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Article

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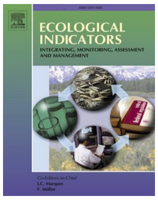

Original Articles

Ecological, environmental, and management data indicate apple production is driven by wild bee diversity and management practices

Timothy Weekers[a,*], Leon Marshall[a], Nicolas Leclercq[a], Thomas J. Wood[b], Diego Cejas[b], Bianca Drepper[c], Michael Garratt[d], Louise Hutchinson[d], Stuart Roberts[a], Jordi Bosch[e], Laura Roquer-Beni[e], Patrick Lhomme[b], Denis Michez[b], Jean-Marc Molenberg[a], Guy Smagghe[f], Peter Vandamme[g], Nicolas J. Vereecken[a]

[a] Agroecology Lab, Université libre de Bruxelles, Brussels B-1050, Belgium
[b] Laboratory of Zoology, Research Institute for Biosciences, University of Mons, B-7000 Mons, Belgium
[c] Division of Forest, Nature and Landscape, University of Leuven, Leuven B-3001, Belgium
[d] School of Agriculture, Policy and Development, University of Reading, Reading RG6 6EU, United Kingdom
[e] Centre de Recerca Ecològica i Aplicacions Forestals, Universitat Autònoma de Barcelona, 08193, Spain
[f] Department of Plants and Crops, Ghent University, Ghent B-9000, Belgium
[g] Department of Biochemistry and Microbiology, Ghent University, Ghent B-9000, Belgium

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ABSTRACT

Climate, landscape composition, management practice, and wild bee pollination are all variables thought to play significant roles in commercial apple production. However, how these variables affect production efficiency under field-realistic conditions has not been investigated at large geographical scales. We combined intensive standardized field surveys (using netting and pan traps) with structural equation models to explore the relative impact of biotic and abiotic variables on bee diversity, apple yield and fruit quality, and their ability to represent reliable proxies of apple production. Here we show that apple yields are mainly driven by management practice, without evidence for a significantly superior contribution by managed honey bees. Total wild bee diversity, while negatively correlated with honey bee dominance, promoted apple quality by enhancing seed set number. Our study demonstrates that even across a broad geographical range there is potential to harness wild bee diversity as nature-based solution and as a substitute to an exclusive reliance on honey bees in the context of commercial apple production.

1. Introduction

Insect pollinators play a pivotal role in the sexual reproduction of wild flowering plants, as well as in the production of fruits and seeds of an estimated 75% of global crop species (Allen-Perkins et al., 2021; Klein et al., 2007; Ollerton et al., 2011). The importance of insect pollination as an (agro-)ecosystem service is currently on the rise, as the global area dedicated to pollinator-dependent crops has increased by over 300% since 1961 (Aizen et al., 2008). Apple (*Malus domestica*) is one of the economically most important fruit crops in the world, with an estimated economic value over $45 billion, and 87 billion tons produced in 2019 (FAOSTAT, 2020). Since they are usually self-incompatible, apple crops rely on insect pollination for their sexual reproduction (Pardo and Borges, 2020). Furthermore, because apple flowers offer readily accessible rewards (pollen and nectar), and since apples are cultivated in different biogeographic regions, apple production can be provided by a broad and regionally-varying range of pollinators worldwide (Prendergast et al., 2021; Ramírez and Davenport, 2013). However, commercial producers around the world have largely converged towards a significant reliance upon managed colonies of the Western honey bee, *Apis mellifera* L., for apple pollination (Garibaldi et al., 2013). This tight link between apple and a single pollinator species despite available suites of non-managed pollinator species (*contra* Prendergast et al., 2021) also extends to many other pollination-dependent crops (Bänsch et al., 2020). Reliance on a single managed pollinator is increasingly viewed as a non-resilient strategy in the context of global change (Garibaldi et al., 2011). Indeed, any major stress affecting the beekeeping sector has the potential to jeopardize the availability of

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* Corresponding author at: Avenue F.D. Roosevelt 50, CP 264/2, Brussels B-1050, Belgium.
E-mail address: Timothy.Weekers@ulb.be (T. Weekers).

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managed hives to support the pollination demand of various pollinator-dependent crops, particularly perennial monocrops, and therefore to threaten both crop production and food security (Potts et al., 2010).

Alternatives to single-pollinator dependence have emerged in recent years, based on reports highlighting the essential role played by wild bees in apple production, and more specifically documenting how the species richness (Blitzer et al., 2016), functional (Roquer-Beni et al., 2021), and phylogenetic diversity (Grab et al., 2019) of wild bees are positively associated with seed set, fruit weight, and overall apple quality (Pardo et al., 2020). From a crop production perspective, commercial output and the quality of pollination services in apple production are generally indicated by measurements of seed set, fruit weight and malformation (Garratt et al., 2014; Grab et al., 2019), or more broadly by the overall crop yield (FAOSTAT, 2020). Although pollination is an essential driver of crop production in apples (Garratt et al., 2021), a series of environmental factors and management practices are

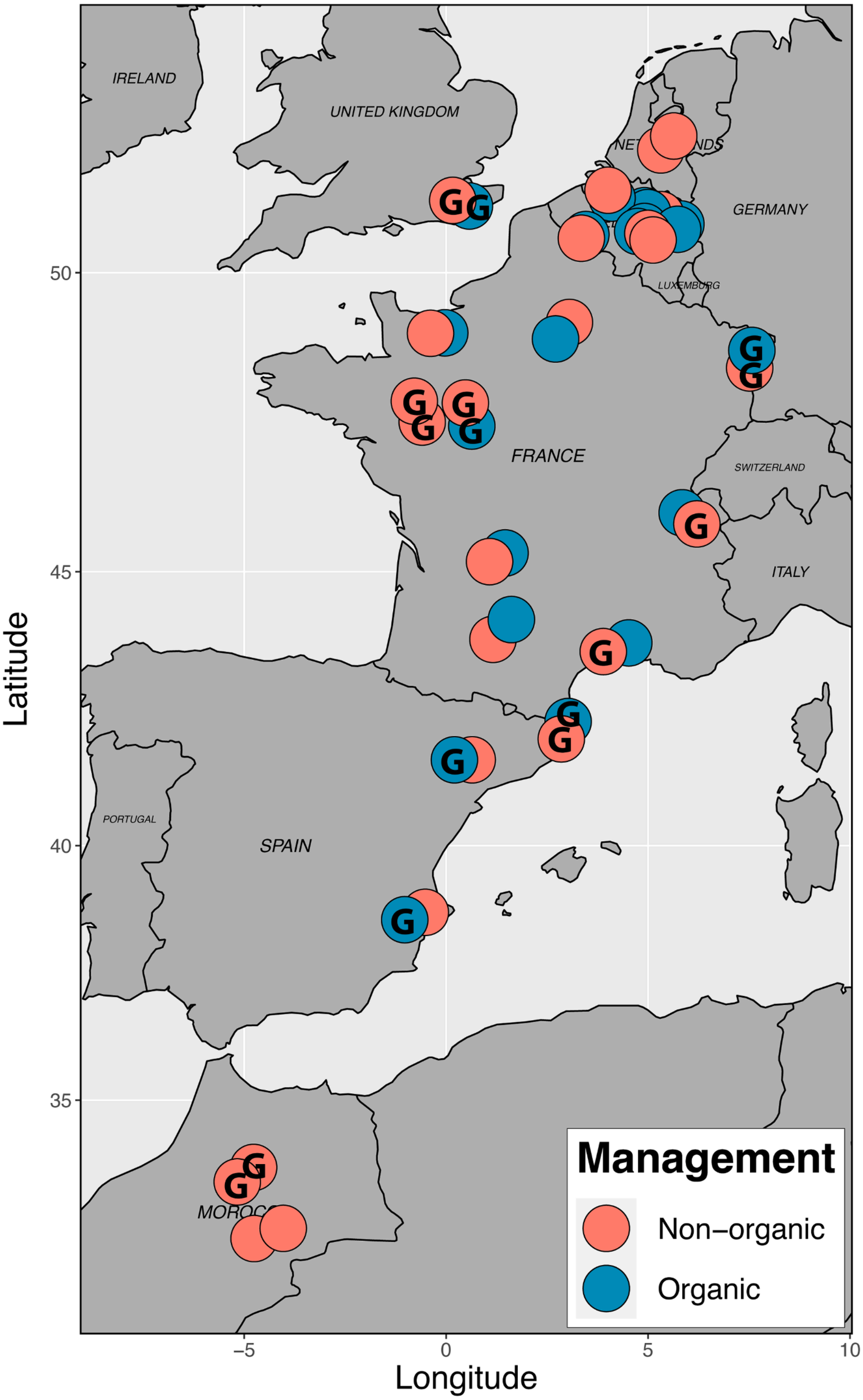

Fig. 1. Map of the study sites. Detailed map of the 46 studied commercial apple orchards in Western Europe and North Africa. Each site is represented by a colored circle, corresponding to the management system observed. The 16 sites for which Gala apples were collected are indicated by a letter “G”. The 6 Jonagold sites are in Belgium, and shown in Fig. A.1.

also involved throughout the growing season and can strongly influence apple production (yield and fruit quality) (Musacchi and Serra, 2018). Recent studies have shown that humidity, temperature, light, wind speed, pesticide use, thinning, nutrition and microclimate conditions are some of the numerous parameters influencing apple quality (Karagiannis et al., 2021; Musacchi and Serra, 2018; Radzevičiūtė et al., 2021). Wildflower diversity and landscape composition around apple orchards also influences apple pollination success, and therefore apple production, by supporting wild pollinator species (Földesi et al., 2016; Kammerer et al., 2016). Indeed, organic management (Council Regulation, 2007) often results in lower apple yield, fruit set and weight than in conventional management, mainly through higher pest damage even with enhanced ecosystem services (Roquer-Beni et al., 2021; Roussos and Gasparatos, 2009; Samnegård et al., 2019; *contra* Pardo et al., 2020). However, other parameters of fruit quality like nutritional value, antioxidant activity, and polyphenolic profile have been found to be equal or higher in organic apples compared to conventionally produced apples (Petkovsek et al., 2010; Valavanidis et al., 2009).

Overall, there is a consensus that climate (Musacchi and Serra, 2018), landscape (Földesi et al., 2016), management practices (Samnegård et al., 2019), and wild bee diversity and abundance (Mallinger and Gratton, 2015) are all significant variables in the complex equation of apple production. How these variables interact in field-realistic conditions of commercial apple orchards, and how these interactions translate into production efficiency (in terms of yield and fruit quality), has not yet been investigated across a large geographic scale (Grab et al., 2019; Pardo and Borges, 2020). In the present study, we used an integrated approach and standardized field methods to fill this important gap in our understanding by exploring and characterizing the causal and embedded effects of (i) honey bee dominance (Weekers et al., 2022), (ii) climatic variables, (iii) landscape composition, and (iv) local factors on bee diversity metrics, apple yields and fruit quality. This approach aimed to disentangle (v) the relative impact of biotic and abiotic variables on apple yield and fruit quality, and (vi) the extent to which pollinator diversity metrics can be used as a proxy to predict apple production. We hypothesize that (i) local factors and management, (ii) climate, and (iii) land use will have an effect on commercial yield and apple quality, both directly and indirectly through effects on bee diversity, which therefore could be potentially used as indicators of apple production.

2. Materials and methods

2.1. Study area and sampling method

During the apple blooming season in 2019, we sampled 46 commercial apple orchards (hereafter referred to as "sites") in Belgium, France, Morocco, the Netherlands, Spain, and the United Kingdom (Fig. 1; see Fig. A.1 and Table A.1 in the Supplementary Material). Sites were managed either according to guidelines and requirements of organic farming practices (hereafter referred to as "organic" and ending with "-O") or according to other practices like integrated pest management and conventional farming (hereafter referred to as "non-organic" and ending with "-N") (Peck et al., 2006). Each site was sampled for three consecutive days during the peak blooming period, using a standardized protocol combining active (netting) and passive (pan traps) collection methods (Droege et al., 2010). Active sampling from apple blossoms allowed surveying the bee community directly associated with the crop, starting at a random point and then following the orchard lanes during two periods of 90 min. The passive sampling was deployed on cleared ground using trios of painted pan traps (fluorescent blue, fluorescent yellow, white), (i.e., nine pan traps in total with three pan traps of each color, set for the day and collected late afternoon) filled with soapy water (Westphal et al., 2008). As the main apple pollinating group, only bee pollinators were considered in this study (Garratt et al., 2016; Pardo and Borges, 2020). All collected specimens were identified to the species level and their entry digitized, except for *Bombus terrestris* and *B. lucorum* which were pooled together as "*Bombus terrestris* agg." (Table A.2 for species list). All specimens are curated in the entomological collection of the Agroecology Lab (Université libre de Bruxelles (ULB), Brussels, Belgium).

2.2. Bee diversity metrics

For all analyses, we pooled the data collected using both methods of trapping. Active and passive sampling are complementary with regard to the spectrum of the species caught, and are most efficiently used in combination when studying richness and diversity (Weekers et al., 2022). We then characterized the entire bee community associated with each site, including honey bees, with the following diversity metrics: Hill-Shannon diversity (Hill-Shannon), functional diversity (FD) and phylogenetic diversity (PD), all computed through Hill-Shannon using the *hill_func* and *hill_phylo* function of the "hillR" package (version 0.5.1) (Li, 2018). Hill numbers, also called "the effective number of species", represent an efficient way of computing the species richness of a community, based on abundance matrices (Chao et al., 2014; Pardo et al., 2020). The functional diversity of a community represents the diversity of life-history traits of bees within each community (Normandin et al., 2017; Petchey and Gaston, 2006) and PD the accumulated evolutionary history of a community (Webb et al., 2002). FD and PD provide additional information on community composition (Cadotte et al., 2011) that can be relevant to study the ecosystem services provided by pollinators (Dorchin et al., 2018; Roquer-Beni et al., 2021). In this study, the following functional traits have been considered for the computed of FD: nesting type, sociality, body size, tongue length, pollen transport, season of flight, diet breadth (Table A.3). To compute PD for each site, we built a multi-gene tree based on fragments from the mitochondrial gene cytochrome oxidase I (COI) and nuclear gene low wavelength opsin (LW Rh) (Boyle and Adamowicz, 2015). See Appendix A.1, Table A.4 for detailed explanation on diversity metrics calculation.

We also calculated the dominance of honey bees in each site, as the proportion of honey bees caught (in percentage of the total population). The number of honey bee hives at each site was also used as a proxy for introduced honey bee pressure on wild bee populations (Mallinger et al., 2017).

2.3. Landscape composition and climate variables

During the sampling period, we characterized the grass height, wildflower abundance and wildflower diversity within the tree rows and the direct perimeter of each orchard using classes. Grass height was scored 1 when below 30 cm, and 2 if above. Wildflower abundance was scored from 1 to 5 according to the proportion of ground covered in the apple orchards. Finally, wildflower diversity was also scored from 1 to 5 according to the diversity of wildflower species found within the orchards. See Table A.5 for more details on the classes used). These variables, along with the management type, the orchard age and size, are referred to as local factors, potentially influencing wild bee communities, crop yield and fruit quality (Scheper et al., 2015) (Table A.1). We also characterized the landscape composition (i.e., proportion of urban, semi-natural habitat, crop and forest cover) in areas surrounding the study sites, known to have a strong influence on bee communities and crop yields (Joshi et al., 2016). Landscape composition was measured within 1000 m buffers around each site after testing correlation between the three diversity metrics and a computed Shannon's landscape diversity index (Radzevičiūtė et al., 2021). For each study site, we computed the proportion of urban, semi-natural habitat, crop (i.e., agriculture fields), and forest cover in a buffer area of 1000 m (Table A.5). This was done using the *geobuffer_pts* function from the "geobuffer" package (version 0.0.0.90) (Stefan, 2019), from the 2019 Copernicus Global Land Cover (100 m × 100 m resolution) (Buchhorn et al., 2020). See Appendix A.2 for more details.

In line with the conclusions of previous studies investigating the links between climate and the diversity of wild bee communities (Hennessy et al., 2020; Marshall et al., 2018), the following climate variables were collected at each study location: precipitation (in mm), average temperature (in Celsius), surface net solar radiation (in J/m^2), surface air pressure (in hPa), and average wind speed (in m/s) per month (Table A.6). This data was collected using ERA5-Land database ranging from March to September (following Bui et al., 2021), from 2006 to 2019, and averaged for the total period (Muñoz-Sabater, 2019).

2.4. Apple production measurements

For all but one site (UKFarmA-N), the producers communicated their final crop yield for the 2019 season, expressed in tons per hectare. As such, it represents the commercial yield on which the apple producers are able to compare the success of their harvests between orchards and from one year to another (FAOSTAT, 2020; Garratt et al., 2014). To measure the relative impact of bee community, local factors, land use, and climate variables on fruit quality, we collected apples in a subset of 22 sites chosen for having shared cultivars (divided in two different cultivars, 16 sites with Gala, and 6 sites with Jonagold), one week before harvest (Garratt et al., 2021, 2014). In each orchard, eleven trees were randomly selected from which five apples were collected from the same mid-size and mid-height branch. Following Grab et al. (2019), a total of 1210 apples were picked randomly in the orchards for the measurement of the three following characteristics reflecting pollination efficiency: number of seeds, weight (in grams), and malformation (considering the shape changes between apples, from perfect shape to distorted) (see Fig. A.3 and Table A.7). When pollen grains are deposited in the stigma by bees, it generally results in fertilization, ultimately leading to seed development (Sheffield et al., 2016). The distribution of seeds within the fruit then influences fruit quality (such as overall weight and shape) (Sheffield et al., 2016). The three parameters can, therefore, be used to reflect pollination efficiency (Grab et al., 2019). See Appendix A.3 for more details.

2.5. Statistical analyses

To study the potential effects of local factors, management, climate and land use on bee diversity, commercial yield and apple quality, we used a piecewise structural equation modelling approach (piecewise SEMs). This method, a form of classical path analysis, allowed to study the interactions between variables in large ecological systems with potential causal implications, by successively testing each solitary link in the light of the entire constructed model (Lefcheck, 2016).

To have a broad view on all possible paths in our system, we first designed a full causal model (explicitly including all possible paths), testing the effects of local factors (including management), climate, landscape composition, honey bee presence (on site hives) and dominance on the bee diversity metrics (Hill-Shannon, FD and PD) and the commercial yield. Generalized linear mixed models (GLMMs) were computed for the different regressions using the *glmer* function of the "lme4" package (version 1.1–28) (Bates et al., 2015). The full model was then computed using the *psem* function from the "piecewiseSEM" package (version 2.1.2) (Lefcheck, 2016).

Similarly, we then computed a second pSEM on the subset of 22 study sites for which additional fruit data had been collected, and focused on the effects of local factors, climate and landscape composition on the bee diversity metrics and apple quality (i.e., seed set, weight and malformation). Apple cultivar (i.e., Gala or Jonagold) was computed as random effect in all the analyses including apple variables (Stevenson et al., 2017).

Finally, we computed a GLMM based on the results obtained from the first and second pSEM, linking apple quality data and commercial yield. More precisely, we tested the relationship between apple quality (i.e., seed set, weight and malformation), Hill-Shannon diversity, honey bee dominance, management, precipitation and temperature on apple commercial yield. After simplification of the GLMs from a full model, based on the Variance Inflation Factors (VIFs), all the retained variables have VIFs below the acceptable threshold of 5 (Menard, 2002). All statistical analyses were performed using RStudio for R version 2021.09.0 for Mac (RStudioTeam, 2020). All assumptions were met. See Appendix A.4 for more details.

3. Results

3.1. Patterns of diversity in commercial apple orchards

During the flowering period in 2019, we collected a total of 12,867 bees from 46 commercial apple orchards in Morocco and Western Europe (Table A.1). They consisted of 173 species from five different families (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae). The Western honey bee, *Apis mellifera* (Apidae), represented 40% of the total abundance in our database, with 5145 individuals caught across all sites; its dominance (expressed as the proportion of honey bees caught, in % of the total population) ranged between 7.5% and 97.1% of sampled individuals per site. The next most abundant species in our dataset were *Bombus terrestris* agg. (Apidae) (n = 1474 individuals), *Lasioglossum malachurum* (Halictidae) (n = 650), *Andrena haemorrhoa* (Andrenidae) (n = 424), *Osmia bicornis* (Megachilidae) (n = 309) and *L. algericolellum* (Halictidae) (n = 300). Discrepancies were observed in the dataset regarding the number of honey bee hives given by the producers and the honey bee dominance measured in the study sites. For example, the Fes2-N site with 100 hives showed a honey bee dominance of 7.5%, while Cothen-N had 97.1% of dominance with 18 hives, and Pescador-N had no hives and 70.8% of measured dominance.

3.2. Structural equation model for commercial yield

Our first causal model explored the potential effects of biotic and abiotic factors on commercial crop yield and bee diversity metrics from the 45 study sites, using commercial apple yield (conditional $R^2 = 0.57$), Hill-Shannon diversity (conditional $R^2 = 0.78$), phylogenetic diversity (conditional $R^2 = 0.76$) and functional diversity (conditional $R^2 = 0.67$) as response variables (Fisher-C = 10.29, df = 6, P = 0.11) (Table 1, Fig. A.2). Though all the predictor variables linked to the commercial yield were included in this large causal model, only management emerged as a significant indicator (CI95% not encompassing 0). Organic management was significantly linked to 36.3% lower crop yields than non-organic management practices, with an estimated average crop yield 16 tons/ha (CI95% = [-26.60, −4.49], $P < 0.01$) less than their non-organic equivalents. Regarding bee diversity, our results also showed a significant and negative effect of honey bee dominance on all bee diversity metrics, with an estimate of −13.77 for Hill-Shannon diversity (CI95% = [-17.52, −10.03], $P < 0.001$), −1.86 for phylogenetic diversity (CI95% = [-2.46, −1.25], $P < 0.001$) and −7.38 for functional diversity (CI95% = [-11.23, −3.53], $P < 0.001$) (Table 1). According to the values of the diversity metrics at each site (Table A.4), our results imply that for a 20 percentage points increase in honey bee dominance, percentage declines of 33.5, 15.3 and 14.1 can be expected for the Hill-Shannon, phylogenetic, and functional diversities of wild bees respectively. The proportion of crop cover surrounding the orchards was also negatively correlated to Hill-Shannon diversity (estimate = -1.23, P = 0.02). Precipitation and temperature had both a significant and negative effect on Hill-Shannon and functional diversity (Table 1). Pearson's correlation coefficients indicated highly significant correlations between Hill-Shannon diversity, phylogenetic (estimate = 0.47, $P < 0.001$) and functional diversity (estimate = 0.81, $P < 0.001$) of wild bees. All other effects were not significant (see Fig. A.2).

Table 1
Parameter significance for the piecewise structural equation model focusing on apple commercial yield (Fisher's C = 10.29, df = 6, P-value = 0.11). Parameters are considered significant with a P-value below the < 0.05 threshold. All significant positive correlations are noted "Yes (+)", while negative ones are noted "Yes (-)". The "/" symbol indicates that a predictor variable is not used in a model. Honey bee dominance has a significant and negative effect on Hill-Shannon, phylogenetic and functional diversity of wild bees. Apple commercial yield is significantly lower in organic orchards. PD and FD were both significantly correlated with Hill-Shannon diversity.

		Response variables			
		Yield	Wild bee Hill-Shannon	Wild bee phylogenetic diversity	Wild bee functional diversity
Predictor variables		Significance (<0.05)	Significance (<0.05)	Significance (<0.05)	Significance (<0.05)
Local factors	Number of honey bee hives	No	Yes (-)	No	No
	Orchard size	No	No	No	No
	Honey bee dominance	No	Yes (-)	Yes (-)	Yes (-)
	Grass height	No	No	No	No
	Orchard age	No	No	No	No
	Management (organic)	Yes (-)	No	No	No
Landscape factors	Urbanization cover (1 km)	No	No	No	No
	Crop cover (within 1 km)	No	Yes (-)	No	No
	Semi-natural habitat cover (within 1 km)	No	No	No	No
Climate	Precipitation	No	Yes (-)	No	Yes (-)
	Atmospheric pressure	No	No	No	No
	Temperature	No	Yes (-)	/	Yes (-)
	Wind speed	No	No	No	No
Diversity	Hill-Shannon	No	/	/	/
	Hill-PD ~~ Hill-Shannon	Yes (+)			
	Hill-FD ~~ Hill-Shannon	Yes (+)			
R^2		0.57	0.78	0.76	0.67

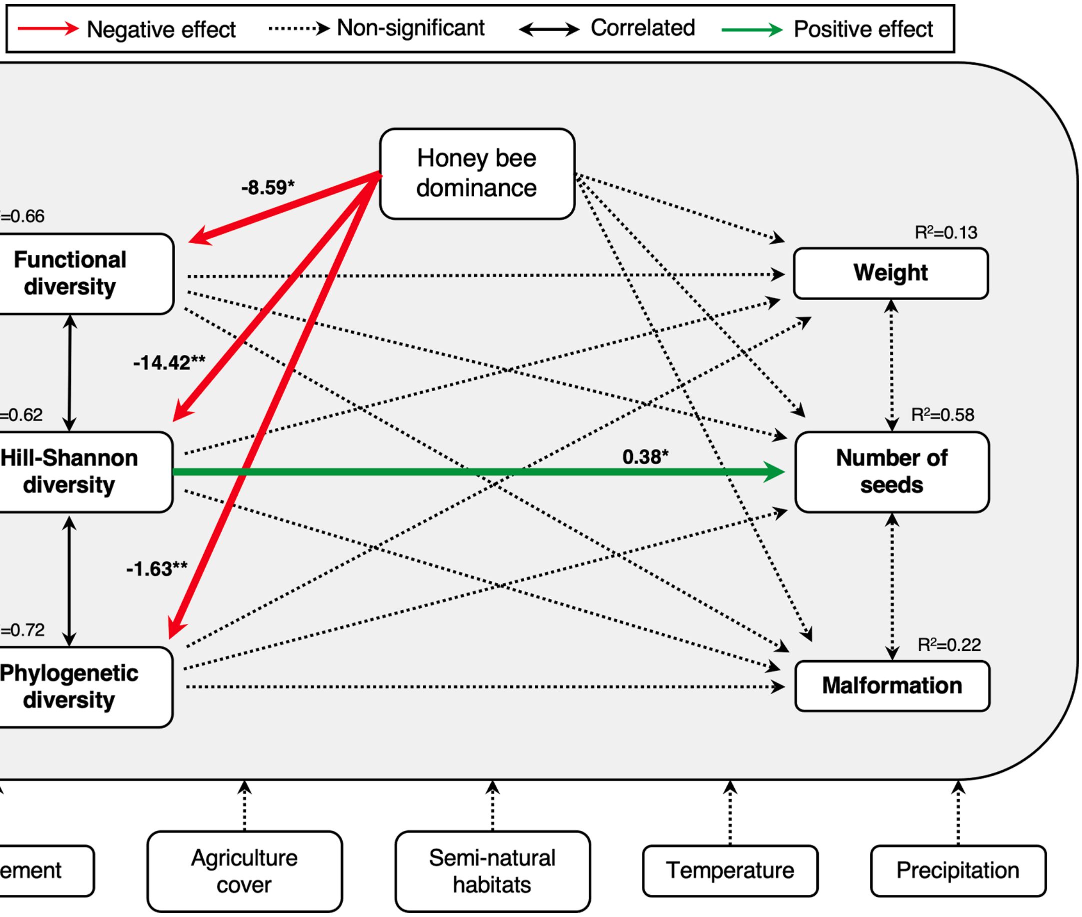

Fig. 2. Structural equation model including apple quality metrics. The R-squared (R^2) is given for each response variable of the model. The asterisk "*" symbol indicates that a link is significant (P-value < 0.5 = "*", P-value < 0.01 = "**"). Honey bee dominance is significantly and negatively correlated to all bee diversity metrics. Hill-Shannon diversity has a significant and positive effect on the number of apple seeds produced. All other links are non-significant.

3.3. Structural equation model for apple quality

Our second pSEM explored the potential effects of biotic and abiotic factors on apple quality measures and bee diversity metrics (Fisher-C = 25.67, df = 18, P = 0.11) (Fig. 2). For apple quality, none of the predictor variables had a significant effect on the number of seeds (conditional $R^2 = 0.58$), individual apple weight (conditional $R^2 = 0.13$), or malformation (conditional $R^2 = 0.22$) (Table 2). The model suggests that a 20.0 percentage points increase in Hill-Shannon diversity is associated with an 11.1 percentage increase in the number of seeds. Landscape composition, along with temperature and precipitation had no significant effect on apple quality. The commercial yields given by the producers ranged from 5 to 91 tons per hectare, with no outliers detected using Grubbs' test. The measured apple weights ranged from 46 to 299 g and were equally distributed for both cultivars (no outliers). Seed number ranged from 0 to 14 (see Fig. A.3). Results for honey bee dominance were similar to those from the first model (Table 2).

3.4. Effects on commercial yield and apple quality

Using the results obtained from the first and second pSEM, we computed the linkage of commercial yield with apple quality, biotic and abiotic factors (Fig. 3). This third model showed that an increased number of deformed apples was significantly correlated with a lower commercial yield, with an estimated decrease of 23 tons/ha for every increment of 0.5 in the mean malformation score (conditional $R^2 = 0.70$, CI95% = [-79.85, −12.17], P = 0.01) (Table 3). Our results showed that the other apple quality metrics (i.e., number of seeds and weight), along with Hill-Shannon diversity, honey bee dominance and precipitation, did not significantly predict the total apple yield (Fig. 3). The random effect (apple cultivar) was removed here as it explained no variance.

4. Discussion

Our study provides a first complex causal model including both biotic and abiotic parameters, using data collected with standardized methods, across a large geographical scale in the same year. Overall, we found that apple yields were mainly driven by management practice, with organic management in particular being associated with lower yields compared with non-organic orchards, and we confirm that honey bee dominance and the number of honey bee hives in the apple orchards had no significant impact on yields.

We found large discrepancies between the quantity of honey bee hives in the sites as given by the producers and the honey bee dominance measured at each site, possibly due to large foraging distances of neighboring honey bees whose hives were not quantified (Härtel and Steffan-Dewenter, 2014). We also confirm recent reports that honey bee dominance is systematically associated with lowered wild bee diversity (Angelella et al., 2021), expressed in terms of Hill-Shannon, phylogenetic, and functional diversity (Lázaro et al., 2021; Weekers et al., 2022). Temperature and precipitation had also a significant effect on Hill-Shannon and functional diversity (Kammerer et al., 2021). We also found that Hill-Shannon diversity of wild bees was negatively correlated with the proportion of surrounding crop cover and positively correlated with apple seed set, confirming the previous findings of Grab et al. (2019) who also found an impact of reduced phylogenetic diversity in the bee community on apple fruit weight and seed set.

Our results do not corroborate those of previous studies reporting a stronger effect of landscape composition on fruit set compared to management practices (Földesi et al., 2016; Martins et al., 2015; Mendoza-García et al., 2018). This is possibly due to a variable effect of surrounding landscapes on pollination services (Gervais et al., 2021), while at the same time apple production can be highly optimized and maintains fruit sets regardless of landscape factors (Jiang et al., 2020). Our results show a predominant effect of management practices on apple yield compared to other biotic and abiotic parameters, with organic management resulting in significantly lower yield than in non-organic orchards. This difference is potentially due to a combination of direct management practices and the indirect consequences of higher pest damage in organic orchards (Samnegård et al., 2019). Direct effects can stem from differences in water and irrigation methods, fertilizer regimes (Klein et al., 2015), but also from fungal disease control, weed management, row density of trees, or cultivar choices (Samnegård et al., 2019). In some cases, organic apple production may benefit from higher abundance of natural enemies and higher pollinator functional diversity and visitation rates, thereby strengthening fruit production (Roquer-Beni et al., 2021; Samnegård et al., 2019). A recent study showed that, through enhanced pollinator diversity, organic orchards reached levels of early fruit set as high as those achieved in conventional orchards (Roquer-Beni et al., 2021). However, our results suggest that these positive aspects fail to mitigate the yield gap resulting from organic management (Samnegård et al., 2019), even considering that organic farming tends to promote ecological resilience and environmental profit (Shennan et al., 2017).

Table 2

Parameter estimates and significance for the piecewise structural equation model for apple quality metrics (Fisher's C = 26.80, df = 18, P-value = 0.08). The model consists of embedded generalized linear models with the following response variables: Hill-Shannon diversity, phylogenetic and functional diversity of bees, number of seeds, apple weight and malformation. Hill-Shannon diversity has a significant effect on the number of seeds, while honey bee dominance negatively influenced all three diversity metrics. Parameters are considered significant with a P-value below the <0.05 threshold. All significant positive correlations are noted "Yes (+)", while negative ones are noted "Yes (-)".

	Response variables					
	Hill-Shannon	Phylogenetic diversity	Functional diversity	Number of seeds	Weight	Malformation
Predictor variable	Significance (<0.05)	Significance (<0.05)	Significance (<0.05)	Significance (<0.05)	Significance (<0.05)	Significance (<0.05)
Honey bee dominance	Yes (-)	Yes (-)	Yes (-)	No	No	No
Crop cover (within 1 km)	No	No	No	No	No	No
Semi-natural habitats (within 1 km)	No	No	No	No	No	No
Temperature	No	No	No	No	No	No
Precipitation	No	No	No	/	No	No
Management (organic)	No	No	No	No	No	No
Number of seeds	/	/	/	/	No	No
Hill-Shannon	/	/	/	Yes (+)	No	No
Hill-PD ∼∼ Hill-Shannon	Yes (+)	Yes (+)	/	/	/	/
Hill-FD ∼∼ Hill-Shannon	Yes (+)	/	Yes (+)	/	/	/
R^2	0.62	0.72	0.66	0.58	0.13	0.22

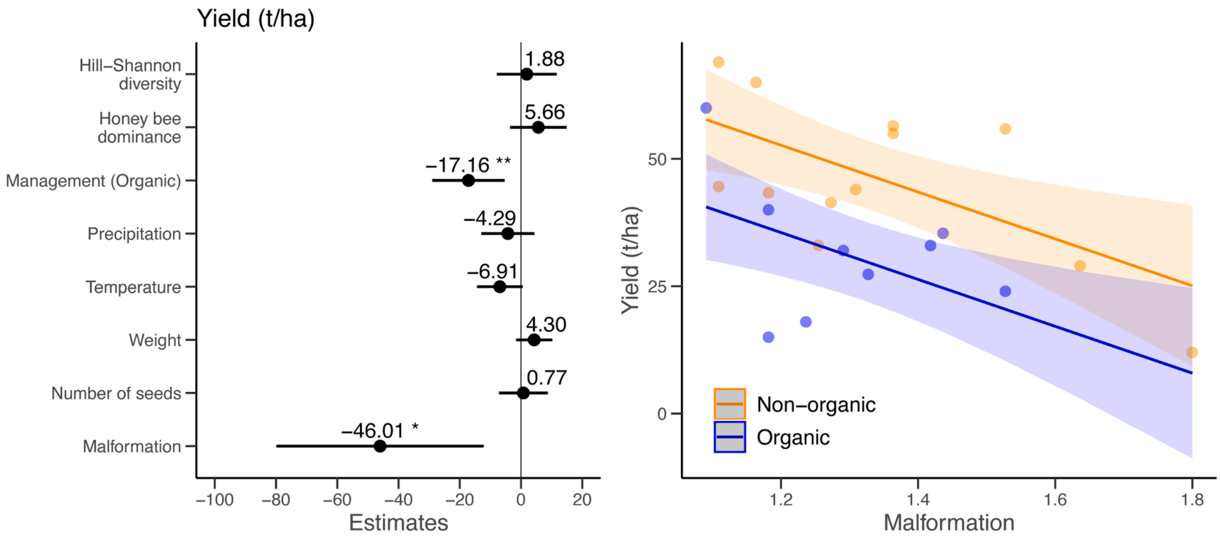

Fig. 3. Generalized linear model focusing on apple yield. The predicting variables are Hill-Shannon diversity, honey bee dominance, management, precipitation, temperature, and apple quality metrics (weight, number of seeds and malformation). Malformation and organic management have both a significant and negative effect on the commercial yield as indicated by an asterisk (P-value < 0.5 = “*”, P-value < 0.01 = “**”). The other predictors are non-significant.

Table 3
Generalized linear model predicting commercial apple yield by using Hill-Shannon diversity, honey bee dominance, number of seeds, weight, malformation, precipitation, temperature and management as predictor variables. For each of the predictors (or fixed effects), estimates are displayed along with confidence interval (95%) and p-values. The random effect (apple cultivar) was removed here as it explained no variance. The proportion of the variance for the response variables explained by the predictor variables is expressed with R^2. The significant effects are highlighted.

Yield			
Predictors	Estimates	Confidence Interval (0.05)	P-value
(Intercept)	107.90	62.32 – 153.49	**<0.001**
Hill-Shannon diversity	1.88	−7.89 – 11.64	0.69
Honey bee dominance	5.66	−3.59 – 14.90	0.21
Management (organic)	−17.16	−28.96 – −5.36	**0.008***
Precipitation	−4.29	−12.99– 4.41	0.31
Temperature	−6.91	−14.35 – 0.53	0.07
Weight	4.30	−1.62 – 10.22	0.145
Number of seeds	0.77	−7.21 – 8.74	0.84
Malformation	−46.01	−79.85 – −12.17	**0.012***
Observations	21		
R^2	0.705		

Despite the tendency for many apple producers to rely primarily or solely on *Apis mellifera* as pollinators, our results provide robust evidence that diverse wild bee assemblages in apple orchards have the potential to ensure all necessary pollination services, irrespective of honey bee dominance (Osterman et al., 2021; Weekers et al., 2022). This is in line with other studies stating that wild insects can be more effective crop pollinators than honey bees (Blitzer et al., 2016; Mallinger and Gratton, 2015), and that honey bees are probably not responsible for the majority of crop pollination services (Breeze et al., 2011; Garibaldi et al., 2013; Rader et al., 2016). Honey bees and wild bees have different foraging behaviors, with the latter visiting trees evenly regardless of floral density (Mallinger and Gratton, 2015). Fruit set also depends on how pollen is collected by bees, with corbicular pollen (i.e., pollen mixed with nectar and compressed into dense pellets on the tibiae, typical of *Bombus* and *Apis* species) being less accessible and adherent to stigmas than pollen collected from non-corbiculate species (found on the scopa and body) (Parker et al., 2015). Nectar is also preferably sought by honey bees, which tend to avoid the stigma and therefore carry pollen less frequently than wild bees (Mallinger and Gratton, 2015). A strong and sometimes exclusive reliance on honey bees for apple pollination, as is often observed by growers seeking “agricultural insurance” (Park et al., 2020), could otherwise have a negative impact on wild bee communities (e.g., through resource competition, see Geslin et al., 2017a) and further diminish efficient pollination services (Blitzer et al., 2016; Garibaldi et al., 2013).

Our findings also suggest a significant potential to harness wild bee diversity as a nature-based solution and as a substitute to this exclusive reliance on honey bees in the context of commercial apple production (Osterman et al., 2021; Pérez-Méndez et al., 2020). To enhance wild bee diversity and promote pollination services in agroecosystems, Potts et al. (2016) proposed three complementary management strategies highly beneficial for pollinators. First, ecological intensification aims to move away from chemical inputs and improve the resilience of farming systems, by including biotic pest-regulation, in-field nutrient cycling increasing fertility and the promotion of unmanaged pollination (Potts et al., 2016; Vanbergen et al., 2020). Secondly, strengthening diversified farming systems by promoting multiple crop types in close proximity with the potential to supporting a wider diversity of pollinating insects compared to monocultures, by maintaining sustainable levels of wildflower abundance and habitats throughout the landscape (Kremen and Miles, 2012; Potts et al., 2016). Thirdly, maintaining and connecting natural habitat patches between the fields using ecological infrastructures such as floral margins, grass margins, hedgerows and tree alleys is likely to form nature-friendly landscapes for many pollinating species (Henríquez-Piskulich et al., 2021; Kleijn et al., 2019; Potts et al., 2016). Fourthly, we think that the management of *Apis mellifera* colonies should be improved to value quality over quantity, and reach low infection rates of the *Varroa* mites and high bee densities to improve the overall pollination efficiency (Geslin et al., 2017b).

Crop pollination involves multiple, complex and interrelated factors, and our study helps to disentangle their effects and hierarchical importance in a globally important insect-pollinated crop, investigated at a large spatial scale, and under field-realistic conditions. We also argue that managing agroecosystems for diverse communities of pollinators is still hindered by a socio-technical “lock-in” in favor of a historical reliance upon honey bees in apples (Park et al., 2020), but also in many other pollinator-dependent crops across the world (Winfree et al., 2008). Future research should scale out recent reports on the use of pollinator-friendly ecological infrastructures (e.g., Blaauw and Isaacs, 2014; Garibaldi et al., 2011) and agroecological practices (Henríquez-

Piskulich et al., 2021; Varah et al., 2020) in redesigning agroecosystems, and explore levers and pathways towards a more balanced reliance in favor of wild bees and other insects for the provision of sustainable pollination services (Blitzer et al., 2016; Weekers et al., 2022).

Author contribution

The study was conceptualized and designed by TWeekers, LM, NL, DM, GS, PV and NJV. TWeekers, LM, NL, TWood, DC, BD, LH, MG, LR, JB, PL, DM, J-MM and NJV found the suitable study sites and collected the data. TWood, LH, DM, J-MM and NJV identified specimens. DC sequenced specimens and built the phylogenetic tree. SR provided functional trait information. TWeekers and DC analyzed the data. TWeekers, LM, NL and NJV led the writing of the original and reviewed manuscript versions. All authors have read and agreed to the published version of the manuscript.

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.

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Data availability statement

Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository (Dryad, Figshare or Hal) and the data DOI will be included at the end of the article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108880.

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