*, etc.). Most visitors were, thus, assigned to one of the following groups: bumblebees, wild bees, hoverflies (predatory hoverflies with aphidophagous larvae or *Eristalis* hoverflies) or flies (Diptera other than hoverflies). In order to better assess species richness, and just after each visitation survey, we also made separate assessments of kiwifruit pollinators by walking slowly along tree rows and catching all floral visitors observed over a 10 min period for each survey event (i.e. a sum of 30 min per orchard per year). Captured specimens were identified in the laboratory.

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

For each blueberry type, a group of 30 consecutive plants 15 m away from the edge were randomly selected and marked at the beginning of the bloom. Before each survey we counted the total number of open flowers in five randomly selected plants (in the group of 30) and used such information to estimate the total number of flowers observed. In each survey we walked slowly along the 30 plants recording all visits to blueberry flowers and catching floral visitors non-identified by sight, during a 10 min period at each survey event (i.e. a sum of 20 min per blueberry type per orchard and per year). Captured specimens were identified in the laboratory.

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

2.3. Pollination effect on crop yield

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

In kiwifruit, in the visit to sample pollinators (see above), 3 similar target female trees per orchard and 40 recently opened flowers per tree were selected each year. Twenty of the flowers were randomly selected, marked with blue wires and left unmanipulated, potentially allowing for pollination through insect and wind vectors (open-pollination treatment). The other 20 flowers were marked with red wires and supplemented with pollen by brushing each of them with three different flowers previously collected from different male trees from the same orchard (supplementary-pollination treatment). These flowers were saturated with pollen, meaning that fruit set and fruit weight in the supplementary-pollination treatment would be the maximum possible for the corresponding tree. In early November, when fruits were ripe, we

counted the number of fruits that had developed from all marked flowers in each treatment. Those fruits were harvested and weighed individually. Then we averaged the weight of all the fruits of each tree and treatment.

In blueberry, on the first visit to sample pollinators (see above), five target plants (included in the 30 for pollinator surveys) per type (highbush and rabbiteye) and orchard were selected each year. Then, two distal clusters of buds with open flowers were selected on each plant and marked with colored flagging and numbered. The total number of flowers (open and closed) of each cluster were counted. One randomly selected cluster was left unmanipulated, potentially allowing for self-pollination and cross-pollination through insect and wind vectors (open-pollination treatment). The other cluster was supplemented with pollen collected previously from the same and different blueberry cultivars from the same orchard and randomly mixed (supplementary-pollination treatment). An electric toothbrush (Oral-B, Procter & Gamble, USA) was placed on the corolla of flowers to vibrate pollen out of donor flowers into a Petri dish, and then a small paint brush was used to immediately apply pollen directly on the stigma of the hand-pollinated flowers (Gibbs et al., 2016). As flowers open sequentially and not all flowers could be pollinated in a single visit, the pollen supplementation was performed twice, once during each visit to sampling pollinators, in order to pollinate as many flowers as possible (average 92.8 %, min-max 71–100 % of flowers per cluster were pollinated). Flowers were allowed to develop normally throughout the bloom and fruit development periods. When at least 50 % of the fruits in the clusters had ripened, and just before the first harvest by growers, all those experimental fruits (the ripe and unripe fruits) were harvested and brought into the laboratory. We counted the number of fruits in each cluster and obtained fruit set by dividing the total number of fruits by the number of flowers counted earlier in the season. Then we weighed all the ripe fruits of each cluster together and obtained the average fruit weight by dividing the total weight of the ripe fruits by the number of ripe fruits in that cluster.

2.4. Landscape structure

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

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

In the studied region, the main trends of landscape change across space are shaped by the complex and interrelated variation of different land cover types, rather than by major changes in single cover types (e.g. Martínez-Sastre et al., 2020). Thus, for an accurate representation of the general landscape gradients surrounding orchards, we used a Principal Component Analysis (PCA, performed with the princomp function in the

R Stats package, R Core Team, 2022) applied to the six general cover types in the R1000 plots around orchards (Table S2). For kiwifruit, the first three principal components accounted for 81.3 % of the variation in our landscape data: PC1 (42.0 % of variance explained) described a gradient ranging from landscapes dominated by other habitats to pasture-dominated landscapes; PC2 (23.7 %) represented a gradient of increased proportions of exotic (eucalyptus) plantations around the orchards; and PC3 (15.6 %) a gradient from semi-natural woody habitats to urbanized landscapes. In the case of blueberry orchards, the first three principal components accounted for 79.8 % of the variation in our landscape data: PC1 (36.8 % of variance explained) described a gradient that ranged from landscapes dominated by semi-natural woody habitats to pasture-dominated landscapes; PC2 (22.6 %) a gradient of increased proportions of exotic (eucalyptus) plantations around the orchards; and PC3 (20.3 %) a gradient from landscapes dominated by fruit tree plantations to urbanized landscapes. In both crop types, these three principal components were used as non-correlated parameters of landscape structure.

2.5. Pollinator management within orchards

In order to account for within-orchard features affecting pollinator occurrence and availability, we asked the growers about the occurrence/absence and the density of honeybee hives and commercial bumblebee colonies (number per ha). Both occurrence and density of honeybee hives and commercial bumblebee colonies varied greatly across kiwifruit and blueberry orchards (Table S1). For kiwifruit, 73 % (year 1) and 64 % (year 2) of the orchards had honeybee hives and/or commercial bumblebee colonies for pollination, with up to 10-fold differences in colony density. In blueberry orchards, around half of the growers had introduced honeybee hives and/or bumblebee colonies for pollination, and differences in colony density were up to 20-fold.

We did not consider other orchard features typically targeted as drivers of pollinator assemblages, such as flowering groundcover or organic management (e.g. Samnegård et al., 2019), as they did not represent large enough environmental gradients in our study cases. Concerning flowering groundcover, both kiwifruit and blueberry producers typically remove flowers from the ground by shredding during crop bloom to avoid expected competition with the crop flowers. In addition, a comparison between organic and conventional management types was not possible in kiwifruit (just one orchard was organic, see above) and it was discarded in blueberry because management is very similar in both certified-organic and non-certified orchards due to the low level of intensification of these crops.

2.6. Statistical analysis

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

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

and open pollination, respectively (Sáez et al., 2022). As fixed-effect predictors, we considered the abundance of honeybee, the abundance of wild pollinators and pollinator richness (orchard-level estimates). In kiwifruit models, we also considered as fixed predictor the proportion of male trees with respect to female trees per orchard, given that kiwifruit is a dieocious plant and the density of male plants could condition the quantity of fertile pollen available to pollinate female flowers. All models included orchard identity as random factor. Correlation between fixed-effect predictors was low (Pearson correlation coefficient: $|r| < 0.450$, $N = 89$) except in the case between the abundance of honeybee and the abundance of wild pollinators ($r = -0.610$, $p < 0.001$, $n = 89$). Thus, values of Variance Inflation Factor (VIF) were estimated for fixed effects in all models, in order to interpret potential effects of collinearity (all VIF values were lower than 2, what is considered indicative of low collinearity; Quinn and Keough, 2002).

In order to evaluate the effects of landscape structure and the management of domestic pollinators in the orchards on pollinator abundances and richness, we used GLMMs, considering honeybee abundance, wild pollinator abundance and pollinator richness per census and orchard as three different response variables for each crop type. Gaussian (identity link) and Gamma (log link) family distributions were considered for abundance measures, and Gaussian (identity link), Gamma (log link) and Poisson (log link) family distributions for richness. Different models with the different family distributions were checked for a given response variable, choosing that with the lowest AICc value. For each crop type and response variable, we considered a whole model incorporating as fixed predictors the three landscape PCA vectors, the occurrence of honeybee hives, the occurrence of bumblebee colonies, and the interaction between occurrence of honeybee hives and that of bumblebee colonies (this interaction proved not significant [$p > 0.1$] in all models and it was subsequently removed in final models). Orchard identity was included as a random factor. Given the high between-site variability in the density of pollinator hives, we compared this model with a second whole model, substituting the occurrences with the densities of honeybee hives and bumblebee colonies (and their interaction), choosing that with the lowest AICc value. Values of PCA vectors and densities of honeybee hives or bumblebee colonies were uncorrelated across orchards, as were densities of honeybee hives and bumblebee colonies (Pearson correlation coefficients, kiwifruit: $|r| < 0.274$, $p > 0.05$, $N = 29$; blueberry: $|r| < 0.286$, $p > 0.05$, $N = 40$). In any case, VIF was estimated for all fixed predictors in all models, resulting lower than 2 in all cases.

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

3. Results

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

In kiwifruit, we recorded 2273 insects visiting flowers (mean number of visits per 100 flowers per 5 min: 10.97 ± 0.53 SE, $N = 435$ censuses). As pollinator assemblages were almost identical in the two years (Fig. S3A), data were pooled for the description of the pollinator community, that was composed by 51 species, mainly hoverflies (21 species) and wild bees from the family Halictidae (17 species; Table S3). Considering all orchards, honeybee, with 69.0 % of the visits, was the dominant pollinator (Fig. 1A), followed by hoverflies (17.1 %; mainly predatory hoverflies) and other dipterans (9.1 %). Wild bees (2.5 %) and bumblebees (2.3 %; mostly *Bombus terrestris*) completed the assemblage. Honeybee was the most numerous flower visitor in all sites but one (Fig. S4A).

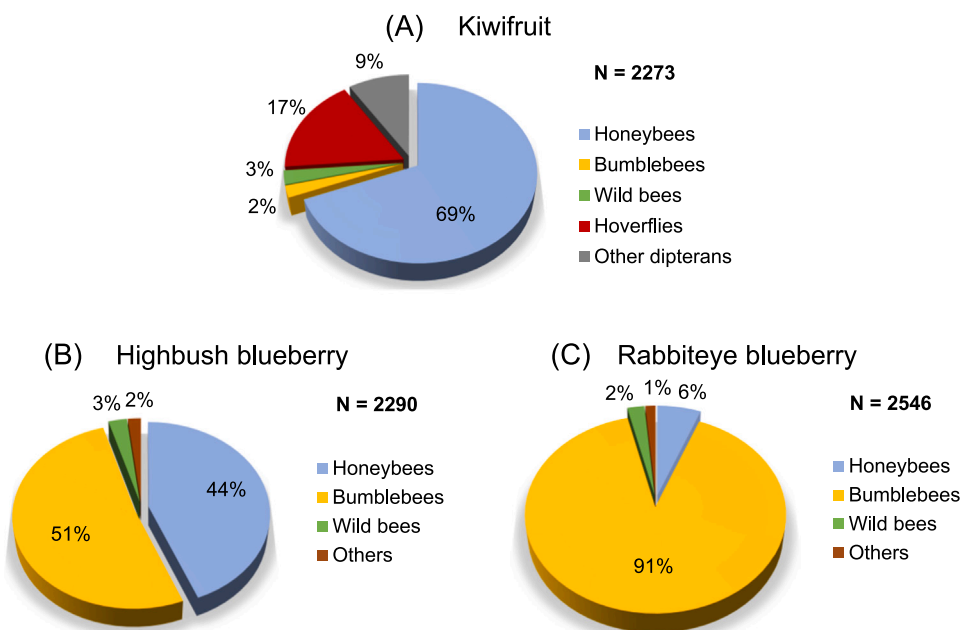


Fig. 1. Pollinator community in kiwifruit (A), highbush blueberry (B) and rabbiteye blueberry (C) crops. N is the number of insect visits recorded for each crop.

We recorded 2290 insects visiting highbush blueberry flowers (0.285 ± 0.022 SE visits/100 flowers/5 min, $N = 80$ censuses). Pollinator assemblages were similar between years (Fig. S3B) and composed of 28 species, mainly wild bees (13 species) and bumblebees (6 species; Table S4). Globally, bumblebees (51.5%), followed closely by honeybee (43.9%), were the dominant pollinators (Fig. 1B). Wild bees (2.7%) and dipterans and butterflies (1.9% in total) completed the assemblage. *Bombus terrestris* (85%) was the most numerous bumblebee species, followed by *B. pascuorum* (10%) and *B. pratorum* (4%). Bumblebees dominated the assemblage in 11 orchards and honeybee in 9 (Fig. S4B).

In rabbiteye blueberry, we recorded 2546 insects visiting flowers (0.178 ± 0.011 SE visits/100 flowers/5 min, $N = 80$ censuses). Again, pollinator assemblages were very similar between years (Fig. S3C). Bumblebees (12 species) and wild bees (11 species) dominated the assemblage of floral visitors (28 species in total; Table S5). Considering all orchards, bumblebees (90.6%) clearly dominated the assemblage, with honeybee representing only 5.8% of total visits, wild bees 2.3% and others 1.3%. *B. terrestris* (77%) was the most numerous bumblebee species, followed by *B. pascuorum* (9%), *B. pratorum* (8%) and *B. hortorum* (5%). Bumblebees were the dominant pollinator in all orchards, whereas honeybee accounted for less than 20% in all sites but one (Fig. S4C).

3.2. Do crop yields suffer from pollination limitation?

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

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

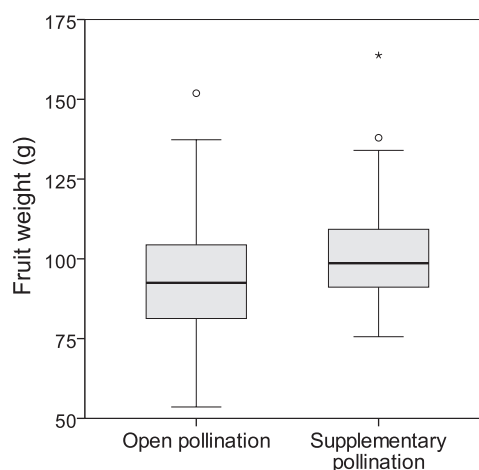


Fig. 2. Distributions of fruit weight in kiwifruit according to pollination treatment (open or supplementary). The difference between treatments reflects pollination limitation. Boxplots are based on per-tree average values and indicate 25–75% quartiles (box boundaries), median (thick horizontal bar),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

84.9%, and fruit weight of 0.83 g and 0.85 g, in open- and in supplementary pollination, respectively (Tables S6 and S7).

3.3. Do pollinator abundance and richness affect crop yields?

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

In highbush blueberry, fruit set responded positively to the abundance of wild pollinators (5.92 ± 0.99 ; $z = 5.98$; $P < 0.001$; Fig. 3C and

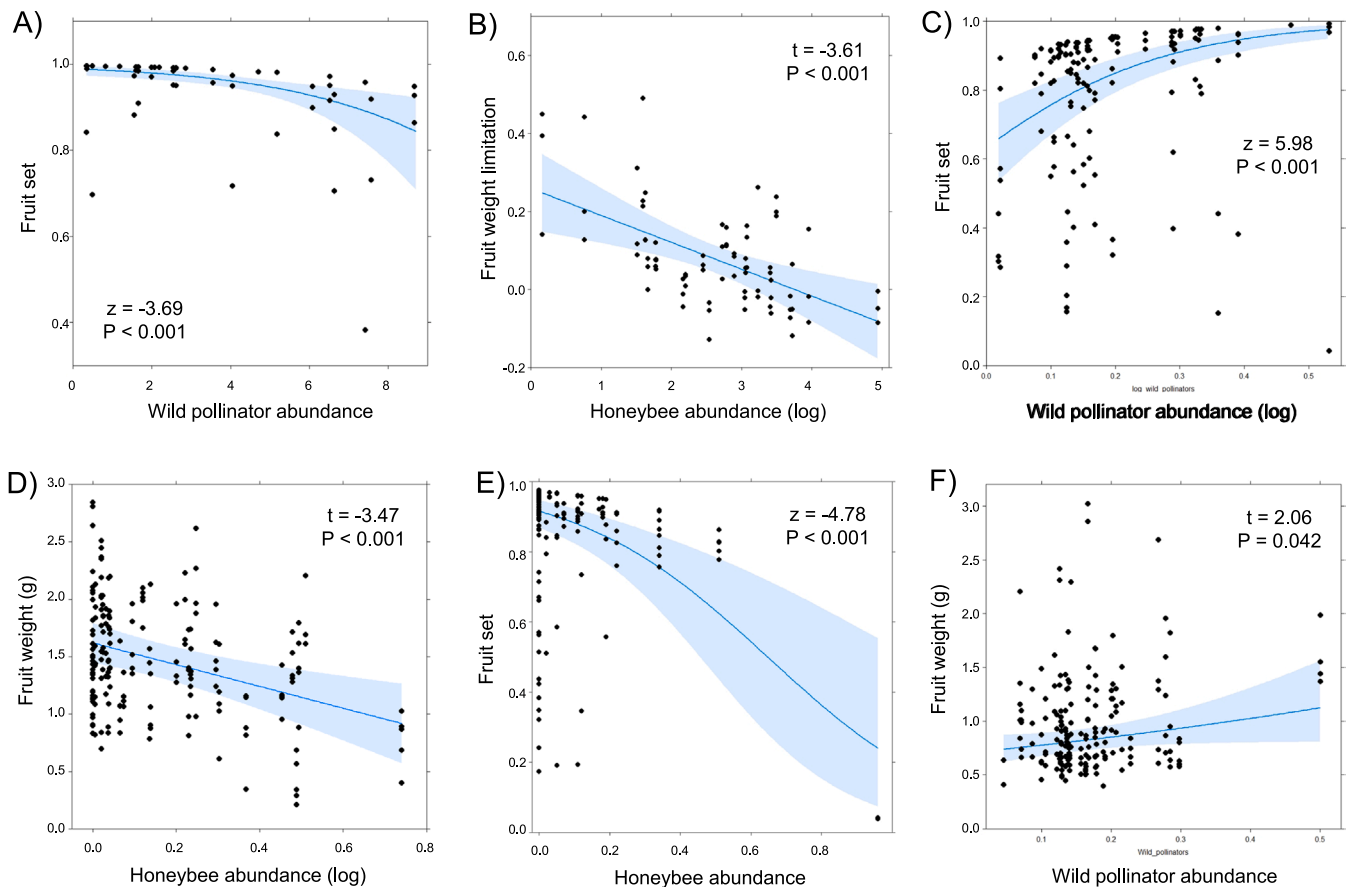


Fig. 3. Examples of significant effects predicted by Generalized Linear Mixed Models of pollinator abundances on pollination effect on crop yields: (A) abundance of wild pollinators on fruit set in kiwifruit; (B) abundance of honeybee on fruit weight limitation (log of the ratio between fruit weight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

Table S8), but fruit weight was negatively related to the abundance of honeybee (-0.95 ± 0.27 ; $t = -3.47$; $P < 0.001$; Fig. 3D and Table S8). In rabbiteye blueberry, fruit set was negatively affected by the abundance of honeybee (-36.82 ± 7.69 ; $z = -4.78$; $P < 0.001$; Fig. 3E and Table S8), whereas fruit weight was positively predicted by the abundance of wild pollinators (0.78 ± 0.38 ; $t = 2.06$; $P = 0.042$; Fig. 3F and Table S8).

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

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

Abundance and richness of pollinators in highbush blueberry also showed significant responses to landscape structure, but not to the management of pollinator hives (Table S10). That is, honeybee abundance was negatively affected by PC1 (gradient from semi-natural

woody habitat to pasture cover; -0.06 ± 0.03 ; $t = -2.40$; $P = 0.016$; Fig. 4C) and PC3 (gradient from fruit tree plantation to urbanized land; -0.05 ± 0.03 ; $t = -1.99$; $P = 0.046$). In contrast, PC1 and PC2 (gradient of intensity of exotic tree plantation cover) had positive effects on wild pollinator abundance (0.27 ± 0.12 ; $t = 2.34$; $P = 0.019$ (Fig. 4D) and 0.27 ± 0.11 ; $t = 2.55$; $P = 0.011$, respectively). In rabbiteye blueberry, landscape structure and domestic pollinators never accounted for more than 13 % of the variability of the abundance and richness of pollinators (marginal $R^2 < 0.134$ in all cases; Table S11). The role of landscape was limited to a negative effect of PC1 (gradient from semi-natural woody habitat to pasture cover) on pollinator richness (-0.15 ± 0.05 ; $t = -2.65$; $P = 0.008$; Fig. 4E). The density of bumblebee colonies negatively affected honeybee abundance (-0.00 ± 0.00 ; $t = -2.04$; $P = 0.041$; Fig. 4F).

4. Discussion

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

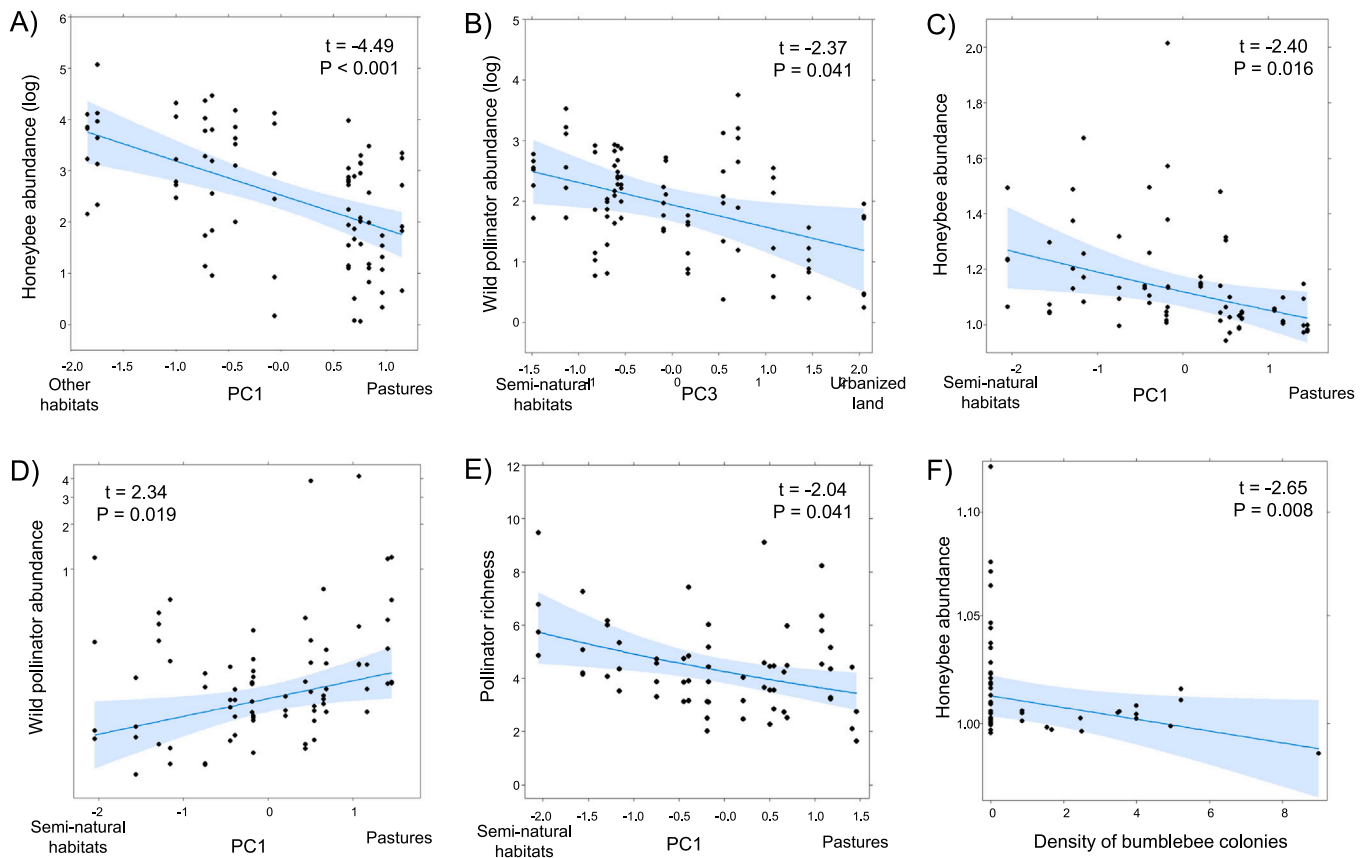


Fig. 4. Examples of significant effects predicted by Generalized Linear Mixed Models of landscape features on pollinator abundances: effect of PC1 on abundance of honeybees (A) and of PC3 on abundance of wild pollinators in kiwifruit (B), effect of PC1 on abundance of honeybees (C) and wild pollinators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

assessing the contribution of extant insects to the pollination service.

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

The three study crops had diverse assemblages of insect pollinators that were each numerically dominated by bees. Honeybee clearly dominated kiwifruit assemblages, representing almost 70% of visits to flowers. Bumblebees and honeybee dominated more or less equally floral visits in highbush blueberry, and, finally, bumblebees accounted for more than 90 % of visits in rabbiteye blueberry. Floral morphology of the different crops partially explains interspecific differences in pollinator assemblages. In this sense, the large open flowers of kiwifruit, and the accessibility to different pollinator types derived from this floral morphology, would explain the generalism (i.e. the richest assemblage of visitors, with 51 species) of this crop species. Many of these floral visitors can also be considered highly generalist themselves, like honeybee and many halictid bees and dipterans (see also Howlett et al., 2017; Gaspar et al., 2022). As expected from their floral traits, blueberry crops were more specialized and, compared to kiwifruit, were visited by a smaller array of pollinator species (28 for both blueberry types) which showed either buzzing behavior to release pollen, long tongues or small size (Sampson et al., 2013; Cortés-Rivas et al., 2022). Specialization degree differed even between blueberry types (and even between highbush cultivars; Courcelles et al., 2013; Cortés-Rivas et al., 2022), being higher in the rabbiteye type, likely due to its longer corolla and narrower flower opening, compared to the highbush type (Sampson et al., 2013; Fig. S1). This would explain why honeybee, despite being abundant in the blueberry orchards (44 % of visits in highbush

blueberry) accounted for only 6 % of visits in the rabbiteye type: this insect had poor access to nectaries due the narrow flower and its short tongue. The specialization of the rabbiteye was also reflected in the characteristics of the assemblage of bumblebees, with more species and a higher occurrence of those with longer tongues (e.g. *B. hortorum*), and those of wild solitary bees (the long-tongued *Anthophora* bees accounted for 64 % of wild bee visits in rabbiteye and only 38 % in highbush). Interestingly, honeybee made a significant numerical contribution to the pollination assemblages of other rabbiteye blueberry cultivars (Sampson and Cane, 2000; Kendall et al., 2020), whereas their contribution to assemblages of other highbush cultivars is lower than that to Duke (Courcelles et al., 2013; Cortés-Rivas et al., 2022). Such intraspecific variability reflects the need of evaluating cultivar differences in pollination considering the relation between pollinators and flower traits.

4.2. Do crop yields suffer from pollination limitation?

Despite its large and diverse pollinator assemblages, kiwifruit crops experienced pollination limitation in the region studied (see Castro et al., 2021 for a similar case in kiwifruit non-native areas). Pollination limitation led to, on average, 7.2 % reductions in fruit weight (40 % in some orchards). In other words, the proper management of pollination could increase fruit weight (and associated yield and economic value) up to 40 %. Fruit weight in kiwifruit is strongly dependent on the number of seeds, which in turn depends on the number of pollen grains fertilizing ovules. A flower contains up to 1500 ovules and a marketable kiwifruit of 100 g has around 1200 seeds (Hopping, 1990; Testolin et al., 1991), which means that the flower received at least 1200 grains of compatible

pollen. Therefore, the fruit weight difference is reflecting insufficient quantity of male compatible pollen reaching the female flowers. This could result from 1) scarcity of pollinators to transfer pollen from male to female flowers (e.g. Abbate et al., 2021; see discussion below, Section 4.3), 2) low pollen availability in the orchard due to low male-female tree ratios (Greatti and Barbattini, 1997; García et al., 2015), or 3) lack of compatibility or bloom synchronization between male and female flowers (Hopping, 1990; García et al., 2015). Our results evidence no effect of male pollen availability on pollination service, suggesting an adequate proportion of male and female trees in the orchards. However, the compatibility between male and female trees remains unexplored.

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

4.3. Do pollinator abundance and richness affect crop yields?

We found marked effects of pollinator abundances on the yields of the exotic crops examined, although both effect type (derived from abundances of honeybees or wild pollinators, and affecting fruit set or fruit weight) and sign (positive or negative) varied considerably across crop types. In kiwifruit, the higher the abundance of honeybees visiting flowers, the lower the limitation of fruit weight (see also Castro et al., 2021), which suggests that abundance can compensate for the low efficiency of honeybee as pollinator in terms of legitimate visits or productivity per single visit (Miñarro and Twizell, 2015). Contrary to previous evidence in other crops (e.g. Garibaldi et al., 2013; Martínez-Sastre et al., 2020; Pérez-Méndez et al., 2020), higher abundance of wild pollinators in kiwifruit led to pollination-derived yield constraints, in this case on fruit-set. Fifty-seven percent of the pollinator species in the present study were dipterans and beetles, which accounted for more than 26 % of visits (Fig. 1; Table S3). These species notably increased wild pollinator abundance locally (Fig. S4A) but probably contributed little to kiwifruit pollination due to their very passive foraging behavior and low rates of legitimate visit (Testolin et al., 1991; Miñarro and Twizell, 2015). However, it remains unknown for us whether the negative relationship between wild pollinator abundance and kiwifruit productivity is direct (due to pollen losses, higher pollen loads of incompatible pollen, damages in stigmas) or mediated by effects of other factors not considered in this study, such as negative interactions between the dominant pollinator and those less efficient wild pollinators (Perfectti et al., 2009).

In both blueberry types, wild pollinator (basically bumblebee) abundance had positive effects on crop yields, whereas that of honeybee affected yield negatively. Bumblebees are known to be better pollinators for blueberry than honeybee, in terms of number of flowers visited per time, pollen transfer, buzzing behavior and resulting yield (Estravis-Barcala et al., 2021; Miñarro and García, 2021; Sun et al., 2021; Cortés-Rivas et al., 2022). Consequently, the negative relationship between honeybee abundance and blueberry yields could be more a consequence of a negative covariation between honeybee and bumblebees rather than a direct detrimental effect of honeybee on pollination. In fact, bumblebees and honeybee clearly have different peaks of activity throughout the blueberry bloom season as well as along gradients of daily temperature and relative humidity (Miñarro and García, 2021). Interestingly, honeybee may accomplish the pollination needs of

highbush blueberry in other situations when local pollinator populations are scarce or absent (Cavigliasso et al., 2021; Martin et al., 2021).

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

We show here that the management of domestic pollinators, at least in terms of the frequencies of occurrence and densities of hives and colonies used currently, had practically no effect on the pollinator assemblages of any of the studied crops. This suggests that extant insect assemblages, spontaneously occurring within orchards, are responsible for the pollination of the exotic crops under study. These extant populations almost certainly combine local wild pollinators with domestic honeybee individuals that spill-over into the orchards from surrounding areas attracted by the mass bloom of fruit crops, thus masking the expected effect of the intentionally introduced colonies. Both this study and previous research in other crops in this region evidence that honeybee and bumblebees occurred spontaneously in the crops in the absence of managed colonies (Miñarro and Twizell, 2015; Martínez-Sastre et al., 2020; Miñarro and García, 2021). Honeybees could originate from the small and profuse domestic apiaries in the surrounding landscape and/or feral populations, whereas *B. terrestris* is an abundant and widely-distributed native pollinator in this region (this study, Miñarro and Twizell, 2015; Miñarro and García, 2018; Martínez-Sastre et al., 2020; Miñarro and García, 2021). During the surveys, we confirmed that commercial bumblebees stayed in the orchards and visited crop flowers (the commercial subspecies had black hairs whereas they are blond in local subspecies), although they accounted for a very low fraction of pollinator visits.

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

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

4.5. Management recommendations

The two main pollinator types, honeybee and bumblebees (especially *B. terrestris*), of the exotic crops studied are ubiquitous in the study

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

CRediT authorship contribution statement

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

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2023.108387](https://doi.org/10.1016/j.agee.2023.108387).

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