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RESEARCH ARTICLE

Management-dependent effects of pollinator functional diversity on apple pollination services: A response–effect trait approach

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Abstract

1. Functional traits mediate the response of communities to disturbances (response traits) and their contribution to ecosystem functions (effect traits). To predict how anthropogenic disturbances influence ecosystem services requires a dual approach including both trait concepts. Here, we used a response–effect trait conceptual framework to understand how local and landscape features affect pollinator functional diversity and pollination services in apple orchards.
2. We worked in 110 apple orchards across four European regions. Orchards differed in management practices. Low-intensity (LI) orchards were certified organic or followed close-to-organic practices. High-intensity (HI) orchards followed integrated pest management practices. Within each management type, orchards encompassed a range of local (flower diversity, agri-environmental structures) and landscape features (orchard and pollinator-friendly habitat cover). We measured pollinator visitation rates and calculated trait composition metrics based on 10 pollinator traits. We used initial fruit set as a measure of pollination service.
3. Some pollinator traits (body size and hairiness) were negatively related to orchard cover and positively affected by pollinator-friendly habitat cover. Bee functional diversity was lower in HI orchards and decreased with increased landscape orchard cover. Pollination service was not associated with any particular trait but increased with pollinator trait diversity in LI orchards. As a result, LI orchards with high pollinator trait diversity reached levels of pollination service similar to those of HI orchards.
4. *Synthesis and applications*. Pollinator functional diversity enables pollinator communities to respond to agricultural intensification and to increase pollination function. Our results show that efforts to promote biodiversity provide greater returns in low-intensity than in high-intensity orchards. The fact that low-intensity orchards with high pollinator functional diversity reach levels of pollination services

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similar to those of high-intensity orchards provides a compelling argument for the conversion of high-intensity into low-intensity farms.

KEYWORDS
agricultural intensification, agri-environmental structures, integrated pest management, organic management, response–effect trait framework, trait diversity, trait identity

1 | INTRODUCTION

Environmental disturbances such as agricultural intensification alter ecosystem function through changes in functional composition of plant and animal communities (Larsen et al., 2005; McGill et al., 2006). Species have traits that affect their ability to cope with environmental changes (response traits) and traits that contribute to specific functions such as pollination (effect traits; Violle et al., 2007). Thus, the degree to which disturbances will affect ecosystem functioning will depend on the overlap between response and effect traits (Schleuning et al., 2015; Suding et al., 2008). For this reason, a response–effect trait framework is necessary to fully understand how specific drivers affect ecosystem function and services (Lavorel & Garnier, 2002). At the community level, the response to environmental changes and the maintenance of ecosystem functions may be affected by the identity and abundance of specific traits (functional identity) but also by the diversity of traits (functional diversity; Leps et al., 2006).

Pollinator diversity and abundance have declined over the last century, and agricultural intensification is considered one of the main drivers of these declines (IPBES, 2016). Agricultural intensification affects pollinators through landscape simplification, including isolation and loss of natural and semi-natural habitats, leading to decreased availability of feeding resources and nesting substrates (Roulston & Goodell, 2011; Shuler et al., 2005). In addition, the increased use of pesticides associated with intensive agriculture has direct negative effects on pollinator fitness and survival (Woodcock et al., 2017). To reverse these effects and enhance on-farm biodiversity, agri-environmental measures have been promoted at both local and landscape scales (Primdahl et al., 2003). These measures include reducing pesticide use, preserving historical land uses and implementing agri-environmental structures (hereafter AES) such as hedgerows and buffer strips to increase connectivity with semi-natural habitats (Ekroos et al., 2016). The effects of agri-environmental measures on pollinator richness and abundance have been widely studied (Marja et al., 2019; Scheper et al., 2013), but much less is known about their consequences on pollinator functional composition.

Pollinator responses to agricultural intensification depend on traits related to mobility, feeding and nesting requirements and physiological tolerance (De Palma et al., 2015; Forrest et al., 2015; Rader et al., 2014). For example, large mobile bee species may be better suited to find floral resources in disturbed habitats compared to small species (Jauker et al., 2013; Klein et al., 2008), but they may also have higher levels of exposure to pesticides (Brittain & Potts, 2011). Although no general patterns have been found between single trait identity and responses to environmental changes (Bartomeus et al., 2018; Bommarco et al., 2010), there is evidence that landscape intensification acts as a filter of specific traits causing decreases in pollinator trait diversity (Forrest et al., 2015; Geslin et al., 2016). Trait diversity is crucial, as it allows for a variety of responses to disturbances over space and time (Mori et al., 2013).

As for effect traits, functional composition appears to be a better predictor of pollination function than taxonomic composition (Gagic et al., 2015). Pollinator traits such as body size, flower-handling behaviour and hairiness have been associated with pollination success (Phillips et al., 2018; Roquer-Beni et al., 2020; Stavert et al., 2016). In addition, based on the complementarity hypothesis (Díaz & Cabido, 2001; Tilman, 2001), communities with high trait diversity should be better suited to provide pollination services under a variety of environmental scenarios (Blüthgen & Klein, 2011; Woodcock et al., 2019).

Some studies have addressed the response of pollinator functional composition to agricultural intensification (De Palma et al., 2015; Forrest et al., 2015; Geslin et al., 2016; Rader et al., 2014; Williams et al., 2010) whereas others have addressed the effects of functional composition on pollination service (Gagic et al., 2015; Hoehn et al., 2008; Woodcock et al., 2019). However, studies analysing pollinator responses and effects simultaneously remain scarce (Bartomeus et al., 2018; Klein et al., 2008).

To address this knowledge gap, we measured functional trait identity and diversity of apple pollinator assemblages in 110 orchards differing in management and in local and landscape features in four European apple-growing regions. Apples *Malus domestica* are one of the most important fruit crops worldwide and are highly dependent on insect pollination (Garratt et al., 2016; Martins et al., 2014). We used a response–effect trait framework to determine how local and landscape features affect pollination service through changes in pollinator functional composition. Our objectives were: (a) to identify functional metrics responding to environmental features and affecting pollination services; b) to establish whether traits that determine pollinator responses to changes in local and landscape factors overlap with traits that affect pollination; (c) to determine whether pollination services are dependent on certain pollinator functional traits and/or on trait diversity; (d) to establish whether the relationship between pollinator trait composition and pollination service is dependent on orchard management.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted in 2015 in 110 commercial apple orchards from four European apple-growing regions: Skåne (Sweden), Baden-Württemberg (Germany), Asturias (Spain) and Catalonia (Spain) (see Figure S1, Table S1; Happe et al., 2019; Miñarro & García, 2018; Samnegård, Alins, et al., 2019 for further details on the study orchards).

In each region, orchards were selected to encompass a range of local and landscape features (Table S1). In Sweden, Germany and Catalonia, half of the orchards followed IOBC guidelines for integrated pest management (Cross, 2002) and used chemical insecticides, fungicides, fertilizers and herbicides (see Happe et al., 2019 for details). These orchards were considered high-intensity (henceforth HI) orchards. The rest of the orchards in Sweden, Germany and Catalonia and all orchards in Asturias were either certified organic or followed close-to-organic guidelines, with very low levels of synthetic inputs and mechanical weed control. These orchards were grouped into a low-intensity orchard management category (henceforth LI).

2.2 | Local features

In each orchard, we established two consecutive 20-m transects on which we conducted pollinator counts (see below). To assess local features, we used aerial photographs combined with on-site inspection to measure the area occupied by AES within a 20-m buffer from the first transect trees. AES included hedgerows, forests fallow lands, orchard meadows and semi-natural grasslands (Table S1). During apple bloom, we estimated flower cover and diversity of entomophilous plant species within and around each orchard. These measures were taken using 12–14 gridded quadrats (1 m^2 in Sweden, Germany and Catalonia; 0.25 m^2 in Asturias). Half of the quadrats were laid between the two orchard transects, and the other half within the 20-m buffer surrounding the orchard. To estimate flower diversity (Shannon's index), we used the mean cover of each flower species. Quadrat size differences among regions were not expected to affect comparative trends in flower diversity because region variability was integrated in the statistical design (see below).

2.3 | Landscape features

We used ArcView 10.3.1, MiraMon v8.2e, R 3.2.3 (R Core Team, 2015) and digital maps (see Table S1) to measure the area covered by different habitat types within 1-km buffers from the surveyed trees and calculated two landscape variables. First, the per cent area occupied by pollinator-friendly habitats (henceforth PFH), defined as habitats free of pesticides and hosting abundant floral resources and potential bee nesting substrates. PFH included shrublands, orchard meadows, semi-natural grasslands, abandoned orchards and hedgerows. Second, the area occupied by orchards, as a proxy of agricultural landscape homogenization (Table S1).

2.4 | Pollinator surveys

Pollinator surveys were conducted during apple bloom (April–May). In Sweden, Germany and Catalonia, observers walked along the two 20-m transects ($M \pm SE$: 35 ± 1.3 trees/transect) and recorded all apple visitors contacting the reproductive parts of apple flowers. Transect walks lasted 5 min and were repeated three times throughout the day, amounting to 30 min of pollinator survey per orchard. In Asturias, observers surveyed a 1-m diameter canopy area for 5 min in five trees per orchard three times throughout the day, for a total of 75 survey minutes per orchard. Pollinators were mostly visually identified in the field, but some specimens were captured and identified in the laboratory.

From these surveys, we calculated abundance of each pollinator species (number of individuals observed visiting flowers) and pollinator visitation rate (number of visits/100 flowers/5 min).

2.5 | Pollination service

At the onset of bloom, we marked two to three branches per tree on six to seven trees per orchard and counted the number of flower buds (1,200–1,300 per orchard). About 3 weeks after petal fall, we assessed initial fruit set as the percentage of flowers that developed into a fruitlet. Initial fruit set is a better measure of pollination service than fruit set at harvest because it is less influenced by post-pollination factors such as natural and/or artificially induced fruit abscission.

2.6 | Pollinator traits

We selected pollinator traits that, based on our knowledge and/or previous studies (Table S2), could either influence the response of pollinators to environmental conditions (response traits, hereafter R), pollination service (effect traits, hereafter E) or both (hereafter R-E). All pollinator species recorded (99 species, Table S3) were characterized with three traits: body length (R-E), hairiness (R-E) and larval diet (R-E). Because bees are the most frequent and effective apple pollinators (Garratt et al., 2016; Vicens & Bosch, 2000a), we conducted separate analyses including only bees. We measured eight traits in this group (45 species): intertegular span (a proxy of body size; R-E), hairiness (R-E), proboscis length (E), forewing aspect ratio (maximum length/maximum width; R), sociality (R), voltinism (R), nesting substrate (R) and pollen transportation structure (E) (see Table S2 for details).

Quantitative traits were measured on pinned specimens from the survey orchards. Categorical traits were based on literature records and our expert knowledge (see Table S2 for methods and sample sizes). We worked with a single mean value per trait and species. We explored correlation between each pair of numerical traits (Table S4). In bees, proboscis length was highly correlated to body size ($r > 0.7$). Thus, we only used body size in the analyses.

2.7 | Functional composition metrics

For each orchard, we calculated the community-weighted mean (CWM) of each trait, a measure of functional identity (Garnier et al., 2004). CWM of numerical traits was calculated as the mean value across species weighted by the relative abundance of each species (Ricotta & Moretti, 2011). CWM of categorical traits was calculated as the proportion of individuals belonging to each trait category. To measure functional diversity, we used the Rao quadratic diversity index (RaoQ), which measures the dissimilarity between two randomly selected individuals and calculates the sum of weighted abundance dissimilarity between each pair of species (Rao, 1982). The RaoQ index has some advantages over other functional diversity metrics: (a) It is easy to interpret (it ranges from 0 to the maximum of Simpson's diversity index); (b) in general, it is relatively unaffected by species richness (Botta-Dukát, 2005) and (c) it can be used to measure both single- and multi-trait diversity (Ricotta & Moretti, 2011).

Honeybees were excluded from calculations of response trait metrics because their presence was mostly (or solely) attributable to managed colonies in all four regions. Conversely, honeybees were included in calculations of effect trait metrics because they affect apple pollination (Vicens & Bosch, 2000b). Measures of CWM and RaoQ were conducted using the dbFD and functcomp functions from FD library (Laliberté & Legendre, 2010) with R (see Appendix S1 for details on functional composition metric calculations). In addition to the RaoQ index, we also measured trait diversity with the Functional Divergence Index (FDiv; Villéger et al., 2008). The results were similar to those obtained with the RaoQ and are provided in the Supporting Information.

2.8 | Statistical analysis

All statistical analyses were conducted with R v3.2.3.

2.8.1 | Response traits

To assess the response of pollinator functional composition to local and landscape features, we performed separate linear mixed-effect models (LMMs) for each functional composition metric (CWM of each trait and RaoQ of all traits combined). These analyses were done separately for all pollinator species and for bee species only. Full models included three local variables (orchard management, AES cover, flower diversity) and two landscape variables (orchard cover, PFH cover) as fixed effects, and region as a random effect. Numerical explanatory variables were not highly correlated ($r < 0.7$, Table S5) and VIF was <5 for all full models.

2.8.2 | Effect traits

To analyse the effect of functional traits on pollination service, we conducted LMMs with initial fruit set as the response variable. Because all pollinators potentially contribute to fruit set, these analyses included honeybees. To discriminate between trait identity and trait diversity effects, we run one model with trait CWMs and another with RaoQ as predictor variables. We checked for correlation between pairs of predictors and excluded variables as required until VIF was <5 (Table S6; Zuur et al., 2010). Whenever two predictors were strongly correlated, we kept the one that we considered more likely to be associated with pollination services. As a result, CWM of hairiness and pollinivorous larvae and RaoQ were the only functional predictor variables included. These models also included two additional variables that could affect initial fruit set: overall pollinator visitation rate and orchard management. To establish whether the relationship between functional composition and pollination services was management dependent, these models also included the interaction between management and the selected functional composition metrics. Finally, apple variety and region were included as independent random effects. Fruit set data were not available for German orchards, so $n = 81$ orchards for these analyses.

Following model selection procedures (MuMIn package; Barton & Barton, 2019), we tested all possible explanatory variable combinations (see above) through a multimodel inference approach (Anderson & Burnham, 2004). We then used a model averaging approach (with averaged variable coefficients) based on AICc to assign a relative importance to each variable. Models with $\Delta\text{AICc} < 2$ were considered equally suitable (see Appendix S1 for details on model selection procedures).

Normality and homoscedasticity assumptions were graphically evaluated by plotting the distribution of residuals of each model. Response variables were square-root- or log-transformed as needed. Numerical explanatory variables were standardized to facilitate comparison across variables. To detect model outliers, we calculated Cook's distance and excluded sites with distances $>4/N$ (Cook, 1977). The exclusion of outliers provided better model adjustments, but trends remained similar (Tables S7 and S8). To rule out spatial autocorrelation, we applied a Moran's I test with the residuals of all our models (Table S9).

TABLE 1 Statistical outputs of model averaging relating wild pollinator and wild bee functional composition response variables to local and landscape features. Estimated coefficients, their 95% intervals (in parentheses) and relative importance (in brackets) are provided. Significant terms are in bold. '—' denotes variables not appearing in the model average. R^2_m and R^2_c are the range of marginal and conditional R^2 of the best-fitted models respectively. R^2 of the best model is indicated in parentheses. 'Sites' indicates the number of orchards included in the model after outlier exclusion (Table S7)

Response variable	Management*	Flower diversity	AES cover	% Orchard cover	% Pollinator friendly habitat cover	R^2_m	R^2_c	Sites
All pollinators								
CWM body length	—	0.145 [0.31] (−0.201, 0.491)	—	**−0.683 [1](−1.078, −0.288)**	**0.986 [1](0.423, 1.550)**	0.28–0.29 (0.28)	0.28–0.29 (0.28)	98
CWM Hairiness[a]	—	—	−0.397 [0.44] (−0.889, 0.095)	**−1.046 [1](−1.627, −0.465)**	**0.676 [0.83](0.054, 1.299)**	0.16–0.23 (0.23)	0.28–0.35 (0.35)	99
CWM Pollinivorous larvae	0.026 [0.18] (−0.076, 0.129)	—	—	−0.031 [0.33] (−0.083, 0.021)	**0.154 [1](0.073, 0.235)**	0.11–0.13 (0.11)	0.56–0.57 (0.56)	94
CWM Insectivorous larvae[a]	−0.026 [0.14] (−0.099, 0.047)	0.033 [0.84] (−0.000, 0.066)	**0.075 [1](0.040, 0.110)**	0.023 [0.20] (−0.018, 0.063)	−0.017 [0.17] (−0.050, 0.017)	0.14–0.17 (0.16)	0.36–0.39 (0.38)	99
Bees								
RaoQ	**4.946 [1](0.655, 9.236)**	—	—	**−3.478 [1](−5.704, −1.252)**	1.657 [0.36] (−1.488, 4.802)	0.18–0.20 (0.18)	0.24–0.26 (0.24)	105

Note: [a]Square-root Log(X + 1).

*Low intensity: reference level of management.

3 | RESULTS

We recorded 8,253 pollinator individuals visiting apple flowers. Most pollinators were honeybees (77.6%), followed by wild bees (9.1%), hoverflies (5.9%), other flies (6.1%), beetles (1%) and others (0.4%) (Table S3). Honeybee visitation rates were similar in LI and HI orchards (LMM, estimate $\beta = 0.08$, $p = 0.24$), but overall pollinator visitation rates were higher in LI orchards ($\beta = 0.15$, $p < 0.05$; Table S10).

3.1 | Response traits

At the local scale, AES cover favoured pollinators with insectivorous larvae (Table 1). There were no effects of local features, landscape features or their interactions on pollinator trait diversity (RaoQ). Landscape orchard cover was negatively associated with body length and hairiness CWMs (Table 1). Pollinator-friendly habitat cover was positively associated with body length, hairiness and proportion of pollinators with pollinivorous larvae (bees).

When considering bees only, the best-fitted models for all CWM variables were the null models. Thus, we could not attribute any effect of local or landscape features to any specific bee trait (Table 1). However, local and landscape features had important effects on functional diversity, which was negatively affected by landscape orchard cover (Figure 1a) and enhanced by LI management (Figure 1b).

3.2 | Effect traits

Models including CWM metrics showed that initial fruit set was enhanced by HI management but was not affected by any particular trait (Table 2). Models including RaoQ revealed an interaction effect between trait diversity and management on initial fruit set (Figure 2). There was a positive effect of trait diversity on initial fruit set in LI orchards but not in HI orchards (Table 2). When trait diversity was low, initial fruit set was lower in LI orchards, but when trait diversity was high, initial fruit set was similar in the two orchard types. In other words, differences between LI and HI orchards in initial fruit set disappeared as pollinator trait diversity increased (Figure 2).

Models computed with FDiv showed similar results (Tables S12 and S13), except that FDiv was not affected by management and was enhanced by PFH cover.

4 | DISCUSSION

Our results show that bee trait diversity was enhanced by LI orchard management and negatively affected by landscape orchard cover. At the same time, pollinator trait diversity enhanced pollination service in LI, but not in HI orchards. Our results provide evidence that pollinator functional diversity is an important mechanism linking responses to agricultural intensification and contribution to pollination services in agricultural systems.

Local factors were important determinants of pollinator functional composition. AES enhanced the abundance of pollinators with insectivorous larvae, probably by providing prey for aphidophagous hoverflies and predatory wasps (Rodríguez-Gasol et al., 2019). Some studies have reported AES to also benefit pollinators with pollinivorous larvae (bees; Blaauw & Isaacs, 2014). However, we found no such effect, suggesting that floral resources may not be limiting during apple bloom.

LI management enhanced bee trait diversity. Various studies show positive effects of organic farming on bee abundance and taxonomic diversity, particularly in homogeneous landscapes, and these results are attributed to reduced use of chemical inputs (Forrest et al., 2015; Rundlöf et al., 2008). As far as we know, effects of agricultural management on bee trait diversity have not been previously reported. Our results show that the increase in species richness caused by LI management also results in an increase in functional diversity.

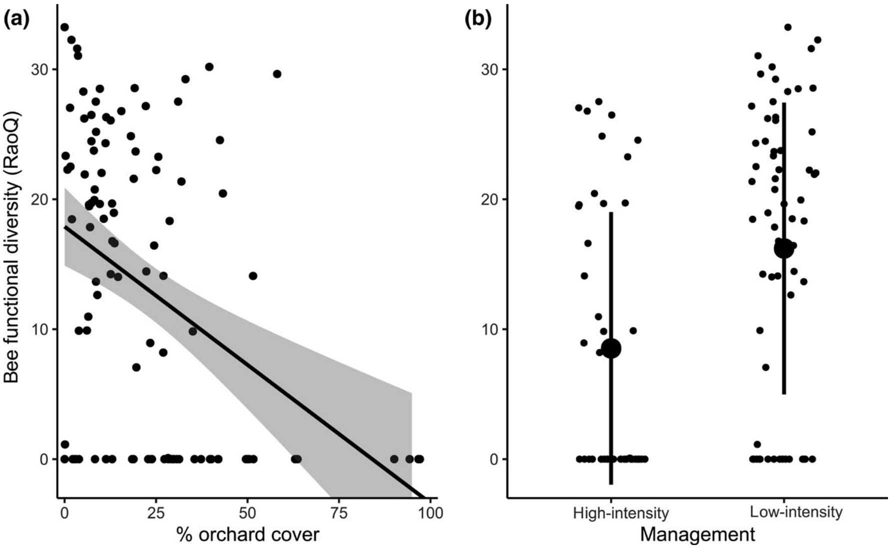

FIGURE 1 Effects of landscape orchard cover (a) and orchard management (high intensity vs. low intensity) (b) on bee multi-trait functional diversity (RaoQ). Grey bands indicate 95% confidence intervals. Vertical bars indicate standard deviations

TABLE 2 Statistical outputs of model averaging relating initial fruit set to management (low intensity vs. high intensity), functional composition metrics, the interaction between management and functional composition metrics and pollinator visitation rate. The first model includes single-trait metrics (CWM of hairiness and pollinivorous larvae). The second model includes functional diversity (multi-trait RaoQ). Estimated coefficients, their 95% intervals (in parentheses) and relative importance (in brackets) are provided. Significant terms are in bold. '—' denotes variables not appearing in the model average. R^2_m and R^2_c are the marginal and conditional R^2 range of the best-fitted model respectively. R^2 of the best model is indicated in parentheses. 'Sites' indicates the number of orchards included in the model after outlier exclusion (Table S8)

Response variable	**Management***	**CWM hairiness**	**CWM pollinivorous**	**CWM hairiness x management**	**CWM pollinivorous x management**	**Visitation rate**	R^2_m	R^2_c	**Sites**
All pollinators									
Initial fruit set^a	**−1.617 [1](−2.304, −0.930)**	0.113 [0.20] (−0.251, 0.477)	—	—	—	0.154 [0.25] (−0.193, 0.500)	0.24–0.25 (0.24)	0.24–0.25 (0.24)	76
Response variable	Management*	RaoQ	RaoQ × management			Visitation rate	R^2_m	R^2_c	Sites
Initial fruit set^a	**−1.580 [1](−2.193, −0.966)**	−0.301 [0.64] (−0.821, 0.219)	**0.749 [0.64](0.089, 1.409)**			—	0.27–0.32 (0.32)	0.27–0.32 (0.32)	76

Note: Data transformations: ^{a}Square-root.

*Low intensity: reference level of management.

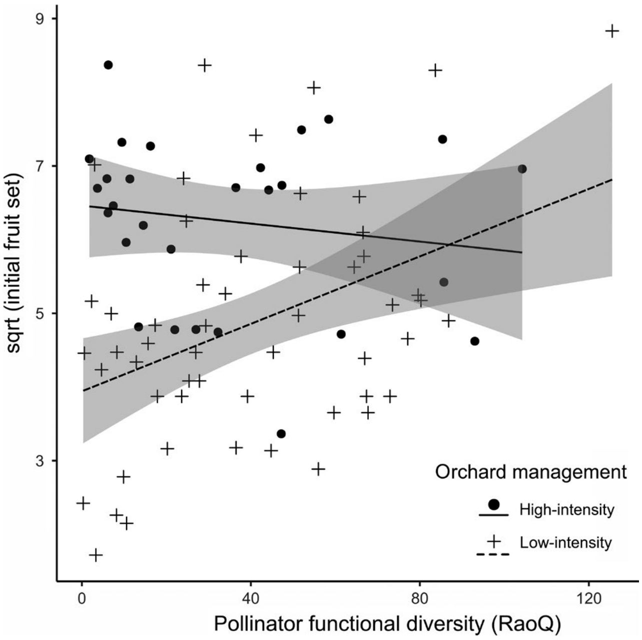

FIGURE 2 Effects of pollinator multi-trait diversity (RaoQ, including wild and managed pollinators) on initial fruit set (square-root transformed) in low-intensity (estimate $\beta = 0.192$; $p = 0.05$) and high-intensity ($\beta = -0.108$; $p = 0.213$) orchards (Table S11). Grey bands indicate 95% confidence intervals

Landscape features also affected pollinator functional composition. Large and hairy pollinators were negatively affected by orchard cover and enhanced by pollinator-friendly habitat cover. The response of body size and other traits to landscape intensification is controversial and appears to be context dependent. According to some studies, small bee species are more sensitive to landscape intensity and isolation from natural habitats (De Palma et al., 2015; Klein et al., 2008). However, other studies show opposite trends (Larsen et al., 2005; Rader et al., 2014) or no clear patterns (Bartomeus et al., 2018; Forrest et al., 2015; Williams et al., 2010). We cannot think of any reason why hairier pollinators should be more abundant in semi-natural habitats than in agricultural areas.

We also found that landscapes with high levels of pollinator-friendly habitat promoted the relative abundance of pollinators with pollinivorous larvae (bees). Semi-natural habitats provide spatio-temporal stability to flower visitors (Klein, 2009) through widespread and continued accessibility to flower resources, especially before and after the crop's flowering period. Pollinator-friendly habitats also provide nesting resources and pesticide-free refuge areas (Holzschuh et al., 2010), thus promoting the colonization and establishment of bee communities in agricultural areas (Kremen et al., 2004). Bee trait diversity was not affected by pollinator-friendly habitat in our study, but it decreased with landscape orchard cover. Bee trait diversity is known to be lower in farmland compared to natural habitats (Forrest et al., 2015; Hass et al., 2018; Woodcock et al., 2014). In addition to higher levels of pesticide exposure, orchard-dominated landscapes are characterized by landscape homogenization and isolation from semi-natural habitats, thus hindering consistent spatio-temporal availability of flower resources not only during but especially before and after apple bloom (Marini et al., 2012). In sum, our results support the need of landscape level initiatives to promote bee communities in agroecosystems (Cole et al., 2020).

HI orchards had higher initial fruit set than LI orchards. Because pollinator visitation rates were higher in LI orchards, we cannot attribute this result to lower pollination levels in LI orchards. We find two possible explanations for the higher initial fruit set in HI orchards. First, the use of chemical fertilizers and lower levels of pests and diseases may enhance fruitlet retention in HI orchards (Peck et al., 2006; Samnegård et al., 2019). Second, to enhance the production of large apples, fruit load is usually chemically thinned. In HI orchards, synthetic thinners are applied during fruitlet growth (Fallahi & Greene, 2010) whereas in LI orchards, organic thinners are applied during bloom (Lordan et al., 2018), effectively lowering the numbers of flowers available for fruitlet development.

No specific pollinator traits emerged as important determinants of pollination service. We found that trait diversity enhanced initial fruit set, but only in LI orchards. The positive effect of trait diversity on pollination services has been previously recognized (Hoehn et al., 2008; Martins et al., 2014; Woodcock et al., 2019), but ours is, as far as we know, the first study showing interactive effects between trait diversity and agricultural management on pollination services. Functionally diverse pollinator communities may enhance pollination function through various spatial and temporal complementarity mechanisms (Blüthgen & Klein, 2011). Our results show that, through the enhancement of pollinator trait diversity, LI orchards may reach levels of initial fruit set similar to those of HI orchards. Importantly, the positive effect of bee trait diversity on initial fruit set in LI orchards was detected despite a very strong background of honeybee visitation.

Some pollinator traits responded to local and/or landscape factors but, as mentioned, no specific traits influenced pollination services. In other words, pollination service could not be explained by sampling effects of dominant traits (Mokany et al., 2008). A recent study shows that pollen deposition in apple flowers is influenced by various morphological and behavioural pollinator traits, possibly diluting the effect of any single trait by itself (L. Roquer-Beni, unpublished data). Bee trait diversity responded negatively to two important features associated with agricultural intensification: HI management and increased orchard cover, and pollinator trait diversity enhanced initial fruit set in LI orchards. These results suggest that the response–effect framework is more relevant for integrative measures (multi-trait diversity) than single traits (Peña et al., 2020). Our results have important implications in the face of the new European Common Agricultural Policy, one of whose strategic objectives is the preservation of landscapes and biodiversity (European Commission, 2019). First, efforts to promote functional biodiversity provide greater returns in low-intensity than in high-intensity farms. Second, the fact that high levels of ecosystem services can be reached in low-intensity farms (as long as functional diversity is preserved) provides a compelling argument for the conversion of high-intensity into low-intensity farms. Measures promoting pollinator functional diversity (e.g. reduction of chemical inputs, implementation of AES enhancing diversified nesting and flower resources, increased landscape heterogeneity and connectivity to semi-natural habitats) could provide environmental benefits and, at the same time, reduce farmer dependence on costly external inputs while maintaining competitive production.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.-M.K., A.-K.H., A.R., D.G., J.B., K.M., L.R.-B., M.M., P.A.H., U.S., V.B. and X.A. conceived and designed the study; A.-K.H., D.G., G.A., J.B., L.R.-B., M.M., M.P., M.T., U.S. and V.B. collected the data; L.R.-B. led data analysis and manuscript writing with assistance from A.R., X.A. and J.B. All authors contributed to draft development and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.63xsj3v39 (Roquer-Beni et al., 2021).

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SUPPORTING INFORMATION

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