



Impact of local practices and landscape on the diversity and abundance of pollinators in an insect-dependent crop

Hugo Gaspar^{*}, João Loureiro, Helena Castro, Catarina Siopa, Mariana Castro, Vinicius Casais, Sílvia Castro

University of Coimbra, Centre for Functional Ecology, Department of Life Sciences, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal

ARTICLE INFO

Keywords:

Actinidia spp.
Insect pollination
In-field management
Kiwifruit
Landscape structure
Pollinator-dependent crop

ABSTRACT

Insects are a functionally diverse group, with economically relevant roles on key ecosystem services, such as pollination. The current trend of biodiversity loss and consequent degradation of ecosystem services delivered by insects is leading to additional pressure on modern agriculture, particularly in crops that depend on insects for pollination. Understanding how insect pollinator diversity varies at local and landscape scales is very important to recognize trends in pollinator populations. The present work quantified the effect of in-field management practices and different landscape types on insect pollinator communities in kiwifruit, a pollinator-dependent crop. Twenty-two orchards were selected and characterized for in-field practices, landscape structure, plant-pollinator interactions, and productivity. We observed that orchards with practices that are less harmful to insect pollinators are related to a higher pollinator diversity and higher abundances of certain wild pollinator groups, although this was not related with increased productivity. Additionally, in the studied production region, agricultural dominated landscapes harbor lower pollinator diversity, lower wild pollinators abundance and higher managed honeybee abundance than forest and herbaceous dominated landscapes, but no differences were detected in productivity among landscape types. In turn, abundance of *Bombus* spp. and the use of pollination support practices were significantly and positively correlated with orchard productivity. Despite the differences in pollinator communities, comparable yields were observed across different landscape types. Additionally, simple changes towards less harmful agricultural practices and the presence of forest and herbaceous habitats can promote wild pollinators and respective pollination services.

1. Introduction

Insects are the most diverse and abundant animal group on the planet (Mittermeier et al., 2011), playing a key role in several ecosystem functions (Weisser and Siemann, 2004). In agricultural areas, insect populations can be present in production fields and inhabit its surroundings, providing economically relevant services like pollination, biocontrol and nutrient recycling (Bommarco et al., 2013; Weisser and Siemann, 2004).

Entomophilous pollination is economically relevant (Lautenbach et al., 2012) for the production of marketable fruits in many crops, increasing not only the quantity but also the quality of the fruits produced (Chaplin-Kramer et al., 2014; Garibaldi et al., 2011; Hoehn et al., 2008). Honeybees (*Apis mellifera* Linnaeus, 1758) are the most recognized and often largely dominating species in entomophilous crops, even

though many other insects, especially wild bees (Hymenoptera:Anthophila) and hoverflies (Diptera:Syrphidae), can efficiently pollinate many crops (Garibaldi et al., 2013; Kleijn et al., 2015; Minckley and Roulston, 2006; Potts et al., 2010; Winfree et al., 2018). Indeed, growing evidence about the relevance of wild pollinators for providing significant contributions to the production levels of entomophilous crops has emerged in the last decades (Fijen et al., 2018; Garibaldi et al., 2013; Rader et al., 2016; Winfree, 2013; Yachi and Loreau, 1999).

Modern agriculture faces a constant pressure to increase production performance, leading to the adoption of high external input-based practices and the increase in land conversion to agricultural use (Bommarco et al., 2013; Tscharntke et al., 2005). The major threats to pollinators in agricultural landscapes include land-use changes causing habitat fragmentation, loss and simplification (Tscharntke et al., 2005), and increased pesticide use (Le Féon et al., 2010). Habitat changes,

^{*} Corresponding author.

E-mail addresses: hgaspar@uc.pt (H. Gaspar), jloureiro@bot.uc.pt (J. Loureiro), hcastro@ci.uc.pt (H. Castro), catarinasiopa@gmail.com (C. Siopa), mcastro@uc.pt (M. Castro), viniciuscasais@gmail.com (V. Casais), scastro@bot.uc.pt (S. Castro).

<https://doi.org/10.1016/j.agee.2021.107804>

Received 26 November 2020; Received in revised form 17 November 2021; Accepted 23 November 2021

0167-8809/© 2021 Elsevier B.V. All rights reserved.

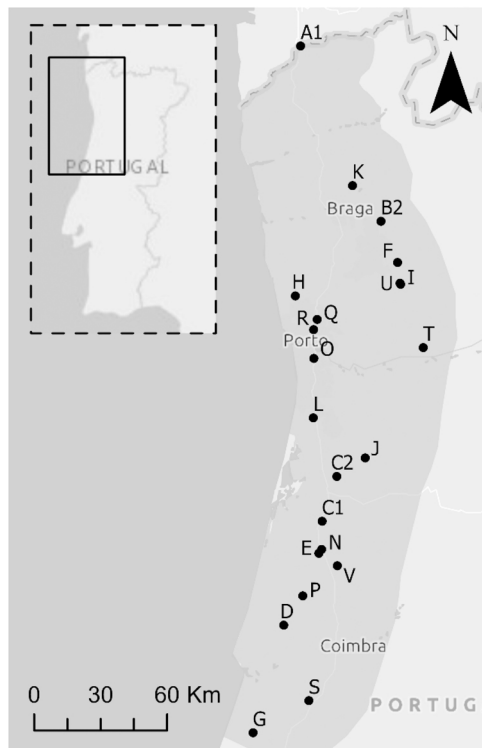


Fig. 1. Distribution of study sites in Portugal mainland for the study of pollinator community in kiwifruit orchards.

alongside with other anthropogenic-related causes, are leading to worldwide declines in insect's abundance and diversity, including pollinators (e.g., Powney et al., 2019; Ellis, 2012; Zattara and Aizen, 2021). To overcome pollinator declines, farmers must resort to supporting practices (e.g., hive rental or even artificial pollination using hand pollination or pollen spraying techniques; Garibaldi et al., 2014; Sáez et al., 2019). These practices are costly and time consuming, and may affect the sustainability of agricultural systems, both environmentally and economically.

Sustainable practices both at local (i.e., in-field practices) and landscape scales are very important for pollinator communities (Kennedy et al., 2013) and can lead towards a better socio-ecological balance (Chapin et al., 2010; Garibaldi et al., 2014). Landscapes can contribute with heterogeneity and higher-quality habitats (i.e., habitats rich in nesting and food resources) to insects in different scenarios and scales (Kennedy et al., 2013; Tscharntke et al., 2005), and are especially important for insects with lower mobility, diet range and fertility (Gámez-Virués et al., 2015; Hall et al., 2019; Rader et al., 2020; Steffan-Dewenter and Kuhn, 2003). However, the real impact of such practices depends on the species/group and/or on the level of stress that each practice poses to biodiversity (Tscharntke et al., 2005). For example, hoverflies can deal with disturbance in agricultural landscapes because of its mobility and ability to fulfill its life cycle within production areas (Jauker and Wolters, 2008). In contrast, wild bees rely on adequate nesting sites and more diversified food sources (Michener, 2007), not always available in agricultural landscapes (Hall et al., 2019; Steffan-Dewenter et al., 2002).

In the last decade, several studies focused in understanding the interplay between the landscape, in-field management practices and pollinator communities available for targeted crops (Tscharntke et al., 2005). These studies have been developed, for example, in orchards of multiple fruit trees (Bartholomée et al., 2020), sweet cherries (Eeraerts et al., 2019; Holzschuh et al., 2012) and apples (Martins et al., 2015; Porcel et al., 2018), and in olive groves (Martínez-Núñez et al., 2019). At the local scale, food resources and nesting sites are directly and

indirectly affected by management practices within and in the surroundings of the field, and the abundance and richness of these resources have been positively related with richness and abundance of insect pollinators (e.g., Holzschuh et al., 2007; Potts et al., 2005). At the landscape scale, proximity and abundance of semi-natural habitats, grasslands and forests have been positively related with diverse and abundant pollinator communities (e.g., Holzschuh et al., 2012; Morandin and Winston, 2005; Somme et al., 2014). In contrast, intensification in land-use through increased crop area and increased crop isolation, negatively impact insect pollinator communities available to crops (e.g., Connelly et al., 2015; Ricketts et al., 2008). Despite the current knowledge, further information across different crops and regions worldwide is still needed to better understand the effect of different factors in pollination ecosystem services provisioning.

Kiwifruit (*Actinidia* spp., Actinidiaceae) is a dioic and mainly entomophilous plant with a mass-flowering period (Guroo et al., 2017; Sáez et al., 2019). Kiwifruit production highly depends on efficient pollination because it directly impacts fruit size, a trait determining kiwifruit commercial value (Costa et al., 1993). The most relevant pollinators of kiwifruit are honeybees (*Apis mellifera*) and bumblebees (*Bombus* spp.) (Pomeroy and Fisher, 2002; Ricketts et al., 2008), but other insects like other wild bees, hoverflies and non-syrphid Diptera are also listed as flower visitors, even though with lower efficiency (Craig and Stewart, 1988; Doreen and Jay, 1984; Miñarro and Twizell, 2015; Sharma et al., 2013). Pollination success is also dependent on abiotic factors, such as winter temperatures (determining flowering phenologies), weather conditions during flowering, and orchard characteristics, such as female: male ratio (Castro et al., 2021b,a; Goodwin et al., 1999; Guroo et al., 2017). Consequently, pollination is currently a challenge for kiwifruit producers and management practices include the installation of honeybee hives and costly artificial pollination (Craig and Stewart, 1988; Hopping and Hacking, 1983). Whilst top producer countries (e.g., New Zealand and Italy) are exploring big scale orchards with frequent use of artificial pollination support (Sáez et al., 2019) and net protection around the orchards (Evans et al., 2019), countries with recent production areas (e.g., Portugal and Spain) are mainly characterized by small orchards that highly rely on the pollinator communities available in the landscape.

The main goals of this work were to assess pollinator's diversity and abundance in orchards of an insect-dependent crop and explore the relationships of pollinator's diversity and abundance with landscape structure and in-field management practices. Additionally, we explored the effect of landscape, in-field practices, and pollinator communities in orchard yield, to provide insights on the factors influencing crop productivity. Kiwifruit orchards were used as study system, given their high dependence on insect pollination (Sáez et al., 2019). We hypothesized that pollinators are influenced by both landscape structure and in-field practices. Landscapes that are richer in food and nesting resources (i.e., landscapes with natural and semi-natural areas), as well as orchards with practices that are less harmful to insects, are expected to harbor diverse and abundant pollinators. In addition, increased diversity and abundance of insect pollinators is expected to provide improved pollination services with positive consequences in yield values. To achieve this, insect pollinator communities were assessed in 22 commercial orchards, covering the entire production area in Portugal, and the effect of landscape type and in-field practices on pollinator's diversity and abundance were explored.

2. Materials and methods

2.1. Study sites and in-field practices

Twenty-two orchards were selected in collaboration with the Portuguese kiwifruit Producers Association (APK – Associação Portuguesa de Kiwicultores) to cover the entire production area in Portugal (central-north coastal region of mainland; Fig. 1; Table A1), and to comprise a

gradient in landscape composition. Fields were at least 3 km apart (except in two cases, in which fields were separated by 2 km and 500 m) and comprised production areas between 0.5 and 28 ha (averaging 6.8 ha; Table A1). Because Portuguese landscapes are highly fragmented due to historical land-use constraints, it was impossible to find a set of orchards with similar production area; however, we note that the mean size did not differ significantly among categories of in-field management practices and landscape types (two-way ANOVA: in-field practices - $F_{1,16} = 0.092$, $P = 0.765$; Landscape types - $F_{2,16} = 1.317$, $P = 0.295$).

Information about in-field management practices and orchard characteristics was collected for each selected orchard, through local inspection and inquiries to field technicians and farmers. The information gathered included: orchard characteristics such as production area, cultivated *Actinidia* varieties and female:male ratio; practices supporting pollination such as presence/absence of artificial pollination (i.e., application of pollen using manual pollen shooters or pollen dispersers machinery), installation of honeybee hives, passage with air turbines (i.e., management practice used to promote wind pollination) and application of developmental regulators (e.g., hormones to promote flower development); and practices affecting insect communities such as frequency of mechanical weed cutting, frequency of herbicide and pesticide application, and presence/absence of net protection. None of the orchards implemented flowers strips in-between lines or in field margins.

Each orchard was classified as having low or high pollinator unfriendly practices (LOW and HIGH, respectively) based on the combination of management practices that may affect pollinator's communities. For this, we scored management practices that may impact insect communities based on expert opinion, as in previous works (Kuldná et al., 2009). The applied criteria were based on expected impacts of management practices as follows: the presence of a physical barrier blocking insect's access to the orchard (net protection) and the use and frequency of agrochemical's application such as pesticides (sub-lethal effects; single annual applications, targeted to Lepidoptera larvae) and herbicides (depletion of food resources) were classified as having high negative impacts on insect communities (10 score – high impact); the mechanical weed cut (depletion of food resources) were classified as having medium negative impacts (5 score – medium impact), and the installation of honeybee hives (competition effects) and the application of developmental regulators as having minor negative impacts on insects (1 score – low impact). Then, we classified each orchard as high pollinator unfriendly (HIGH, $n = 11$) when the sum of the score values of management practices was higher or equal to 6 (i.e., high impactful in-field practices), and as low pollinator unfriendly (LOW, $n = 11$) when it was lower than 6 (i.e., low impactful in-field practices). High pollinator unfriendly orchards included orchards with two or more high and/or medium impact practices; low pollinator unfriendly orchards included orchards with none or only one medium or low impact practice.

Orchard productivity in tons per hectare was obtained from the producers for 2019 (kiwifruits harvested in October–November 2019). Finally, the number of registered honeybee colonies in 2019 within a 10 km radius area around each study site was obtained from the National Food and Veterinary Department (DGAV – *Direção Geral de Alimentação e Veterinária*; September 2019).

2.2. Landscape structure

Landscape parameters were extracted from four concentric radii (0.5, 1.0, 1.5 and 2.0 km) centered on each of the 22 orchards (Fig. A1), using the software ArcGIS (10.6 for Desktop Advanced Single Use, California, Esri). The distances selected were based on previous evidence demonstrating landscape effects in insect communities at these distances (e.g., Bartholomée et al., 2020; Bartholomée and Lavorel, 2019; Holland et al., 2004) and spanning the foraging ranges of most wild bees (e.g., Greenleaf et al., 2007). Polygons with more than 100 m² were classified

based on the Land Use Maps of Portugal (*Carta do Uso e Ocupação do Solo – 2010* COS 2010, available online at dgterritorio.gov.pt and provided by the National Territory Department – *Direção Geral do Território*), namely the COS 2010 categories (DGT 2018) (Table A2), and on 2018 Google Earth satellite imagery. The number of polygons (fragmentation) and the number of polygon types (fragment diversity) were obtained for COS 2010 Level 5. A conversion of COS Level 3 categories into the following five habitat types was carried out: forest, herbaceous, agricultural, urban, and water bodies (Table A2; Fig. A2); the percentual coverage of each habitat type was obtained, totaling 26,200 ha and 85 polygon types according to COS Level 5.

The study region is characterized by a human-dominated landscape, with a gradient in land-use from forest habitats to agricultural areas, and almost absence of natural and semi-natural areas. Based on field observations and preliminary data exploration of the main habitat types, the percentage of forest and herbaceous vegetation combined, and the percentage of agricultural area were the strongest variables describing the landscape. Thus, we used Principal Component Analyses to obtain the combined contribution of these landscape elements in the four concentric radii and extracted the values of the first component that explained 70% of the variance; the first component depicted a gradient in the coverage of landscape elements: from orchards with high coverage in forest and herbaceous vegetation and low agricultural area to orchards with low coverage in forest and herbaceous vegetation and high agricultural cover. Then, each orchard was classified in one of the following three categories depicting a gradient in these landscape elements: F+H ($n = 7$), when the landscape is dominated by forest and herbaceous habitats (mean \pm SD coverage for 2.0 km radius: $68.7 \pm 13.1\%$) and has low agricultural coverage ($19.8 \pm 13.1\%$); AGR ($n = 8$), when the landscape is dominated by agricultural habitats ($46.5 \pm 10.4\%$) and has low forest coverage ($27.0 \pm 12.3\%$); and MIX ($n = 7$), when intermediate to low values for forest, herbaceous and agricultural habitats are found ($30.7 \pm 8.3\%$ and $33.0 \pm 10.5\%$, respectively). Herbaceous coverages had a small representation accounting with only 1.0% coverage on average (ranging from 0.0% to 4.5%). The forest coverage accounted with 40.3% on average (ranging from 12.1% to 86.3%) and the agricultural areas accounted with 33.7% on average (ranging from 1.4% to 61.9%).

2.3. Insect pollinator community

Direct observations of plant-pollinator interactions were used to assess insect pollinator community in kiwifruit orchards. Observations were carried out during the flowering peak of kiwifruit, defined as 80–100% opened flowers within the orchard, from end of April to beginning of June 2019, in sunny days with low wind.

Direct observations were carried out during 2 min observation periods from 09:00 to 17:00 (GMT) in randomly chosen spots, with male and female flowers on sight, as many times as possible (between 52 and 189 observation periods per orchard, averaging 116; Table A3). Monitoring spots were selected along transects from the edge to the center of the orchard to account with edge-center effects in the sampling. Due to the short flowering period, only one day of field observations per orchard was possible (but it enabled us to attain >90% sampling completeness; see Section 2.5 Statistical analyses). The observer was set at approximately 2 m from the flower patch to monitor the interactions without disturbing foraging activity. Only insect species interacting with the flowers' anthers and/or stigmas was registered as pollinators. Photographs of insect visitors were taken to assist insect identification and validated with a reference collection of insects from the same kiwifruit orchards (FLOWer Lab, CFE, University of Coimbra). All insects were identified to the family level; Syrphidae (Diptera) were identified to the genus level; and Anthophila (Hymenoptera) were identified to the species level.

Table 1

Effect of in-field practices (LOW and HIGH pollinator unfriendly practices) on the following pollinators response variables: pollinator richness, Shannon-Wiener index (H'), Wild pollinators abundance, *A. mellifera* abundance, *Bombus* spp. abundance, Other wild bees abundance, and Syrphidae abundance. Significant differences at $P < 0.05$ are highlighted in bold.

Response variables	Factor: in-field practices		
	DF	WALD	P value
Pollinator RICHNESS	1	0.486	0.485
H' (Shannon-Wiener index)	1	4.591	0.032
Wild pollinators ABUNDANCE	1	6.831	0.009
<i>A. mellifera</i> ABUNDANCE	1	0.321	0.571
<i>Bombus</i> spp. ABUNDANCE	1	8.325	0.004
Other wild bees ABUNDANCE	1	0.203	0.653
Syrphidae ABUNDANCE	1	4.590	0.032

2.4. Insect pollinator community characterization

Pollinator species richness (estimated by simple counts) and Shannon-Wiener diversity index [$H' = \sum p_i (\ln p_i)$ in which p_i represents the abundance of each pollinator species, (Shannon, 1948)] were calculated. Because sampling effort varied among orchards due to various field work constraints (Table A3), we used rarefaction curves and an extrapolation and interpolation procedure following Hsieh et al., 2016 to obtain comparable species richness across orchards. Sampling effort of 150 observation periods was used because it enabled to achieve a plateau of species richness across all the surveyed orchards. Regardless of different sampling efforts, overall, sampling completeness ranged from 90% to 100%. Original and intra-/extrapolated values are provided in Table A3.

Pollinators were described also by species abundance per orchard, i. e., total abundance recorded in the orchard divided by the total number of observation periods performed in the orchard. For this, pollinators were organized in groups depending on whether they were managed or wild pollinators, and based on their efficiency, as follows: all pollinators – all insects observed interacting with sexual structures of kiwifruit flowers; wild pollinators – the fraction of pollinators excluding the managed *Apis mellifera*; *A. mellifera* – the only managed pollinator species in the study (Miñarro and Twizell, 2015; Steffan-Dewenter et al., 2002); *Bombus* spp. – the most effective kiwifruit pollinator using buzz foraging (Corbet et al., 1988; Craig and Stewart, 1988; King and Ferguson, 1994); other wild bees – an important group of pollinators that may pollinate kiwifruit, although rarely observed (Miñarro and Twizell, 2015); Syrphidae – an important pollinator group after bees (Miñarro et al., 2018; Miñarro and Twizell, 2015).

2.5. Statistical analyses

Generalized linear models (GLMs) were used to evaluate the effect of in-field practices (LOW and HIGH pollinator unfriendly orchards) and landscape structure (AGR, MIX and F+H categories) on insect pollinator's diversity and abundance variables. First, we explored differences between low and high pollinator unfriendly orchards (LOW and HIGH, respectively) in the following response variables: pollinator richness, H' (Shannon-Wiener index), wild pollinators abundance, *A. mellifera* abundance, *Bombus* spp. abundance, other wild bees abundance, Syrphidae abundance. Pollinator richness was adjusted to a Poisson distribution with a log link function; a square root transformation was applied to the remaining response variables and a Gaussian distribution with an identity link function was used to model responses. Model validation was performed by visual inspection of the residuals for checking heteroscedasticity and normality, as well as overdispersion (Zuur et al., 2009). Although the mean number of honeybee colonies at 10 km radius area around each site did not differ significantly among categories of in-field management practices and landscape types (two-way ANOVA: in-field practices - $F_{1,16} = 1.948$, $P = 0.182$; landscape types - $F_{2,16} =$

0.045, $P = 0.957$), for the analyses of *A. mellifera* abundance, the number of beehives was included as covariable. Second, we explored differences among landscape categories (i.e., AGR, MIX and F+H) in the above-mentioned response variables following the same statistical approach. Differences between estimated-marginal means were tested pairwise through multiple comparisons (Tukey contrasts).

GLMs were also used to evaluate the impact of in-field practices and landscape structure on orchard productivity (given as tons per hectare). For that, productivity was used as response variable (adjusted to a Gaussian distribution and an identity link function) and in-field practices, landscape structure and their interaction were defined as fixed factors. Additionally, the information on practices supporting pollination, such as, the application of pollen (artificial pollination), use of turbines (promoting wind pollination) and installation of beehives within the orchard, was used to create the variable 'pollination support practices' (orchards with and without pollination support practices) that was included in the analyses as a factor. Finally, linear regression analysis was used to explore the relationship between productivity and key pollinators variables, namely the diversity index, *A. mellifera* abundance, *Bombus* spp. abundance (considered the main pollinators of kiwifruit; Pomeroy and Fisher, 2002; Ricketts et al., 2008) (with variables standardized before the analyses) and 'pollination support practices'. Wild pollinator abundance was not used because it was significantly correlated with *Bombus* spp. abundance, and the later variable produced models with lower AIC values.

Statistical analyses were performed using R (v.3.6.2; <https://www.r-project.org/>), packages: iNEXT (Hsieh et al., 2016), pscl (Jackman, 2020), multcomp (Hothorn et al., 2008), car (Fox and Weisberg, 2019) and effects (Fox, 2003; Fox and Weisberg, 2019).

3. Results

A total of 4568 insect pollinators were observed visiting the flowers of kiwifruit, including a total of 44 morphospecies. The pollinator community was dominated by *A. mellifera* (53.3%), followed by other major groups, such as syrphids (14.7%; e.g., *Syrphus* sp. and *Sphaerophoria* sp.), *Bombus* spp. [10.3%, of which 98.8% were *B. terrestris* (Linnaeus, 1758)] and other wild bees (11.4%; e.g., *Halictus* spp. and *Andrena* spp.).

3.1. Effect of in-field practices in pollinator's community

In-field practices significantly impacted Shannon-Wiener diversity index and abundance of wild pollinators, *Bombus* spp. and Syrphidae, while no significant differences were observed for the remaining variables (Table 1, Fig. 2). LOW pollinator unfriendly orchards showed higher Shannon-Wiener diversity values than HIGH pollinator unfriendly orchards; a similar but non-significant trend was observed for pollinator's richness (Table 1, Fig. 2). LOW pollinator unfriendly orchards also showed significantly higher wild pollinators abundances than HIGH pollinator unfriendly orchards. The higher wild pollinators abundance was driven by overall higher abundances of all wild pollinator groups, in particular of *Bombus* spp. and Syrphidae (Table 1, Fig. 2). The managed *A. mellifera* tended to show an opposite pattern, but no significant differences were observed between LOW and HIGH pollinator unfriendly orchards (Fig. 2); also, *A. mellifera* abundance was not affected by the available beehives in the surrounding landscape ($Wald = 2.68$, $P = 0.102$).

3.2. Effect of landscape structure in pollinator's community

Landscape structure significantly impacted pollinators richness, Shannon-Wiener diversity index and the abundance of wild pollinators and *A. mellifera* (Table 2, Fig. 3). AGR landscapes presented significantly lower species richness and Shannon-Wiener diversity values than F+H landscapes, with MIX landscape presenting intermediate values

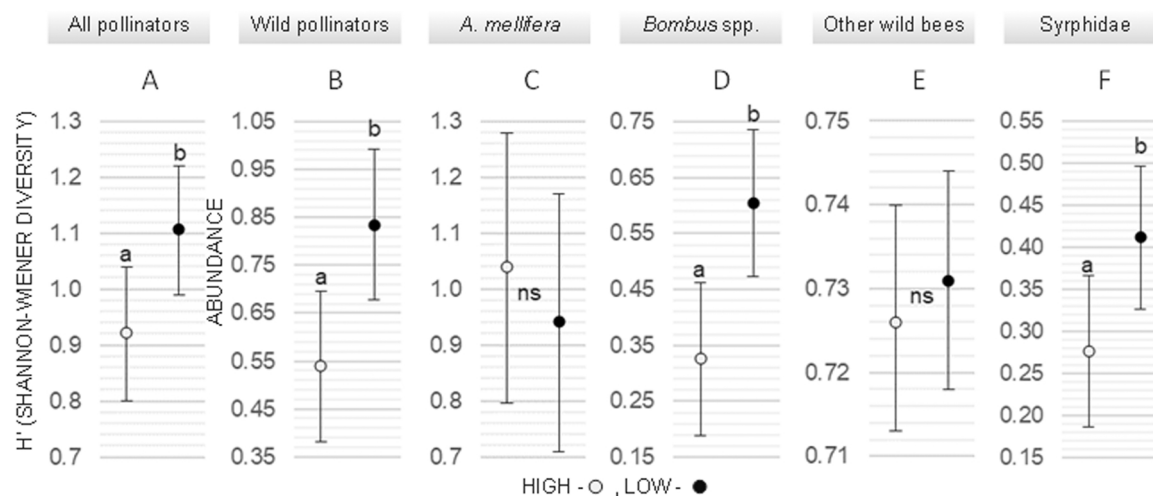


Fig. 2. Pollinator's diversity (H' , Shannon-Wiener index) and abundance according to in-field practices (HIGH – white mark – high pollinator unfriendly orchards; LOW – black mark – low pollinator unfriendly orchards) in kiwifruit orchards. Abundance is provided for different pollinator groups: wild pollinators, managed *Apis mellifera*, *Bombus* spp., other wild bees and Syrphidae. Values are provided as estimated marginal means as 95% confidence intervals. Different letters denote significant differences at $P < 0.05$; ns denotes non-significant differences ($P > 0.05$).

Table 2

Effect of landscape type (AGR, MIX and F+H) on the following pollinator response variables: pollinators richness, Shannon-Wiener index (H'), Wild pollinators abundance, *A. mellifera* abundance, *Bombus* spp. abundance, Other wild bees abundance, and Syrphidae abundance. Significant differences at $P < 0.05$ are highlighted in bold.

Response variables	Factor: landscape type		
	DF	WALD	P value
Pollinators RICHNESS	2	6.404	0.041
H' (Shannon-Weiner index)	2	18.080	< 0.001
Wild pollinators ABUNDANCE	2	7.549	0.023
<i>A. mellifera</i> ABUNDANCE	2	8.427	0.015
<i>Bombus</i> spp. ABUNDANCE	2	2.868	0.238
Other wild bees ABUNDANCE	2	3.854	0.146
Syrphidae ABUNDANCE	2	4.940	0.085

(Table 2, Fig. 3). AGR landscapes also presented significantly lower wild pollinator abundances than F+H landscapes ($P < 0.05$), once again with MIX landscape presenting intermediate values ($P > 0.05$) (Fig. 3). In contrast with wild pollinator's abundance, the managed *A. mellifera* was significantly more abundant in AGR landscapes than in F+H landscapes ($P < 0.05$), with MIX landscape presenting intermediate values ($P > 0.05$) (Fig. 3); also, its abundance was not affected by the available beehives in the surrounding landscape ($Wald = 2.98$, $P = 0.084$). No significant differences between landscape categories were observed for the abundance of *Bombus* spp., other wild bees and Syrphidae (Table 2, Fig. 3).

3.3. Effects of in-field practices and landscape structure on crop productivity

No statistically significant differences were observed in orchard productivity between LOW and HIGH pollinator unfriendly orchards, nor among landscape types (in-field practices: $Wald = 1.316$, $P = 0.251$; Landscape: $Wald = 1.822$, $P = 0.402$, interaction: $Wald = 0.382$,

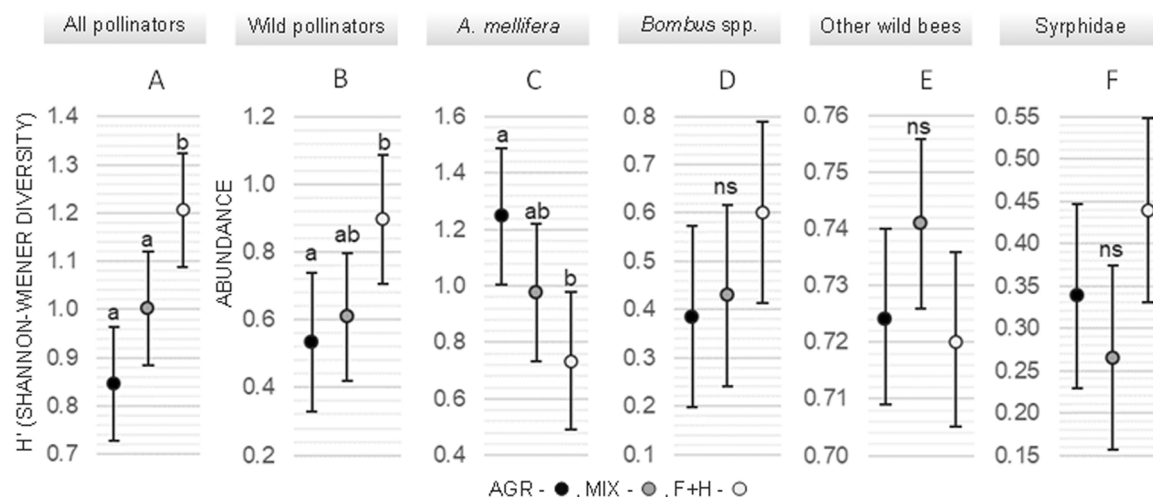


Fig. 3. Pollinator's diversity (H' , Shannon-Wiener index) and abundance according to the landscape type (AGR – black mark, dominance of agricultural habitats; MIX – gray mark, combination of agricultural and forest categories; F+H – white mark, dominance of forest and herbaceous habitats) in kiwifruit orchards. Abundance is provided for different pollinator groups: wild pollinators, managed *Apis mellifera*, *Bombus* spp., other wild bees and Syrphidae. Values are provided as estimated marginal means as 95% confidence intervals. Different letters denote significant differences at $P < 0.05$; ns denotes non-significant differences ($P > 0.05$).

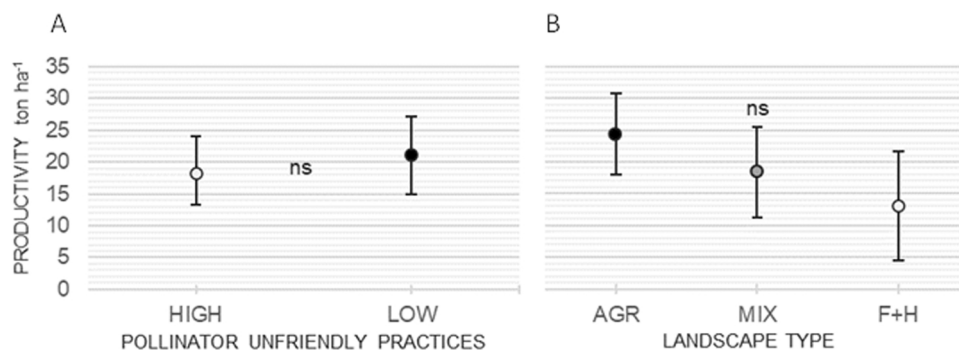


Fig. 4. Effect of in-field practices (HIGH – high pollinator unfriendly practices; LOW – low pollinator unfriendly practices) and landscape type (LANDSCAPE TYPE: AGR – black mark, agricultural habitats dominance; MIX – gray mark, combination of agricultural and forest categories; F+H – white mark, forest and herbaceous habitats) in the kiwifruit productivity (tons per hectare). ns denotes non-significant differences ($P > 0.05$).

Table 3

Linear regression analyses of productivity as a function of pollinator richness, *Apis mellifera* abundance, *Bombus* spp. abundance and pollination support practices. Significant differences at $P < 0.05$ are highlighted in bold.

Explanatory variables	Coefficient	T value	P value
H' (Shannon-Wiener index)	-9.182	-4.645	< 0.001
<i>A. mellifera</i> ABUNDANCE	-3.384	-1.364	0.196
<i>Bombus</i> spp. ABUNDANCE	6.173	3.723	0.003
Pollination support practices	5.828	2.203	0.046

$P = 0.826$) (Fig. 4).

Significant correlations were found between productivity and the explored explanatory variables (Adjusted $R^2 = 0.655$, $F_{4,13} = 9.060$, $P = 0.001$). A significant and positive correlation was found between productivity and *Bombus* spp. abundance, with higher *Bombus* spp. abundances being related with higher productivity levels (Table 3, Fig. 5). Additionally, orchards having pollination support practices were also related with higher productivity values (Table 3, Fig. 5). In contrast, a significant negative correlation was found between productivity and the Shannon-Wiener diversity index (Table 3, Fig. 5), with higher diversities being related with lower productivity values. No significant correlation was found between *A. mellifera* abundance and productivity

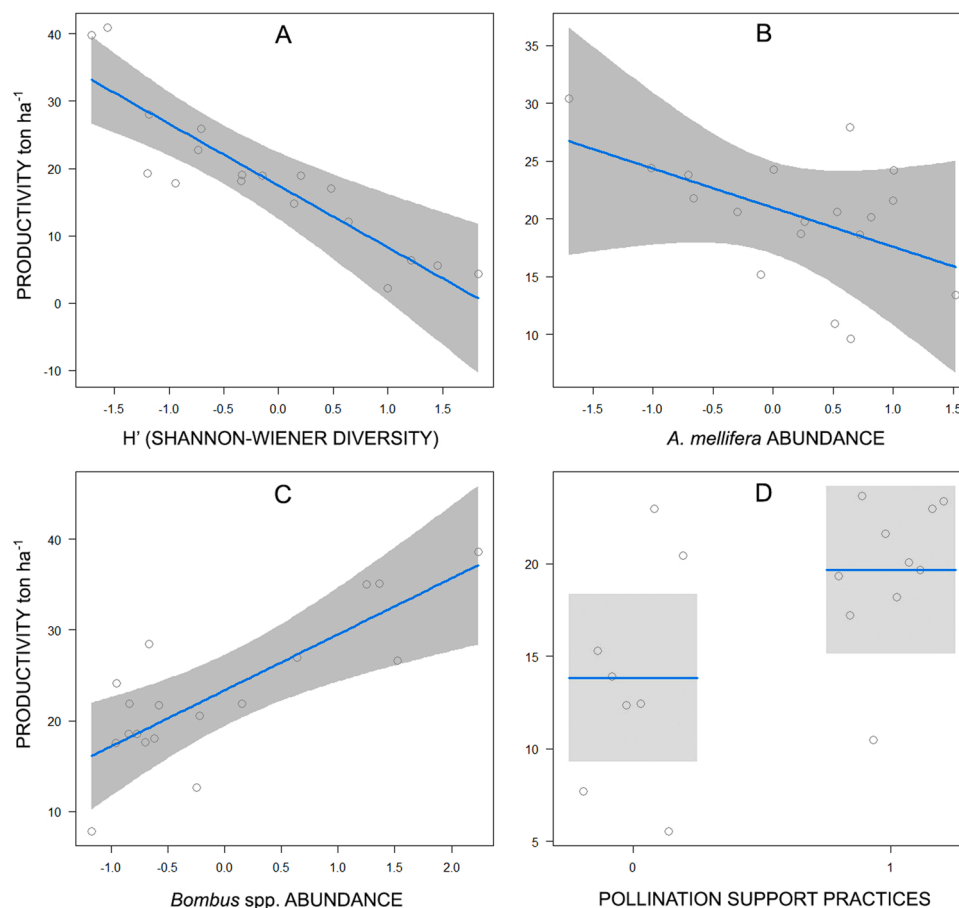


Fig. 5. Linear regression analyses of productivity (given in tons per hectare) as a function of pollinator richness (A), *Apis mellifera* abundance (B), *Bombus* spp. abundance (C), and pollination support practices (D) where 0 denotes no pollination support practices and 1 denotes presence of pollination support practices.

Table A1

Study sites identification codes (ID), location (including district and locality names), area (in hectares, ha), and categories of in-field management practices (IN-FIELD PRACTICES: LOW – low pollinator unfriendly practices; HIGH – high pollinator unfriendly practices) and landscape type (LANDSCAPE: F+H – dominance of forest and herbaceous habitats, AGR – dominance of agricultural habitats, MIX – combination of agricultural and forest + herbaceous habitats).

ID	District: locality	Area (ha)	In-field practices	Landscape
A1	VC: Valença	28.0	HIGH	AGR
K	BR: Amares	10.0	LOW	MIX
B2	BR: Guimarães	4.0	LOW	MIX
F	VC: Viana do Castelo	10.0	HIGH	MIX
U	PO: Felgueiras	3.0	HIGH	AGR
I	PO: Felgueiras	2.0	HIGH	AGR
H	PO: Vila do Conde	12.0	HIGH	AGR
Q	PO: Maia	6.6	LOW	AGR
R	PO: Gondomar	1.9	LOW	MIX
T	PO: Marco de Canavezes	4.0	LOW	F+H
O	PO: Vila Nova de Gaia	27.0	HIGH	MIX
L	AV: Santa Maria da Feira	6.0	HIGH	MIX
J	AV: Sever do Vouga	0.9	LOW	F+H
C2	AV: Albergaria-a-Velha	0.5	LOW	F+H
C1	AV: Aveiro	3.3	LOW	F+H
N	AV: Oliveira do Bairro	5.0	HIGH	MIX
E	AV: Oliveira do Bairro	0.9	LOW	AGR
V	AV: Anadia	3.0	LOW	F+H
P	CO: Cantanhede	2.3	HIGH	F+H
D	CO: Montemor-o-Velho	4.0	HIGH	MIX
S	CO: Soure	10.0	HIGH	AGR
G	LE: Pombal	6.9	LOW	F+H

Table A2

Landscape polygon classification categories (HABITAT TYPE) based on the Land Use Maps of Portugal – COS 2010 (*Carta do Uso do Solo* from 2010) levels 1 and 3.

COS 2010 Level 1	Habitat type	COS 2010 Level 3
Forests and semi to natural	Forest (F)	Hardwood forests
		Mixed forests
		Open, cut and new forests
	Herbaceous (H)	Softwood forests
		Shrubs
		Natural herb vegetation
Agricultural and agro-forest	Agricultural (AGR)	Open and low vegetation
		Sclerophyll vegetation
		Agricultural and agri-forest areas
		Complex and cultural systems
		Temporary and/or permanent crops
		Temporary irrigated crops
Artificialized	Urban	Temporary dry crops
		Orchards
		Olive orchards
		Vineyard
		Urban green areas
		Discontinuous urban area
		Land communication pathways
		Construction sites
		Recreation areas
Water bodies	Water bodies	Industry, trading and services
		Continuous urban area
		Inert material extraction
		Waste deposition areas
		Water courses
		Water plans

(Table 3, Fig. 5).

4. Discussion

4.1. In-field practices and pollinator's communities

Our study shows that orchards with practices that are less harmful to insect pollinators harbored more diverse pollinator communities and higher abundances of some wild pollinator groups, in particular *Bombus* spp. and Syrphidae. In-field practices that may impact negatively insect communities in kiwifruit orchards include the use of agrochemicals and weed mowing, and the use of net covers and managed pollinators. The regular application of agrochemicals has direct negative impacts in insect communities through effects on insect's life cycle (e.g., pesticides; Bengtsson et al., 2005; Hole et al., 2005), or indirect negative impacts through changes in food resources (e.g., herbicides; Bretagnolle and Gaba, 2015; Russo et al., 2020). Kiwifruit orchards are characterized by a low use of insect targeted agrochemicals but have a frequent application of herbicides or regular weed mowing (especially during spring). Because these practices significantly impact the amount and diversity of food resources for pollinators, orchards with practices promoting in-field wildflower's resources may provide attractive feeding resources for wild pollinators and promote its populations. Still, our data does not allow us to know if the differences in pollinator communities between management categories were due to pollinator movement among foraging areas, or due to real population increases. Previous studies have shown that the diversity of in-field floral resources is positively correlated with the diversity and abundance of insect pollinator communities in different systems (Holzschuh et al., 2007; Knapp et al., 2019; Roulston and Goodell, 2011), including orchards (Martínez-Núñez et al., 2020; Rosas-Ramos et al., 2020; Wu et al., 2021). Diverse flower resources provide pollen and nectar resources to support different pollinator taxa, such as wild bees and flies, but also different foraging types, like generalist and specialist pollinators (Häussler et al., 2017; Knapp et al., 2019; Torné-Nogueira et al., 2014). Further supporting the importance of diverse floral resources are the positive effects of implemented floral stripes or hedgerow improvement in the abundance and diversity of insect pollinators (e.g., Carvalheiro et al., 2011; Feltham et al., 2015; Pywell et al., 2011; Zamorano et al., 2020), including *Bombus* spp. (e.g., Carvell et al., 2007). Indeed, previous studies showed that the presence of wildflower's resources are related with increased bumblebee abundances (e.g., Carvell et al., 2007; Knapp et al., 2019). Considering that bumblebees are the most effective kiwifruit pollinators (Pomeroy and Fisher, 2002), management practices that promote their abundance would promote pollination services in kiwifruit orchards.

Additionally, net cover is being increasingly used in kiwifruit orchards to protect the plants and fruits from environmental factors (Cutting et al., 2018) and decrease the susceptibility to *Pseudomonas syringae* pv. *Actinidiae* (Psa) (Donati et al., 2018). However, Evans et al. (2019) showed that the implementation of net cover significantly impacted honeybee foraging behavior, decreasing bee densities and visitation rates, as well as significantly reducing the number of bees returning to the colonies. These changes in honeybee behavior due to net cover have expectable negative impacts in colony health and in kiwifruit productivity (Evans et al., 2019). Likewise, our field observations also recorded insect pollinators being trapped in the nets of covered kiwifruit orchards (author's field observations). However, we were not able to evaluate the direct effects of net cover for wild insects, as such practice is still rarely used in the Portuguese kiwifruit orchards (e.g., only a single orchard presented net covering at the sampling moment, although two additional producers implemented it afterwards). Still, considering the impacts of net cover in honeybee behavior, it is important to evaluate its impacts also in wild pollinators and the cost/benefits of its implementation before it becomes a more common practice.

Honeybees are currently a ubiquitous factor when considering

Table A3

Direct observation data obtained in the field and corrected for the same sampling effect using extrapolation or interpolation procedures. ID – orchard identification code; N – Number of monitoring periods of 2 min; SC% – Sampling Completeness; O – Observed value; I/E – Inter- or Extrapolated value.

ID	N	SC%	Species Richness		Wild pollinators Abundance		<i>Apis mellifera</i> Abundance		<i>Bombus</i> spp. Abundance		Other wild bees Abundance		Syrphidae Abundance	
			O	I/E	O		O		O		O		O	
A1	117	100	3	3	48		139		47		0		1	
B2	111	98	13	14	72		278		29		7		26	
C1	128	98	17	17	136		115		94		4		31	
C2	165	99	13	13	399		236		177		2		86	
E	158	98	14	14	172		300		98		13		40	
F	89	96	8	10	20		137		15		2		2	
G	120	95	10	11	85		1		44		1		8	
H	75	98	8	9	25		128		8		0		17	
I	151	99	9	9	79		244		8		6		41	
J	67	94	8	8	78		5		48		0		8	
K	70	91	6	8	12		37		7		0		5	
L	105	96	9	10	39		53		7		2		9	
N	52	90	8	11	15		18		4		4		4	
O	92	95	7	9	22		107		16		4		1	
P	103	95	11	12	25		78		9		4		11	
Q	129	98	8	8	22		198		12		2		8	
R	189	100	9	9	166		185		126		23		15	
S	129	99	9	9	25		182		4		0		10	
T	145	98	13	13	71		234		14		3		28	
U	167	97	11	10	27		318		9		6		10	
V	88	95	9	10	29		9		6		2		21	

pollination services, and even with a high provision of colonies at the landscape level (in our study area the number of colonies ranged between 800 and 3800 in a 10 km radius), kiwifruit producers are still more prone to install honeybee colonies within the orchard than to promote practices that favor wild pollinators. Indeed, the implementation of honeybee colonies is a widely used and well-established practice in several crops, and the valorization of wild pollinators is yet less fostered (e.g., Boecking and Veromann, 2020; Eraerts et al., 2020). Our results showed that an increase in the number of installed colonies in the landscape does not affect the abundance of honeybees within kiwifruit orchards, supporting a global dominance of these pollinators, although their foraging patterns across different landscape elements is still largely unknown. The development of practices supporting wild pollinator communities and their services to crop systems could promote a freely available and highly efficient service (Boecking and Veromann, 2020; Miñarro and Twizell, 2015). The current honeybee dominance not only may intensify potential negative ecological effects on wild pollinators and plant communities (Mallinger et al., 2017), but also increase the dependence on a single pollinator species (Fijen et al., 2018; Garibaldi et al., 2013; Kleijn et al., 2015), which is not necessarily the most effective pollinator (as it is the case of kiwifruit; Craig, 1988; Pomeroy and Fisher, 2002).

4.2. Landscape structure and pollinator communities

Overall, our results support the role of landscape structure shaping pollinator communities, with different landscape structures being associated with different pollinator communities. We observed that agricultural dominated landscapes harbored lower pollinator diversity, lower wild pollinators abundance and higher managed honeybee abundance than forest and herbaceous dominated landscapes, while mixed landscapes harbor, in general, intermediate values. Our results further support previous studies showing that more complex pollinator communities are expected to exist when high-quality habitats are prevalent in the landscape (Bartholomé et al., 2020; Beduschi et al., 2018; Hall et al., 2019; Holland et al., 2017). These higher-quality habitats have been characterized by diverse and abundant food and nesting resources and have been identified as non-crop areas (areas not covered by arable fields; Tscharnke et al., 2005), such as forests and grasslands (Hall et al., 2019; Holland et al., 2017; Potts et al., 2006).

Consequently, increased coverage or decreased distance to natural and semi-natural areas, such as forests and grasslands, has been observed to promote diverse pollinator communities (Holzschuh et al., 2012; Kennedy et al., 2013; Morandin and Winston, 2005; Shackelford et al., 2013), as observed in our study. In contrast, more simplified pollinator communities are expected in landscapes with high agricultural coverage (Carré et al., 2009), with increased crop area being associated with lower pollinator's abundance and richness (Benjamin et al., 2014; Connelly et al., 2015; Landaverde-González et al., 2017).

The central-north coastline of Portugal is marked by a highly dominated anthropogenic landscape, being devoted to forest exploitation and agriculture, with many small agricultural properties and complex landscapes (complexity here used to designate landscapes with small and diverse patches). Grasslands, one of the most attractive habitats for pollinator populations (Hall et al., 2019; Holland et al., 2017), are very scarcely represented (4.5%), while forests account for 41.3% of the study area around the orchards. These forests harbor high diversity as they can range from plantations of *Eucalyptus globulus* (28.2%, from the forest area) to mixed forests of eucalyptus and other tree species (19.1%), pinus forests (20.2%) and forests of caducifolious trees (8.3%), with diverse herbaceous and shrub vegetation within. Thus, such habitat type harbors permanent and highly heterogeneous and diverse food and nesting resources and may promote wild pollinator's groups. Wild pollinators, such as wild bees (*Bombus* spp. and other wild bees), rely on the availability of a diverse set of resources due to specific nesting and diet requirements and smaller foraging ranges in comparison to honeybees (Gámez-Virués et al., 2015; Hall et al., 2019; Steffan-Dewenter et al., 2002). Syrphids can also benefit from forest habitats, especially those that belong to dead wood feeding guilds (De Souza et al., 2014; Meyer et al., 2009; Rader et al., 2020). In contrast, agricultural landscapes, although structurally complex with abundant hedgerows with ruderal vegetation (as a result of small farms) and diverse crop systems, are subjected to continuous disturbance and are dominated by temporary crops (58.0%, including several cereals, such as, maize and rye), thus not providing reliable resources in time and space.

Conversely, honeybees were more abundant in agricultural dominated landscapes. Our results are in accordance with previous findings showing that honeybee abundance decreases with increased natural or semi-natural habitat (Steffan-Dewenter et al., 2002). Honeybees do not depend so heavily as other wild pollinators groups on landscape



Fig. A1. Representation of the landscape around the 22 kiwifruit orchards studied for pollinator community with the five habitat types (as provided in Table A3) represented (generated in ArcGIS). Each image presents the kiwifruit orchards in the center of concentric 500 m, 1000 m, 1500 m and 2000 m radii circles (some pairs are represented in the same image). (A–G) Orchards located in forest + herbaceous dominated landscapes. (H–N) Orchards located in a mixture of agricultural and forest + herbaceous landscapes (note that in panel I, only the left orchard belongs to this landscape category; the right orchard belongs to agricultural dominated landscapes). (O–T) Orchards located in agricultural dominated landscapes.

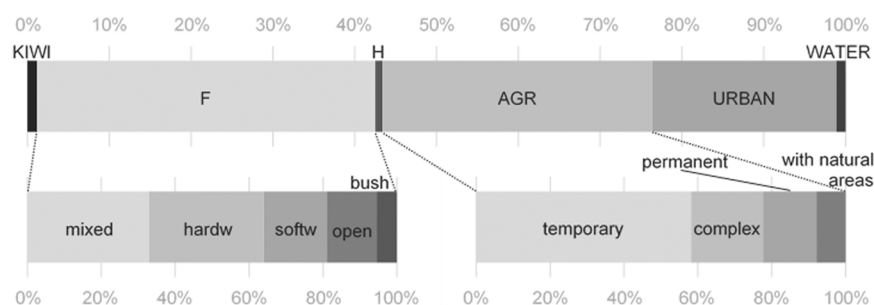


Fig. A2. Overall habitat description of the landscape given as percentage of area from the 2000 m radius around the studied kiwifruit orchards, according to COS 2010 Level 3 categories. Abbreviations: KIWI – studied kiwifruit orchards; F – Forest; H – herbaceous habitats; AGR – agricultural areas; URBAN – urban areas; WATER – water bodies; mixed – hardwood and softwood forests; hardw – hardwood forests; softw – softwood forests; open – open forests and young plantations; bush – shrublands with small bushes; temporary – annual crops; complex – mixed crop systems; permanent – vineyards and orchards; with natural areas – agricultural areas with natural areas.

structure as they take advantage of their higher mobility and social behavior that enables an easy recruitment to food sources. Additionally, honeybees have less restricted life cycle requirements that are facilitated by artificial management (Steffan-Dewenter et al., 2002). Honeybee traits, together with a close relationship between farming and

beekeeping, may promote honeybee abundance in agricultural landscapes. Although we did not find any relationship between wild pollinator and honeybee abundances, given the ubiquitous nature of honeybees in the landscape, it remains unclear if in the context of the studied region they may drive negative effects on wild pollinators, for

example through direct competition, as observed in other regions (Cane and Tepedino, 2017), or through indirect changes in plant communities (Fontaine et al., 2006). Yet, it is worth noticing that, when analyzing several crops, including analyses in kiwifruit orchards, Garibaldi et al. (2013) found no correlation in visitation rates by wild pollinators and honeybees, with no evidence for resource competition at the field level, most probably because mass flowering crops provide floral resources in excess in comparison with what can be exploited by local pollinator's populations (Garibaldi et al., 2013).

4.3. Productivity and pollinator communities

Regardless of the differences observed in pollinator communities described above, we observed no significant differences in kiwifruit yield, neither between low and high pollinator unfriendly orchards, nor across landscape types (Fig. 4). On one hand, these results in particular suggest that the different pollinator communities observed at each in-field management category may provide pollination services that enabled to attain similar yield values. Therefore, having less harmful in-field practices to insect pollinators may be an effective way for boosting the diversity and abundance of wild pollinators (including the efficient kiwifruit pollinator *Bombus* spp.), thereby benefiting pollinator's conservation, without compromising kiwifruit yield. On the other hand, the observed lack of differences in productivity across landscape types (Fig. 4) could suggest that higher *Apis mellifera* abundances in agricultural dominated areas may complement, in some degree, the pollination services provided by the less abundant wild pollinators (but see below).

However, our results also show that kiwifruit productivity was significantly impacted by the abundance of *Bombus* spp., while no significant relationship was detected with honeybee abundance. This result is not surprising because, although honeybees are the main floral visitor of kiwifruit (results herein; 88% of the visits in the review by Garibaldi et al., 2013; Pomeroy and Fisher, 2002; Ricketts et al., 2008; Craig and Stewart, 1988; Doreen and Jay, 1984; Miñarro and Twizell, 2015; Sharma et al., 2013), bumblebees are the most efficient pollinator of kiwifruit (Craig, 1988; Pomeroy and Fisher, 2002). Comparative studies have shown that bumblebees have lower flower handling times, contact more stigmatic lobes per visit and transfer significantly more pollen in single visits to female flowers than honeybees (10 times more according with Macfarlane and Ferguson 1983; and 4.5 times more according with Craig, 1988). The increased pollination efficiency by bumblebees is linked with the 'buzz-pollination' syndrome of kiwifruit flowers (Buchmann, 1983), namely, the dehiscent dry male pollen via small apical slits, which bumblebees (but not honeybees) collect by sonicating the flowers. Thus, higher abundances of honeybees may not compensate for their lower pollination efficiency of kiwifruit as no significant relationship was detected between honeybee abundance and kiwifruit productivity. Likewise, in a global survey by Garibaldi et al., 2013, visitation rates by honeybees were shown to significantly increase fruit set in only a small fraction of the crop systems surveyed (14% of surveyed crops; Garibaldi et al., 2013). These authors also showed that a higher abundance (and diversity) of wild pollinators positively impacted productivity regardless of *A. mellifera* abundance in many crops (Garibaldi et al., 2013). However, when analyzing kiwifruit separately, wild pollinator communities (and honeybees) did not significantly increase pollen deposition with increased visitation rates (Garibaldi et al., 2013, Fig. S4). It remains unknown if the same pattern would have been observed if the authors would have analyzed *Bombus* spp. (or other pollinators able to sonicate the flowers) separately.

Expectedly, we observed that productivity was highly influenced by pollination support management practices that directly improved pollination levels, and consequently, kiwifruit yield. Practices such as the use of turbines and artificial pollination, complement insect pollination in kiwifruit orchards when pollination deficits are identified. Pollination deficits are common in kiwifruit orchards (Tacconi et al., 2016; Castro et al., 2021b,a), and are generated by unfavorable

environmental conditions for insect pollination, low pollen availability due to flowering asynchrony or insufficient number of male plants, and management practices that reduce pollinator activity (e.g., net cover) (Antunes et al., 2007; Evans et al., 2019; Gonzalez et al., 1998; Miñarro and Twizell, 2015; Tacconi and Michelotti, 2018). In the studied region, pollination management practices are not so common as in intensive kiwifruit production areas such as in Italy and New Zealand (Tacconi and Michelotti, 2018), where they are routinely applied. Their application to Portuguese landscapes might have low economic potential because of the costs associated with the spread of diseases; also, the implementation of nature-based solutions presents a higher potential than such practices.

Finally, kiwifruit productivity was negatively related with pollinator diversity. Several empirical studies have shown links between pollinator diversity and plant reproduction, with a higher diversity of wild pollinators positively impacting productivity (e.g., Carvalheiro et al., 2011; Eeraerts et al., 2019; Garibaldi et al., 2013; Hoehn et al., 2008). Pollinator richness is expected to increase mean fruit set and reduce fruit set variability through effects such as complementary pollination and/or facilitation among pollinator species (e.g., Greenleaf and Kremen, 2006; Blüthgen and Klein, 2011). However, simulations of the effect of pollinator diversity on plant reproduction revealed that the relationship between these two components may vary widely depending on the interactions between among-pollinator differences in effectiveness and visitation frequency (Perfectti et al., 2009). As described above, kiwifruit is a crop with a specialized pollination system. In one hand, the flower needs to receive a high amount of pollen (2000–3000 viable pollen grains) to ensure a good pollination (fruits with > 100 g and 1000 seeds; Ferguson et al., 1984; Tacconi et al., 2016; Testolin et al., 1991). On the other hand, the most efficient pollinators are restricted to a specific group of insects with the ability to buzz pollinate (King, 1993; King and Ferguson, 1994), and thus, able to release and transport high amounts of pollen. Consequently, productivity might be more related with abundance of specific and highly efficient pollinator guilds than with the entire pollinator community. In our study region, insects that are able to sonicate the flowers of kiwifruit are almost exclusively represented by *Bombus* species. Indeed, our surveys showed that this genus was largely dominated by one species, *Bombus terrestris*, that accounted with 98.8% of the visits, with a few additional species (e.g., *B. pascuorum* and *B. hortorum*) being rarely observed. In contrast, diversity indexes were incremented by flower visitors from other taxonomic groups, such as Syrphidae, that might not contribute heavily to kiwifruit productivity because of their significantly lower pollination effectiveness when compared with *Bombus* spp. Under this scenario, we would expect that kiwifruit productivity would be particularly linked with *Bombus* spp. abundance (as described in the previous paragraph) and would not be impacted by pollinator diversity. However, when exploring diversity-functioning relationships using different functions, Perfectti et al. (2009) found that low pollinator diversity benefited plant fitness when the most abundant pollinators were the most effective floral visitors, or, alternatively, an optimal value of pollinator diversity maximizing plant fecundity would depend on the frequency of the most-effective pollinators. For example, in *Lavandula latifolia* the most abundant pollinator is also the most effective one, and simulations yielded a decreasing relationship between pollinator diversity and plant fitness (Perfectti et al., 2009). This occurs because increasing pollinator diversity may encompass an increment of inefficient floral visitors leading to increased pollen losses or higher pollen loads of unviable, incompatible, or inter-specific pollen, with negative impacts in pollination success. In an experimental design using potted petunias in vineyards, (Brittain et al., 2010) also observed a negative relationship between seed set and species richness and attributed the results to different pollinator efficiencies. Additionally, competitive interactions mediated by the most abundant pollinator groups (*Bombus* and honeybees) might also drive behavioral changes in pollinator communities, although here no correlations were found between wild pollinator diversity and *Bombus* and

honeybee's abundances. For example, *Bombus* species impacted differently two species of small syrphids, significantly reducing the foraging time of one, while indirectly favoring the other species due to the different syrphid foraging strategies (Morse, 1981). Yet, it remains unknown whether the negative relationship between pollinator diversity and kiwifruit productivity is direct or mediated by effects of other factors not considered in this study.

5. Conclusions

Here we show that orchards with practices that are less harmful to insect pollinators harbor more diverse and abundant pollinator communities, contributing to both wild pollinator's conservation and crop pollination services. Thus, even with simple and inexpensive in-field practices, as promoting natural vegetation, there can be significant positive changes in pollinator's community, including increased abundance of the most efficient pollinator of kiwifruit (i.e., *Bombus* spp.), without compromising yield. Orchard productivity was significantly and positively impacted by *Bombus* spp. abundance as well as by pollination support practices. Thus, cost/benefits analyses for the use of in-field pollinator friendly practices and pollination support practices such as artificial pollination and/or the use of turbines are needed to understand their economic impact in kiwifruit production. Additionally, different landscape structures were associated with specific pollinator's communities, but no differences were detected in productivity among landscape types. While forest and herbaceous dominated landscapes harbored higher pollinator diversity and wild pollinator's abundance, agricultural landscapes were characterized by higher abundances of managed honeybees. The lack of differences in productivity across landscape types could suggest that honeybees may complement wild pollinators services in agricultural landscapes, but no significant impacts were detected in productivity.

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.

Acknowledgments

We thank the many specialists that helped in the insect identification, namely Andrei Humala, Angel M. Moreno, Boris Büche, Even Dankowicz, Francisco A. López Núñez, Ian Cross, John Ascher, José Manuel Grosso-Silva, Louis Raginwulf, Patrícia Garcia Pereira, Peter Slingsby, Rui Andrade, Sílvia Pina, Spencer K. Monckton, Steven Wang, Susanna Heideman, Thomas J. Wood and Villu Soon. This work was supported by the Rural Development Programme 2014–2020 (*Programa de Desenvolvimento Rural* 2014–2020 (PDR)) under the research programme PDR2020101-031204 'i9K – Development of strategies for the sustainability of the kiwifruit industry through the creation of a value-added product' and by FCT – *Fundação para a Ciência e a Tecnologia*, I. P. within the project UID/BIA/04004/2020. FCT also financed the work of CS through the fellowship SFRH/BD/145962/2019. Project ReNATURE – (Regional Operational Programme Centro 2020, CENTRO-01-0145-FEDER-000007) financed the work of HC, SC and MC; SC was also financed by the Integrated Program of Scientific Research and Technological Development CULTIVAR (CENTRO-01-0145-FEDER-000020), co-financed by the Regional Operational Programme Centro 2020, Portugal 2020 and European Union, through European Fund for Regional Development (ERDF). HC was also financed by national funds (OE), through FCT, I.P., in the scope of the framework contract foreseen in the numbers 4–6 of the article 23, of the Decree-Law 57/2016, August 29, changed by Law 57/2017, July 19.

Appendix A

See Tables A1–A3, and Figs. A1 and A2.

References

- Antunes, M.D.C., Oliveira, M., Teixeira, M., Veloso, A., Veloso, F., Panagopoulos, T., 2007. Evaluation of the effect of complementary pollination on *Actinidia deliciosa* "Hayward" in northwest Portugal. *Acta Hort.* 753, 347–352. <https://doi.org/10.17660/ActaHortic.2007.753.43>.
- Bartholomé, O., Lavelle, S., 2019. Disentangling the diversity of definitions for the pollination ecosystem service and associated estimation methods. *Ecol. Indic.* 107, 105576 <https://doi.org/10.1016/j.ecolind.2019.105576>.
- Bartholomé, O., Aulio, A., Becquet, J., Vannier, C., Lavelle, S., 2020. Pollinator presence in orchards depends on landscape-scale habitats more than in-field flower resources. *Agric. Ecosyst. Environ.* 293, 106806 <https://doi.org/10.1016/j.agee.2019.106806>.
- Beduschi, T., Kormann, U.G., Tschamntke, T., Scherber, C., 2018. Spatial community turnover of pollinators is relaxed by semi-natural habitats, but not by mass-flowering crops in agricultural landscapes. *Biol. Conserv.* 221, 59–66. <https://doi.org/10.1016/j.biocon.2018.01.016>.
- Bengtsson, J., Ahnström, J., Weibull, A.C., 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *J. Appl. Ecol.* 42, 261–269. <https://doi.org/10.1111/j.1365-2664.2005.01005.x>.
- Benjamin, F.E., Reilly, J.R., Winfree, R., 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. *J. Appl. Ecol.* 51, 440–449. <https://doi.org/10.1111/1365-2664.12198>.
- Blüthgen, N., Klein, A.M., 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic Appl. Ecol.* 12 (4), 282–291.
- Boecking, O., Veromann, E., 2020. Bee pollination of crops: a natural and cost-free ecological service. In: *Entomovectoring for Precision Biocontrol and Enhanced Pollination of Crops*. Springer, Cham, pp. 53–62.
- Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28, 230–238. <https://doi.org/10.1016/j.tree.2012.10.012>.
- Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. *Agron. Sustain. Dev.* 35, 891–909.
- Brittain, C., Bommarco, R., Vighi, M., Settele, J., Potts, S.G., 2010. Organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biological Conservation* 143, 1860–1867. <https://doi.org/10.1016/j.biocon.2010.04.029>.
- Buchmann, S.L., 1983. Buzz pollination in angiosperms. *Handbook of Experimental Pollination Biology*. Scientific and Academic Editions, New York, pp. 73–113.
- Cane, J.H., Tepedino, V.J., 2017. Gauging the effect of honey bee pollen collection on native bee communities. *Conserv. Lett.* 10, 205–210. <https://doi.org/10.1111/conl.12263>.
- Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyörgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M., Vaissière, B.E., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agric. Ecosyst. Environ.* 133, 40–47. <https://doi.org/10.1016/j.agee.2009.05.001>.
- Carvalho, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S., Nicolson, S.W., 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecol. Lett.* 14, 251–259. <https://doi.org/10.1111/j.1461-0248.2010.01579.x>.
- Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D., Nowakowski, M., 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J. Appl. Ecol.* 44, 29–40.
- Castro, H., Siopa, C., Casais, V., Castro, M., Loureiro, J., Gaspar, H., Castro, S., 2021a. Pollination as a key management tool in crop production: Kiwifruit orchards as a study case. *Scientia Horticulturae* 290, 110533. <https://doi.org/10.1016/j.scienta.2021.110533>.
- Castro, H., Siopa, C., Casais, V., Castro, M., Loureiro, J., Gaspar, H., Dias, M.C., Castro, S., 2021b. Spatiotemporal Variation in Pollination Deficits in an Insect-Pollinated Dioecious Crop. *Plants* 10 (7), 1273. <https://doi.org/10.3390/plants10071273>.
- Chapin, F.S., Carpenter, S.R., Kofinas, G.P., Folke, C., Abel, N., Clark, W.C., Olsson, P., Smith, D.M.S., Walker, B., Young, O.R., Berkes, F., Biggs, R., Grove, J.M., Naylor, R. L., Pinkerton, E., Steffen, W., Swanson, F.J., 2010. Ecosystem stewardship: sustainability strategies for a rapidly changing planet. *Trends Ecol. Evol.* 25, 241–249. <https://doi.org/10.1016/j.tree.2009.10.008>.
- Chaplin-Kramer, R., Dombeck, E., Gerber, J., Knuth, K.A., Mueller, N.D., Mueller, M., Ziv, G., Klein, A.M., 2014. Global malnutrition overlaps with pollinator-dependent micronutrient production. *Proc. R. Soc. B Biol. Sci.* 281. <https://doi.org/10.1098/rspb.2014.1799>.
- Connelly, H., Poveda, K., Loeb, G., 2015. Landscape simplification decreases wild bee pollination services to strawberry. *Agric. Ecosyst. Environ.* 211, 51–56. <https://doi.org/10.1016/j.agee.2015.05.004>.
- Corbet, S.A., Chapman, H., Saville, N., 1988. Vibratory pollen collection and flower form: bumble-bees on *Actinidia*, *Symphytum*, *Borago* and *Polygonatum*. *Funct. Ecol.* 2, 147. <https://doi.org/10.2307/2389689>.
- Costa, G., Testolin, R., Vizzotto, G., 1993. Kiwifruit pollination: an unbiased estimate of wind and bee contribution. *N. Z. J. Crop Hortic. Sci.* 21, 189–195. <https://doi.org/10.1080/01140671.1993.9513767>.

- Craig, J.L., Stewart, A.M., 1988. A review of kiwifruit pollination: where to next? *N. Z. J. Exp. Agric.* 16, 385–391. <https://doi.org/10.1080/03015521.1988.10425667>.
- Cutting, B.T., Evans, L.J., Paugam, L.I., McBrydie, H.M., Jesson, L.K., Pomeroy, N., Janke, M., Jacob, M., Pattimore, D.E., 2018. Managed bumble bees are viable as pollinators in netted kiwifruit orchards. *N. Z. Plant Prot.* 71, 214–220. <https://doi.org/10.30843/nzpp.2018.71.178>.
- De Souza, J.M.T., Marinoni, R.C., Marioni, L., 2014. Open and disturbed habitats support higher diversity of syrphidae (diptera)? a case study during three yr of sampling in a fragment of araucaria forest in southern Brazil. *J. Insect Sci.* 14, 1–8. <https://doi.org/10.1093/jisesa/ieu098>.
- Donati, I., Cellini, A., Buriani, G., Mauri, S., Kay, C., Tacconi, G., Spinelli, F., 2018. Pathways of flower infection and pollen-mediated dispersion of *Pseudomonas syringae* pv. *actinidiae*, the causal agent of kiwifruit bacterial cancer. *Hortic. Res.* 5. <https://doi.org/10.1038/s41438-018-0058-6>.
- Doreen, J., Jay, C., 1984. Observations of honeybees on Chinese gooseberries ('Kiwifruit') in New Zealand. *Bee World* 65, 155–166. <https://doi.org/10.1080/0005772X.1984.11098804>.
- Eeraerts, M., Smagghe, G., Meeus, I., 2019. Pollinator diversity, floral resources and semi-natural habitat, instead of honey bees and intensive agriculture, enhance pollination service to sweet cherry. *Agric. Ecosyst. Environ.* 284, 106586 <https://doi.org/10.1016/j.agee.2019.106586>.
- Eeraerts, M., Borremans, L., Smagghe, G., Meeus, I., 2020. A growers' perspective on crop pollination and measures to manage the pollination service of wild pollinators in sweet cherry cultivation. *Insects* 11, 1–8. <https://doi.org/10.3390/insects11060372>.
- Ellis, J., 2012. The honey bee crisis. *Outlooks Pest Manag.* 23, 35–40. <https://doi.org/10.1564/22feb10>.
- Evans, L.J., Cutting, B.T., Jochym, M., Janke, M.A., Felman, C., Cross, S., Jacob, M., Goodwin, M., 2019. Netted crop covers reduce honeybee foraging activity and colony strength in a mass flowering crop. *Ecol. Evol.* 9, 5708–5719. <https://doi.org/10.1002/eece3.5154>.
- Feltham, H., Park, K., Minderman, J., Goulson, D., 2015. Experimental evidence that wildflower strips increase pollinator visits to crops. *Ecol. Evol.* 5, 3523–3530. <https://doi.org/10.1002/eece3.1444>.
- Ferguson, A.R., 1984. Kiwifruit: a botanical review. In: Janick, J. (Ed.), *Horticultural Reviews*. AVI Publishing Company, INC, Westport, CT, USA, pp. 1–64.
- Fijen, T.P.M., Scheper, J.A., Boom, T.M., Janssen, N., Raemakers, I., Kleijn, D., 2018. Insect pollination is at least as important for marketable crop yield as plant quality in a seed crop. *Ecol. Lett.* 21, 1704–1713. <https://doi.org/10.1111/ele.13150>.
- Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2006. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biol.* 4, 0129–0135. <https://doi.org/10.1371/journal.pbio.0040001>.
- Fox, J., 2003. Effect displays in R for generalised linear models. *J. Stat. Softw.* 8, 1–27.
- Fox, J., Weisberg, S., 2019. *An R Companion to Applied Regression*, third ed. Sage, Thousand Oaks CA.
- Gómez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., De Jong, H., Simons, N.K., Klein, A.M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C.N., Weisser, W., Werner, M., Tschamtkke, T., Westphal, C., 2015. Landscape simplification filters species traits and drives biotic homogenization. *Nat. Commun.* 6 <https://doi.org/10.1038/ncomms9568>.
- Garibaldi, L.A., Steffan-dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608–1611. <https://doi.org/10.1126/science.1230200> (80-).
- Garibaldi, L.A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A.M., Janssen, C., Morandin, L., Scheper, J., Winfree, R., 2014. From research to action: enhancing crop yield through wild pollinators. *Front. Ecol. Environ.* 12, 439–447. <https://doi.org/10.1890/130330>.
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentesi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14 <https://doi.org/10.1111/j.1461-0248.2011.01669.x>, 1062–1072.
- Gonzalez, M.V., Coque, M., Herrero, M., 1998. Influence of pollination systems on fruit set and fruit quality in kiwifruit (*Actinidia deliciosa*). *Ann. Appl. Biol.* 132, 349–355. <https://doi.org/10.1111/j.1744-7348.1998.tb05210.x>.
- Goodwin, R.M., Houten, A., Ten, Perry, J.H., 1999. Effect of staminate kiwifruit vine distribution and flower number on kiwifruit pollination. *N. Z. J. Crop Hortic. Sci.* 27, 63–67. <https://doi.org/10.1080/01140671.1999.9514081>.
- Greenleaf, S.S., Kremen, C., 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl. Acad. Sci.* 103 (37), 13890–13895.
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596. <https://doi.org/10.1007/s00442-007-0752-9>.
- Guroo, I., Wani, S.A., Wani, S.M., Ahmad, M., Mir, S., Massodi, F., 2017. A review of production and processing of kiwifruit. *J. Food Process. Technol.* 8 <https://doi.org/10.4172/2157-7110.1000699>.
- Hall, M.A., Nimmo, D.G., Cunningham, S.A., Walker, K., Bennett, A.F., 2019. The response of wild bees to tree cover and rural land use is mediated by species' traits. *Biol. Conserv.* 231, 1–12. <https://doi.org/10.1016/j.biocon.2018.12.032>.
- Häussler, J., Sahlin, U., Baey, C., Smith, H.G., Clough, Y., 2017. Pollinator population size and pollination ecosystem service responses to enhancing floral and nesting resources. *Ecol. Evol.* 7, 1898–1908.
- Hoehn, P., Tschamtkke, T., Tylanakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. B Biol. Sci.* 275, 2283–2291. <https://doi.org/10.1098/rspb.2008.0405>.
- Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V., Evans, A.D., 2005. Does organic farming benefit biodiversity? *Biol. Conserv.* 122, 113–130. <https://doi.org/10.1016/j.biocon.2004.07.018>.
- Holland, J.D., Bert, D.G., Fahrig, L., 2004. Determining the spatial scale of species' response to habitat. *Bioscience* 54, 227. [https://doi.org/10.1641/0006-3568\(2004\)054\[0227:dtssos\]2.0.co;2](https://doi.org/10.1641/0006-3568(2004)054[0227:dtssos]2.0.co;2).
- Holland, J.M., Douma, J.C., Crowley, L., James, L., Kor, L., Stevenson, D.R.W., Smith, B.M., 2017. Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agron. Sustain. Dev.* 37 <https://doi.org/10.1007/s13593-017-0434-x>.
- Holzschuh, A., Dudenhöffer, J.H., Tschamtkke, T., 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biol. Conserv.* 153, 101–107. <https://doi.org/10.1016/j.biocon.2012.04.032>.
- Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tschamtkke, T., 2007. Diversity of flower-visiting bees in cereal fields: Effects of farming system, landscape composition and regional context. *J. Appl. Ecol.* 44, 41–49. <https://doi.org/10.1111/j.1365-2664.2006.01259.x>.
- Hopping, M.E., Hacking, N.J.A., 1983. A comparison of pollen application methods for the artificial pollination of kiwifruit. *Acta Hort.* 139.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biom. J.* 50, 346–363.
- Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7 (12), 1451–1456. <https://doi.org/10.1111/2041-210X.12613>.
- Jackman, S., 2020. *pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory*.
- Jauker, F., Wolters, V., 2008. Hover flies are efficient pollinators of oilseed rape. *Oecologia* 156, 819–823. <https://doi.org/10.1007/s00442-008-1034-x>.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16, 584–599. <https://doi.org/10.1111/ele.12082>.
- King, M.J., 1993. Buzz foraging mechanism of bumble bees. *J. Apic. Res.* 32, 41–49. <https://doi.org/10.1080/00218839.1993.11101286>.
- King, M.J., Ferguson, A.M., 1994. Vibratory collection of *Actinidia deliciosa* (Kiwifruit) Pollen. *Ann. Bot.* 74, 479–482.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tschamtkke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldman, R., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6.
- Knapp, J.L., Shaw, R.F., Osborne, J.L., 2019. Pollinator visitation to mass-flowering courgette and co-flowering wild flowers: implications for pollination and bee conservation on farms. *Basic Appl. Ecol.* 34, 85–94. <https://doi.org/10.1016/j.baee.2018.09.003>.
- Kuldná, P., Peterson, K., Poltina, H., Luig, J., 2009. An application of DPSIR framework to identify issues of pollinator loss. *Ecol. Econ.* 69, 32–42. <https://doi.org/10.1016/j.jecolecon.2009.01.005>.
- Landaverde-González, P., Quezada-Euán, J.J.G., Theodorou, P., Murray, T.E., Husemann, M., Ayala, R., Moo-Valle, H., Vandame, R., Paxton, R.J., 2017. Sweat bees on hot chillies: provision of pollination services by native bees in traditional slash-and-burn agriculture in the Yucatán Peninsula of tropical Mexico. *J. Appl. Ecol.* 54, 1814–1824. <https://doi.org/10.1111/1365-2664.12860>.
- Lautenbach, S., Seppelt, R., Liebscher, J., Dormann, C.F., 2012. Spatial and temporal trends of global pollination benefit. *PLoS One* 7. <https://doi.org/10.1371/journal.pone.0035954>.
- Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., Burel, F., 2010. Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. *Agric. Ecosyst. Environ.* 137, 143–150. <https://doi.org/10.1016/j.agee.2010.01.015>.
- Mallinger, R.E., Gaines-day, H.R., Gratton, C., 2017. Do managed bees have negative effects on wild bees? A systematic review of the literature. *PLoS One* 12, 1–32. <https://doi.org/10.1371/journal.pone.0189268>.
- Martínez-Núñez, C., Manzaneda, A.J., Lendínez, S., Pérez, A.J., Ruiz-Valenzuela, L., Rey, P.J., 2019. Interacting effects of landscape and management on plant-solitary bee networks in olive orchards. *Funct. Ecol.* 33, 2316–2326.
- Martínez-Núñez, C., Manzaneda, A.J., Isla, J., Tarifa, R., Calvo, G., Molina, J.L., Salido, T., Ruiz, C., Gutiérrez, J.E., Rey, P.J., 2020. Low-intensity management benefits solitary bees in olive groves. *J. Appl. Ecol.* 57, 111–120. <https://doi.org/10.1111/1365-2664.13511>.

- Martins, K.T., Gonzalez, A., Lechowicz, M.J., 2015. Pollination services are mediated by bee functional diversity and landscape context. *Agric. Ecosyst. Environ.* 200, 12–20. <https://doi.org/10.1016/j.agee.2014.10.018>.
- Meyer, B., Jaunker, F., Steffan-Dewenter, I., 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl. Ecol.* 10, 178–186. <https://doi.org/10.1016/j.baae.2008.01.001>.
- Michener, C.D., 2007. *The Bees of the World*, 2nd ed. The Johns Hopkins University Press, Baltimore. [https://doi.org/10.1016/0047-2484\(91\)90057-3](https://doi.org/10.1016/0047-2484(91)90057-3).
- Minarro, M., Twizell, K.W., 2015. Pollination services provided by wild insects to kiwifruit (*Actinidia deliciosa*). *Apidologie* 46, 276–285. <https://doi.org/10.1007/s13592-014-0321-2>.
- Minarro, M., García, D., Martínez-Sastre, R., 2018. Los insectos polinizadores en la agricultura: importancia y gestión de su biodiversidad. *Rev. Ecosistemas* 27, 81–90. <https://doi.org/10.7818/RE.2014.27-2.00>.
- Minckley, R.L., Roulston, T.H., 2006. Incidental mutualisms and pollen specialization among bees. In: Waser, N.M., Ollerton, J. (Eds.), *Plant-Pollinator Interactions: From Specialization to Generalization*. Univ. Chicago Press, Chicago, pp. 69–98.
- Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., Gascon, C., 2011. Global biodiversity conservation: the critical role of hotspots. In: Zacher, F.E., Habel, J.C. (Eds.), *Biodiversity Hotspots*. Springer-Verlag Berlin Heidelberg, pp. 3–22.
- Morandin, L.A., Winston, M.L., 2005. Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecol. Appl.* 15, 871–881. <https://doi.org/10.1890/03-5271>.
- Morse, D.H., 1981. Modification of bumblebee foraging: the effect of milkweed pollinia. *Ecology* 62 (1), 89–97. <https://doi.org/10.2307/1936672>.
- Perfectti, F., Gómez, J.M., Bosch, J., 2009. The functional consequences of diversity in plant-pollinator interactions. *Oikos* 118 (9), 1430–1440.
- Pomeroy, N., Fisher, R.M., 2002. Pollination of kiwifruit (*Actinidia deliciosa*) by bumble bees (*Bombus terrestris*): effects of bee density and patterns of flower visitation. *N. Z. Entomol.* 25, 41–49. <https://doi.org/10.1080/00779962.2002.9722093>.
- Porcel, M., Andersson, G.K.S., Pålsson, J., Tasin, M., 2018. Organic management in apple orchards: higher impacts on biological control than on pollination. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.13247>.
- Potts, S.G., Vulliamy, B., Roberts, S., 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.* 30, 78–85.
- Potts, S.G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A., Willmer, P., 2006. Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. *Biol. Conserv.* 129, 519–529. <https://doi.org/10.1016/j.biocon.2005.11.019>.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>.
- Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., Isaac, N.J.B., 2019. Widespread losses of pollinating insects in Britain. *Nat. Commun.* 10, 1–6. <https://doi.org/10.1038/s41467-019-08974-9>.
- Pywell, R.F., Meek, W.R., Loxton, R.G., Nowakowski, M., Carvell, C., Woodcock, B.A., 2011. Ecological restoration on farmland can drive beneficial functional responses in plant and invertebrate communities. *Agric. Ecosyst. Environ.* 140, 62–67. <https://doi.org/10.1016/j.agee.2010.11.012>.
- Rader, R., Cunningham, S.A., Howlett, B.G., Inouye, D.W., 2020. Non-bee insects as visitors and pollinators of crops: biology, ecology, and management. *Annu. Rev. Entomol.* 65, 391–407. <https://doi.org/10.1146/annurev-ento-011019-025055>.
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffitt, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggard, S., Jaunker, F., Klein, A.M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., Pereira, N.D.O., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci. USA* 113, 146–151. <https://doi.org/10.1073/pnas.1517092112>.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdansk, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng', A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns. *Ecol. Lett.* 11, 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>.
- Rosas-Ramos, N., Baños-Picón, L., Tormos, J., Asís, J.D., 2020. Natural enemies and pollinators in traditional cherry orchards: Functionally important taxa respond differently to farming system. *Agric. Ecosyst. Environ.* 295, 106920. <https://doi.org/10.1016/j.agee.2020.106920>.
- Roulston, T.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* 56, 293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>.
- Russo, L., Buckley, Y.M., Hamilton, H., Kavanagh, M., Stout, J.C., 2020. Low concentrations of fertilizer and herbicide alter plant growth and interactions with flower-visiting insects. *Agric. Ecosyst. Environ.* 304, 107141. <https://doi.org/10.1016/j.agee.2020.107141>.
- Sáez, A., Negri, P., Viel, M., Aizen, M.A., 2019. Pollination efficiency of artificial and bee pollination practices in kiwifruit. *Sci. Hortic.* 246, 1017–1021. <https://doi.org/10.1016/j.scienta.2018.11.072> (Amst.).
- Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C., Sait, S.M., 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. *Biol. Rev.* 88, 1002–1021. <https://doi.org/10.1111/brv.12040>.
- Shannon, C.E., 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27, 623–656. <https://doi.org/10.1002/j.1538-7305.1948.tb00917.x>.
- Sharma, M., Mattu, V.K., Thakur, M.L., 2013. Pollination studies on kiwi crop (*Actinidia deliciosa* Chev.) in Himachal Pradesh, India. *Int. J. Adv. Biol. Res.* 3, 545–548.
- Somme, L., Mayer, C., Jacquemart, A.L., 2014. Multilevel spatial structure impacts on the pollination services of *Comarum palustre* (Rosaceae). *PLoS One* 9. <https://doi.org/10.1371/journal.pone.0099295>.
- Steffan-Dewenter, I., Kuhn, A., 2003. Honeybee foraging in differentially structured landscapes. *Proc. R. Soc. B Biol. Sci.* 270, 569–575. <https://doi.org/10.1098/rspb.2002.2292>.
- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tscharnkte, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1–12.
- Tacconi, G., Michelotti, V., 2018. Artificial pollination in kiwifruit and olive trees. *Pollinat. Plants*. <https://doi.org/10.5772/intechopen.74831>.
- Tacconi, G., Michelotti, V., Cacioppo, O., Vittone, G., 2016. Kiwifruit pollination: the interaction between pollen quality, pollination systems and flowering stage. *J. Berry Res.* 6, 417–426. <https://doi.org/10.3233/jbr-160138>.
- Testolin, R., Vizzotto, G., Costa, G., 1991. Kiwifruit pollination by wind and insects in Italy. *N. Z. J. Crop Hortic. Sci.* 19 (1), 381–384. <https://doi.org/10.1080/01140671.1991.10422880>.
- Torné-Nogueira, A., Rodrigo, A., Arnan, X., Osorio, S., Barril-Graells, H., Correia da Rocha-Filho, L., Bosch, J., 2014. Determinants of spatial distribution in a bee community: nesting resources, flower resources, and body size. *PLoS One* 9, 1–10. <https://doi.org/10.1371/journal.pone.0097255>.
- Tscharnkte, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* 8, 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>.
- Weisser, W.W., Siemann, E., 2004. The various effects of insects on ecosystem functioning. *Ecol. Stud.* 173, 3–24. https://doi.org/10.1007/978-3-540-74004-9_1.
- Winfree, R., 2013. Global change, biodiversity, and ecosystem services: what can we learn from studies of pollination? *Basic Appl. Ecol.* 14, 453–460. <https://doi.org/10.1016/j.baae.2013.07.004>.
- Winfree, R., Reilly, J.R., Bartomeus, I., Cariveau, D.P., Williams, N.M., Gibbs, J., 2018. Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science* 359, 791–793. <https://doi.org/10.1126/science.aao2117> (80-).
- Wu, P., Dai, P., Wang, M., Feng, S., Olhnuud, A., Xu, H., Li, X., Liu, Y., 2021. Improving habitat quality at the local and landscape scales increases wild bee assemblages and associated pollination services in apple orchards in China. *Front. Ecol. Evol.* 9, 1–10. <https://doi.org/10.3389/fevo.2021.621469>.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Ecology* 96, 1463–1468.
- Zamorano, J., Bartomeus, I., Grez, A.A., Garibaldi, L.A., 2020. Field margin floral enhancements increase pollinator diversity at the field edge but show no consistent spillover into the crop field: a meta-analysis. *Insect Conserv. Divers.* <https://doi.org/10.1111/icad.12454>.
- Zattara, E.E., Aizen, M.A., 2021. Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* 4, 114–123.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed effects models and extensions in ecology with R*. Statistics for Biology and Health. Springer.