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RESEARCH ARTICLE

Differential effects of agricultural expansion on wild bee taxonomic and functional diversity

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Abstract

1. Pollinators, especially bees, are in global decline, threatening biodiversity and food security. While intensive agriculture is a primary driver, its impact on bee functional diversity—particularly in the diverse Mediterranean region—remains understudied. Understanding how natural habitat loss in farmed landscapes affects functional diversity is crucial for developing land management that preserves pollination services.
2. We assessed how natural area proportion affects wild bee taxonomic and functional diversity in apple and sweet cherry orchards in central Chile. Over 2 years, bees were sampled using coloured pan traps in orchards categorized by surrounding natural vegetation. Taxonomic diversity was analysed via richness and composition indices, while functional diversity was calculated from morphological and life-history traits, analysed separately for males and females.
3. We found that the increasing proportion of natural areas positively affected wild bee taxonomic and functional diversity in orchards. Bee taxonomic diversity significantly increased with surrounding natural area proportion, but functional diversity responses were contrasting between male and female bee traits. In particular, functional homogenization (based on RaoQ) was significantly associated with male functional traits in orchards with low natural areas (%) and, in some cases, functional richness (FRic) increased with more surrounding natural area. We found that bee taxonomic and functional diversity responded differently for apple and sweet cherry orchards. Further, the fourth-corner analysis showed

some sex-specific and temporal associations between traits and natural areas percentage.

4. Natural areas seem to promote pollinator taxonomic and functional bee diversity in different ways. Sex-specific trait approaches reveal differential ecological associations. Thus, making future studies include intra-specific trait variability (like sexual dimorphism) seems relevant and a deeper understanding of how different taxonomic and functional bee diversity aspects respond to environmental filters imposed by natural areas neighbouring crops is needed.

KEYWORDS
bees, Central Chile, ecological intensification, functional diversity, functional traits, natural areas, pollinators, wild-bee diversity

1 | INTRODUCTION

In the last couple of decades, a global pollination crisis has become evident, with multiple threats to pollinator diversity and declines in their abundance, often linked to habitat loss, excessive pesticide use and invasive species (Brondizio et al., 2019; Garratt et al., 2023; Goulson et al., 2015; Kennedy et al., 2013; Potts et al., 2016; Powney et al., 2019; Vieli et al., 2021; Zattara & Aizen, 2021). Intensive agriculture practices have rapidly aggravated the effects of these threats on insect pollinators in a drive to meet increasing demand for food production. This is paradoxical because such effects negatively affect agricultural production and ecosystem functioning, considering 87% of angiosperm species, including many key crops, depend on animal-mediated pollination (Losey & Vaughan, 2006; Ollerton et al., 2011; Outhwaite et al., 2022). One of the consequences of intensive agriculture is crop isolation from natural environments, which is strongly associated with the reduction of flower-visiting insect diversity (Dainese et al., 2019; Garibaldi et al., 2011). Additionally, the dramatic increase in pesticide use with low target-specificity significantly impacts beneficial insects like wild pollinators at different spatial scales (Galetto et al., 2022; Wan et al., 2025). Moreover, introducing exotic species, such as the globally commercialized European bumblebee (*Bombus terrestris*) and honeybee (*Apis mellifera*), poses risks to native pollinators, such as increasing interspecific competition and potential novel pathogen transmissions (Arbetman et al., 2013; Morales et al., 2013; Plischuk et al., 2009).

Bees are among the most important insect pollinators affected by global pollinator decline (Bartomeus et al., 2013; Bascompte et al., 2003). Wild bees (comprising native and naturalized species) are fundamental for agricultural production and ecosystem functioning (Garibaldi et al., 2013, 2014; Hoehn et al., 2008; Klein et al., 2007; Russo et al., 2017). Changes in bee diversity are becoming apparent from a taxonomic standpoint, as local species richness and abundance decline in various countries (Bartomeus et al., 2013; Biesmeijer et al., 2006; Powney et al., 2019). Besides species diversity, bee functional diversity has been found to play a fundamental role in delivering pollination services; functional traits (e.g. body size, hair density, flower handling behaviour and visit duration) have a positive direct relationship to pollen deposition, which is related to pollinator effectiveness and also crop yield (Földesi et al., 2021; Garibaldi et al., 2015; Russo et al., 2017; Woodcock et al., 2019). Empirical evidence shows that functional diversity is threatened by land-use change, with more conspicuous effects on certain species, such as those with large body sizes or solitary behaviour (Rader et al., 2014; Woodcock et al., 2019). Also, landscape heterogeneity is known to favour bee functional diversity (Coutinho et al., 2021). A recent review by Ostwald et al. (2024) shows an increasing number of articles that not only include a functional diversity approach to bee ecology in the last decades, but also emphasizes that in the southern hemisphere—and specifically in South America—these kinds of studies are underrepresented.

Central Chile is a global biodiversity hotspot, particularly for bees, due to its high endemism (Gould, 2015). The above becomes important, considering that the southern hemisphere faces major perceived risks associated with global pollinator decline (Dicks et al., 2021), not least the expansion of agricultural production. In the last decades, Chile has increased the area of pollinator-dependent crops, with direct consequences for biodiversity mainly due to loss of natural vegetation, increase in the use of commercial pollinators and pesticide which may be related to pollinator decline (Vieli et al., 2021) including pollinator species that are important for crop pollination. In other countries, primarily from the northern hemisphere, it has been observed that wild pollinators (e.g. wild bees) are important for pollinating apple and sweet cherry crops, and their activity and resulting pollination services are linked to non-crop habitats in and around crop fields (Eeraerts, 2022; Eeraerts et al., 2020; Mateos-Fierro et al., 2022). However, studies on how wild bee communities are affected by intensive agricultural practices are scarce, particularly in the southern hemisphere (Osterman et al., 2024).

In this study, we assessed how the proportion of natural areas surrounding apple and sweet cherry crops affects bee taxonomic and functional diversity in agricultural landscapes of central Chile. We hypothesized that local landscape context affects bee communities found in orchards as natural vegetation areas host a higher richness of wild bee species by meeting habitat requirements. Therefore, orchards surrounded by more natural areas will have a greater wild bee diversity than those in more intensive areas, with taxonomic diversity more sensitive to land-use change than functional diversity, given functional redundancy among wild bee species present in fruit orchards.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in agricultural landscapes in the Mediterranean biodiversity hotspot ecosystems of central Chile from O'Higgins to Maule administrative regions (34°–36° S; Figure 1). Today, these landscapes comprise a mosaic of remnant natural and semi-natural habitats of the dominant sclerophyllous native vegetation, rural settlements and intensive agricultural areas. In this region, two of the most common fruit crops are sweet cherry and apple, which are highly pollinator-dependent crops that occupy 48,960 and 31,967 ha, respectively, in the country (ODEPA fruit registre, 2021).

2.2 | Site selection

Our study was conducted in a total of 54 orchards across six 15 × 15 km quadrants (3 in apple- and 3 in sweet cherry-producing regions). To select these orchards, we first characterized the landscape context of all potential sites by calculating the proportion of different land uses within a 1 km radius buffer around each orchard edge. This analysis used national land-use data from Zhao et al. (2016), later updated by CONAF (2020). Based on the percentage of native sclerophyllous vegetation (i.e. forests and shrublands) within each buffer, we assigned orchards to one of three categories: Low (L: 0%–35%), Medium (M: 36%–70%) or High (H: >71%). Within each of the six pre-defined quadrants (Soto et al., 2023), we selected three random orchards from each native vegetation category with minimum 3 km separation requirement, resulting in nine orchards per quadrant. Bee sampling was subsequently carried out in all 54 orchards (Figure 1).

2.3 | Bee sampling

At each apple and sweet cherry orchard selected, we set up three 20 × 20 m plots 50 m apart, starting from the edge of each orchard into the interior to reduce any edge effect. Each plot had three pan trap sets randomly placed 10 m apart at 1 m above ground level (at the height of crop flowers). Each set of pan traps (8 cm in diameter, 9 cm tall) had three plates painted in white, yellow and blue (following Hutchinson et al. (2022)) filled with water and detergent to reduce the surface tension to capture the insects (Figure S1). We placed pan traps for 10 days in each orchard during the crop blossom period (September to October for sweet cherry and October to November for apple in 2021 and 2022) as we focused on responses on the pollination period of these crops. Farmers in all sampled farms used commercial honeybee (*A. mellifera*) colonies to supplement pollination with a density of 5–6 hives/ha. Thus, the presence of individuals of *A. mellifera* is not related to the proportion of natural habitat, but to hives, those farmers placed in every orchard. Consequently, we did not consider *A. mellifera* a wild bee and excluded it from the analysis. Although *Bombus ruderatus* and *B. terrestris* are introduced species, we consider them wild bees because farmers in our sampled orchards do not use them as managed pollinators (i.e. there are no hives of both species within or in the surrounding orchards, so the individuals found in our pan traps came from naturalized populations). We stored collected bees in 70% ethanol using 50 mL Falcon tubes. All specimens used in the analysis were identified to genus or species level, except for one Colletid bee that we left as Colletidae sp. We used literature for identification; in some cases, expert entomologists were consulted to confirm identifications.

2.4 | Wild bee functional traits

We selected a mixture of both effect (i.e. morphological) and response (i.e. behavioural and life history) functional traits. We measured morphological traits separately between female and male bees to consider marked sexual dimorphism and ecological roles of both sexes (e.g. usually females are larger than males and forage more often for pollen), which affects pollination process (Frank et al., 2016). For sexing the bees, we used taxonomical literature and presence or absence of morphological structures (tibial scopa, abdominal scopa, number of flagellomers, sting, etc.) but due to the high number of individuals in some species, we extrapolated a sex proportion with a representative subset for both years. We selected intertegular distance and wing size, which are proxies of body size and positively correlated with foraging distances (i.e. the distance that bees may fly from their nest sites to visit flowers and forage; Cane, 1987; Gathmann & Tscharntke, 2002; Greenleaf et al., 2007). We also measured facial hairiness (also an effect trait), which is linked to facial pollen load (Goulnik et al., 2020). We selected bee response traits from the literature, focusing on behavioural patterns, life-history characteristics, floral resource use and nesting substrate preferences (Table S1, available online as Supporting Information), which are likely affected by landscape configuration.

We measured morphological traits from pinned specimens belonging to the native bee collection of the Pontificia Universidad Católica de Valparaíso (Chile) and the entomological collection from Instituto de Entomología (Universidad Metropolitana de Ciencias de la Educación, Santiago de Chile). We measured every species identified in our sampling. Specimens we could not identify at the species level were excluded from the functional trait analysis, which represented 58% of the specimens collected. We measured intertegular distance and wing size using a stereo

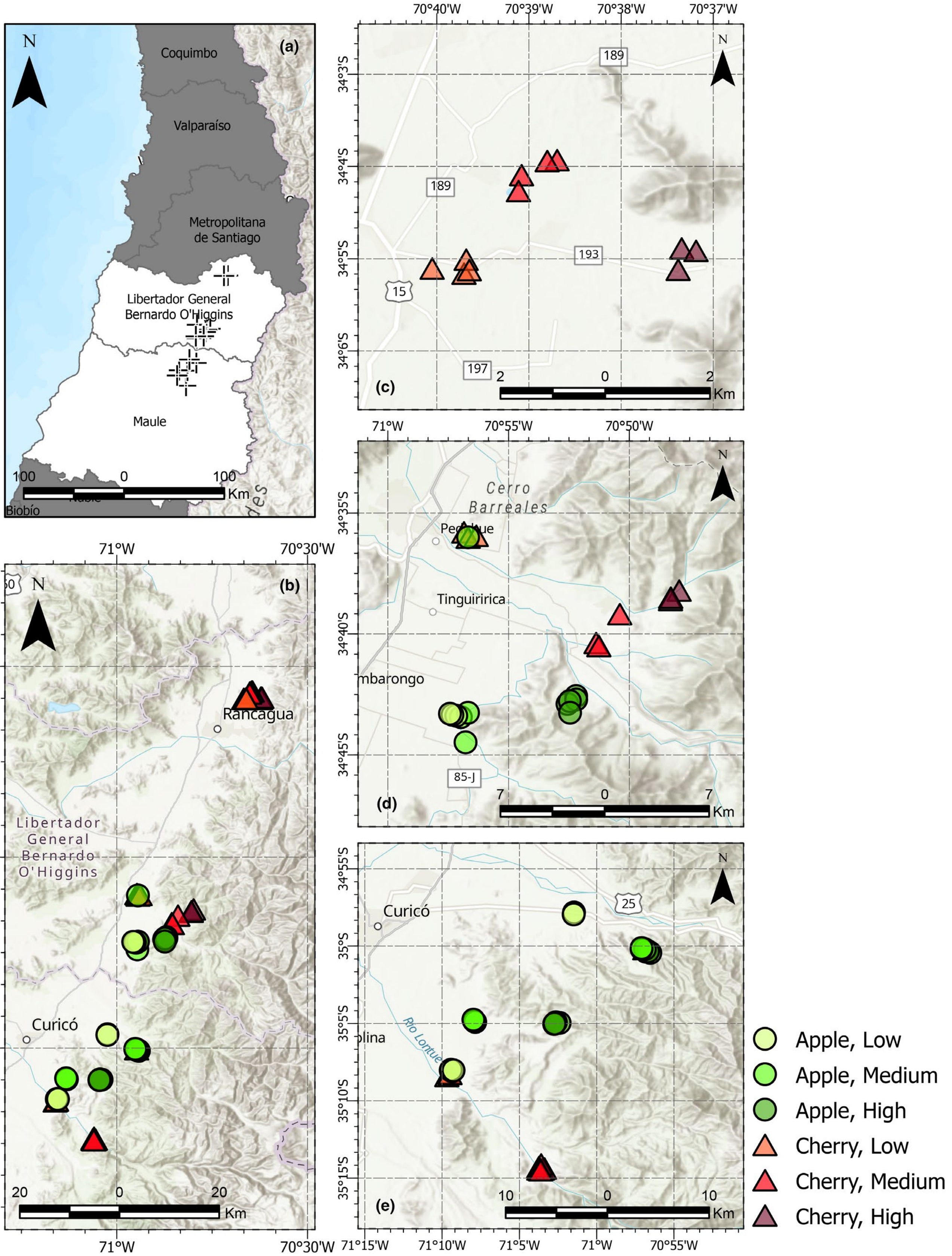


FIGURE 1 (a) Location of the study area in continental Chile, detailing apple and sweet cherry orchards sampled. (b) O'Higgins and Maule regions where sampling areas are located, (c–e) details of sampled landscapes, where green tones represent natural area categories (low: 0%–35%, medium: 36%–70%, high: >71%) for apple crop orchards, and red tones present natural area categories for cherry crop orchards.

microscope (ZEISS Stemi 305 with Axiocam 208 color, Labscope 3.1.1 software). Face hairiness was measured following a standard protocol (Stavert et al., 2016), using MATLAB with Image Processing ToolBox. For face hairiness measurements, we captured stacked images using a motorized rail system (StackShot Macro Rail, Cognisys) and processed them in Helicon Focus v8 (see Figure S2 for examples of the photographs obtained to measure hairiness). We measured five male and five female individuals per species to assess sexual dimorphism, using specimens sampled across latitudinal ranges, when possible, to account for intraspecific variability. Quantitative traits for *B. terrestris* and *B. ruderatus* were obtained from Stavert et al. (2016) due to limited specimen availability in our reference collections.

2.5 | Taxonomic diversity analysis

We calculated species richness using the Shannon diversity and evenness indices (Jost, 2006) for wild bee taxa collected and identified to species or genus level in apple and sweet cherry crops. We used the BiodiversityR (Kindt & Coe, 2005) package in R version 4.2.0 (R Development Core Team, 2022) to conduct diversity analyses. We also used the iNEXT package (Chao et al., 2014; Hsieh et al., 2024) to conduct a rarefaction-based diversity estimation. This approach compares Hill numbers ($q=0$: richness, $q=1$: exponential Shannon, $q=2$: inverse Simpson) with 84% confidence intervals (when these intervals do not overlap, we can assume significant differences at $p<0.05$). Then, we fitted generalized linear mixed-effects models (GLMM) with a Gaussian error distribution to compare species richness, diversity and evenness across natural area categories and crop types, including quadrants as a random effect. Then, we conducted Type III ANOVAs over GLMM results to assess the overall effect of natural area category on taxonomic diversity metrics.

2.6 | Species composition analysis

We then performed an analysis of similarities (ANOSIM) to test wild bee compositional differences among natural area categories for apple and sweet cherry crop types, as they have slightly different blooming periods. ANOSIM is a non-parametric multivariate analysis that uses similarity matrices (Clarke, 1993); here, we used the Bray–Curtis index to perform ANOSIM tests, and we used 999 permutations to estimate its significance values. Then, we used a non-metric multidimensional scaling (nMDS) to visualize the results obtained from the test. When we obtained significant ANOSIM results, we used a Similarity Percentage test (SIMPER) to determine the individual contribution of each bee species to compositional differences among landscape categories. SIMPER test is a similarity test that enables us to decide the contribution of each species in the different categories (Rees et al., 2004). We used the vegan (Oksanen et al., 2013) package to perform these analyses and the ggplot2 (Wickham, 2016) package to plot the results.

2.7 | Functional diversity analysis

To assess bee functional diversity, we estimated metrics based on quantitative data. Therefore, we had to transform qualitative traits (nesting substrate, floral visit range, resources used and sociality) into Spearman rank correlation coefficients (following Legendre and Legendre (2012)). After that, we generated two matrices, one with the functional traits for each species separated by female and male bees (matrix B) and another with the species-relative abundance in each orchard (matrix W). According to Villéger et al. (2008), we calculated multidimensional indices that consider abundance (Laliberté & Legendre, 2010). With matrices B and W, we calculated four functional diversity complementary indices (Botta-Dukát, 2005; Mason et al., 2005; Villéger et al., 2008): (1) Functional richness index (FRic hereafter), which constitutes the amount of functional space occupied by a subset of species within the community; (2) Rao's quadratic entropy index (RaoQ hereafter), obtained as the sum of the differences of weighted traits and represents the mean distance of a given trait between two randomly selected bees; (3) Functional Evenness index (FEve hereafter), which represents the regularity of species abundance distributions along the functional volume; and (4) Functional divergence index (FDiv hereafter), which describes patterns of niche differentiation within the community. We calculated these functional indices using the FD package (Laliberté et al., 2014). These four indices capture different, complementary aspects of functional diversity and collectively provide a complete characterization of community functional structure, as these indices can respond differently to the same ecological processes or environmental gradients (Fontúrbel et al., 2022; Mouchet et al., 2010; Velásquez-Trujillo et al., 2021).

To assess the relationships of the four functional diversity indices and proportion of natural areas (we used the exact value of natural area proportion for each orchard), we fitted Markov chain Monte Carlo generalized linear models (MCMCGLM, hereafter) with a Gaussian error distribution using the MCMCglmm package (Hadfield, 2010). We fitted separate models for each index, year, crop and bee sex (no random terms were included). MCMCGLMs provide a Bayesian inference framework that provides posterior distribution for parameters along with credible intervals (that are interpreted in the same way as 95% confidence intervals), which perform better for challenging data and small sample sizes (Bolker et al., 2009). We assessed model fit by examining posterior predictive checks and residuals using posterior mean predictions.

2.8 | Fourth-corner analysis

To evaluate the relationship between bee functional traits and the environmental gradient represented by the percentage of natural area, we performed a fourth-corner analysis separately for males and females in apple and cherry crops, for each sampling year (Dray & Legendre, 2008). This approach allows identification of significant associations between bee functional traits and the percentage of natural area through the species abundance matrix. In each analysis, we treated the natural area percentage variable as continuous and performed 999 permutations to assess the statistical significance of the observed associations. We performed the analyses using the ade4 package (Dray & Dufour, 2007).

2.9 | Permits and bioethics

In Chile, no capture permits are required for field studies involving insects. This study was approved by the bioethics committee of the Pontificia Universidad Católica de Valparaíso (authorization BIOEPUCV-BA 331-2020).

3 | RESULTS

We found a total of 12,361 bee individuals for both years and crops, from which we were able to identify 42 taxa to species or genus level, represented by the families Apidae, Andrenidae, Colletidae, Halictidae, and Megachilidae (Table S2). In 2021, we recorded 42 taxa with 8150 individuals; in 2022, we found 36 taxa with 4211 individuals; 78% of those species were recorded in both years. Among those bee species, we found the exotic bumblebees *B. terrestris* and *B. ruderatus*, considered naturalized individuals in the study area. The remaining species were native or endemic. Although we excluded *A. mellifera* from the analyses (because it came from managed hives), it is important to mention that it was by far the most abundant species in the focal crops, with a total of 55,987 individuals (~81% of the overall abundance).

3.1 | Taxonomic diversity

In both years, we found the highest values of species richness (*S*) in those crops surrounded by >71% of natural area. We found similar results for the Shannon Index (*H′*) except in the second year (2022) for apple crops surrounded by a high proportion of natural areas (H). In contrast, Evenness (*J*) was greater for both years and crop types when surrounding natural habitat proportion was low (Table 1). In both sampling years, species richness significantly increased with natural area (2021: $F=23.66$, df=44, $p<0.001$; 2022: $F=30.53$, df=44, $p<0.001$), landscapes dominated by natural areas (H) supported approximately twice as many species per orchard as intensively managed landscapes (H: 16.4±4.9 vs. L: 8.7±3.2 species in 2021; H: 11.4±4.1 vs. L: 5.7±2.1 species in 2022). A similar pattern was observed for Shannon diversity (2021: $F=8.28$, df=44, $p<0.001$; 2022: $F=8.02$, df=44, $p=0.001$). In contrast, we found no significant effects of natural areas on Evenness (2021: $F=3.14$, df=44, $p=0.053$; 2022: $F=1.18$, df=44, $p=0.320$). These results are confirmed by the rarefaction-based diversity estimations (Figures S3–S6).

TABLE 1 Wild bee species richness (*S*), species diversity (*H′*) and evenness (*J*) among crop types (Apple=A, Sweet cherry=C), natural area categories (low=L, medium=M, high=H) found in both years (2021, 2022).

Year	Category	Crop	*S*	Diversity (*H′*)	Evenness (*J*)
2021	L	A	20	1.471	0.614
	M	A	28	1.606	0.402
	H	A	32	2.031	0.509
	L	C	21	1.078	0.363
	M	C	28	1.219	0.292
	H	C	34	1.458	0.289
2022	L	A	15	1.523	0.723
	M	A	20	1.356	0.413
	H	A	24	1.480	0.420
	L	C	11	0.607	0.561
	M	C	20	1.095	0.518
	H	C	22	1.455	0.507

3.2 | Community composition

We found significant differences in bee community composition between apple and sweet cherry crops in both years (ANOSIM $R=0.179$, $p=0.001$ for 2021 and ANOSIM $R=0.083$, $p=0.008$ for 2022). We found significant differences in wild bee community composition in apple and sweet cherry among all natural area categories in 2021 (apple; $R=0.207$, $p=0.009$; Figure 2a; sweet cherry; $R=0.120$, $p=0.021$; Figure 2c) and for 2022 (apple; $R=0.341$, $p=0.001$; Figure 2b; sweet cherry; $R=0.07$, $p=0.098$; Figure 2d; individual species contributions to those differences are detailed in Tables S3–S6). These differences were more evident between orchards belonging to (L) and (H) categories, as they had less polygon overlap, reflected in the nMDS plot (Figure 2).

3.3 | Functional diversity components

The relationship between functional diversity indices and percentage of natural area showed contrasting patterns across bee sex, year and crop type. For female wild bees, functional richness (FRic) had a significant positive relationship with natural area in apple orchards during 2021 ($p=0.040$) and a highly significant positive relationship in cherry orchards during 2022 ($p<0.001$; Figure 3i,l). Functional divergence (FDiv) showed a significant negative relationship only in cherry orchards during 2022 ($p=0.016$; Figure 3d), while functional evenness (FEve) had a marginally negative trend in apple orchards during 2021 ($p=0.056$; Figure 3e). Rao's quadratic entropy (RaoQ) showed no significant relationships for female bees in any case. In contrast, male bees showed more consistent patterns, particularly for RaoQ, which showed significant positive relationships in all cases: apple 2021 ($p=0.004$), cherry 2021 ($p=0.030$), apple 2022 ($p=0.002$) and cherry 2022

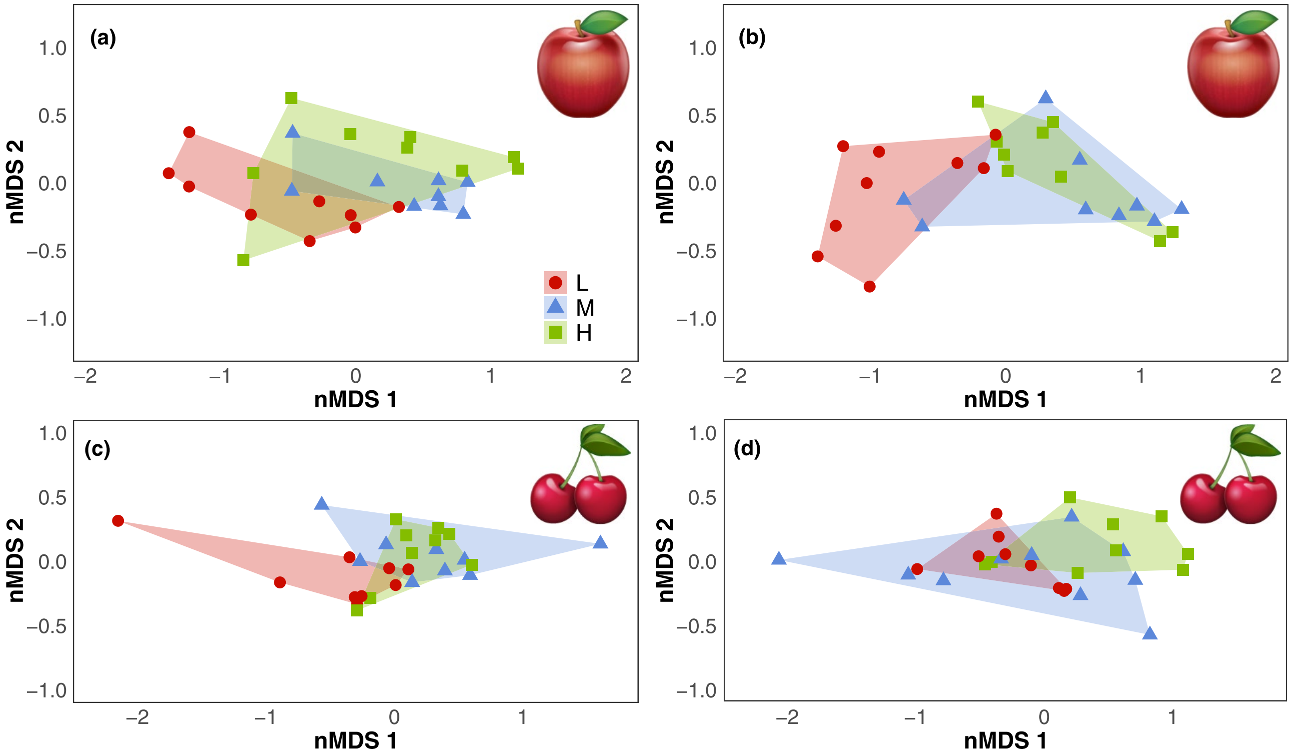


FIGURE 2 Wild bee species compositional differences among crops including (a) apple orchards (ordination stress = 0.085) in 2021 and (b) apple orchards (ordination stress = 0.061) in 2022; and (c) sweet cherry orchards (ordination stress = 0.075) in 2021 and (d) sweet cherry orchards (ordination stress = 0.064) in 2022. Polygon overlap implies that bee species composition is similar. Crop categories: L = intensive crops with <35% of natural area (red circles), M = crops with 36%–70% of natural area (blue triangles) and H = crops surrounded by >71% of natural area (green squares).

(*p* = 0.001; Figure 4m–p). Also, FRic showed a significant positive relationship with natural areas in apple orchards during 2021 (*p* = 0.038; Figure 4i), while FEve showed a highly significant negative relationship in apple during 2022 (*p* = 0.004; Figure 4g). These results suggest that male bee functional diversity, particularly Rao's quadratic entropy, is more consistently influenced by the percentage of neighbouring natural area than female bees, whose functional richness appears more responsive in apple orchards during the first sampling year and in cherry orchards during the second sampling year. Detailed MCMCGLM results are available in Table S7.

3.4 | Fourth-corner analysis

The fourth-corner analysis revealed specific associations by sex and year between bee functional traits and the percentage of natural area surrounding apple and cherry crops. In the case of males in apple orchards during 2021 (Figure 5a), the morphological trait intertegular distance (IM) showed a positive association with natural area (coefficients close to 0.2), while wing size (WM) showed a negative association. Among life-history and behavioural traits, nesting in branches and stems (BS) was positively associated with natural area, in contrast to nesting on the ground (So), which showed a negative association. In 2022, in the same apple orchards, we observed that intertegular distance (IM) became negatively associated with natural area (Figure 5c). In cherry orchards, the functional traits of males also showed associations with natural area in both 2021 and 2022 (Figure 5b,d). In 2021, the patterns were similar to those observed in apple orchards: IM showed a positive association with natural area, and in terms of life-history and behaviour, BS was positively associated while So was negatively associated (Figure 5b). However, in 2022, the morphological patterns were different: hairiness (HM) showed a positive association with natural area, while IM and WM showed negative associations (coefficients between −0.1 and −0.2) (Figure 5d). In contrast, life-history and behavioural traits maintained the same pattern observed in 2021.

In general, the functional traits of females showed fewer associations with the natural area than those of males in all crop types and years (Figure 5e–h). In apple orchards during 2021 (Figure 5e), life-history and behavioural traits showed that solitary sociality (Sl) was positively associated with natural area, while social bees (Sc) showed a negative association. In 2022 (Figure 5g), the functional associations were different: life-history and behavioural traits showed no relationship with the natural area, but the morphological traits wing size (WF) and intertegular distance (IF) were negatively associated with it. In cherry orchards in 2021 (Figure 5f), the morphological traits WF and IF showed positive associations with natural area. Consistently, the life history and behavioural traits of nesting in existing cavities (EC) and social sociality (Sc) were also positively

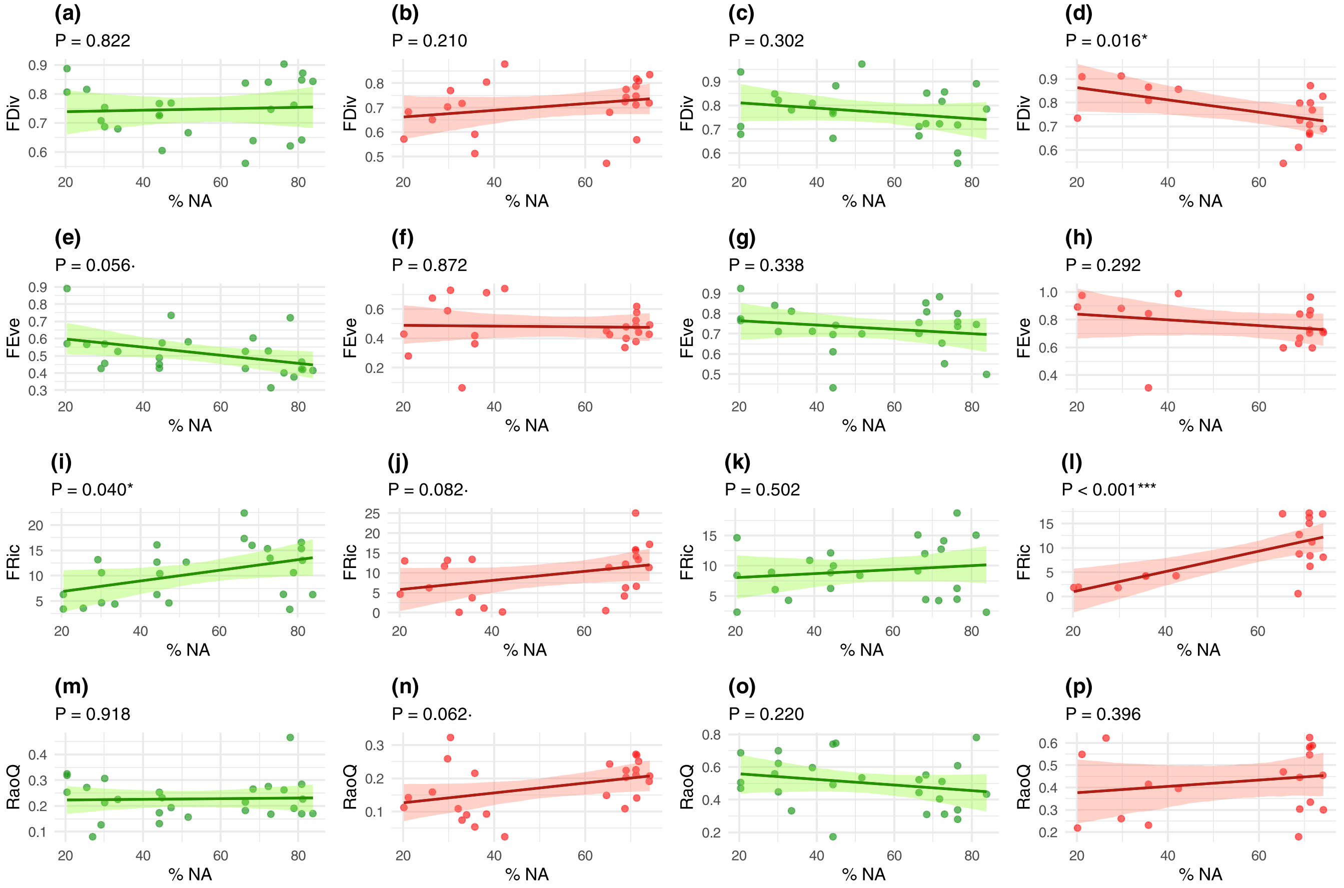


FIGURE 3 Relationships of functional diversity indices (FDiv = functional divergence (a–d), FEve = functional evenness (e–h), Fric = functional richness (i–l), and RaoQ = Rao's quadratic entropy (m–p)) and the percentage of surrounding natural area (%NA) on female bees of apple (in green) and cherry (in red) crops in 2021 (left panels) and 2022 (right panels). Significance values were estimated using MCMCGLM models.

associated, while ground nesting (So) and solitary sociality (Sl) showed negative associations. In 2022 (Figure 5h), the associations changed again: hairiness (HF) showed a positive association with natural area, while WF showed a negative association compared to the previous year. In terms of life history and behavioural traits, both Sc and Sl increased their strength of association with natural cover compared to 2021.

Overall, the fourth-corner analysis showed that the associations between the functional traits of bees and the percentage of neighbouring natural area were clearly dependent on sex, crop type and sampling year. Morphological effect traits (IM, WM and HM), selected for their relationship to body size and foraging distance, exhibited the greatest variation in their associations with natural area, especially in males. In contrast, response traits, such as nesting substrate and sociality, showed more consistent patterns, maintaining similar associations between years within each crop, although with evident differences between apple and cherry orchards. In females, both effect and response traits showed fewer associations, suggesting that the influence of the percentage of surrounding natural area is more pronounced in males. Taken together, these results indicate that the proportion of natural area available in the landscape differentially modulates functional effect and response traits, and that this modulation is strongly dependent on the ecological context determined by sex, crop and year.

4 | DISCUSSION

Our study demonstrates that across crops, neighbouring natural areas are an important factor that has differential effects on bee taxonomic and functional diversity, depending on their proportion in the landscape. Firstly, as we expected, taxonomic diversity increased with natural areas in terms of richness and Shannon index (*H*′), which concurs with our hypothesis (apple and sweet cherry; see Table 1). Also, the composition of bee species in orchards with lower natural area proportion (L) differs significantly from those with a higher proportion of natural area (H). Interestingly, we encountered more variability as we explored functional diversity. We see that male and female bee traits respond differentially to natural areas (see Figures 3–5). Furthermore, we found that some trait groups are associated more positively or negatively with natural areas. As we will further discuss, other variables might also be involved in modulating bee functional diversity, as we found differences between crop types (apple and sweet cherry) and between male and female bees.

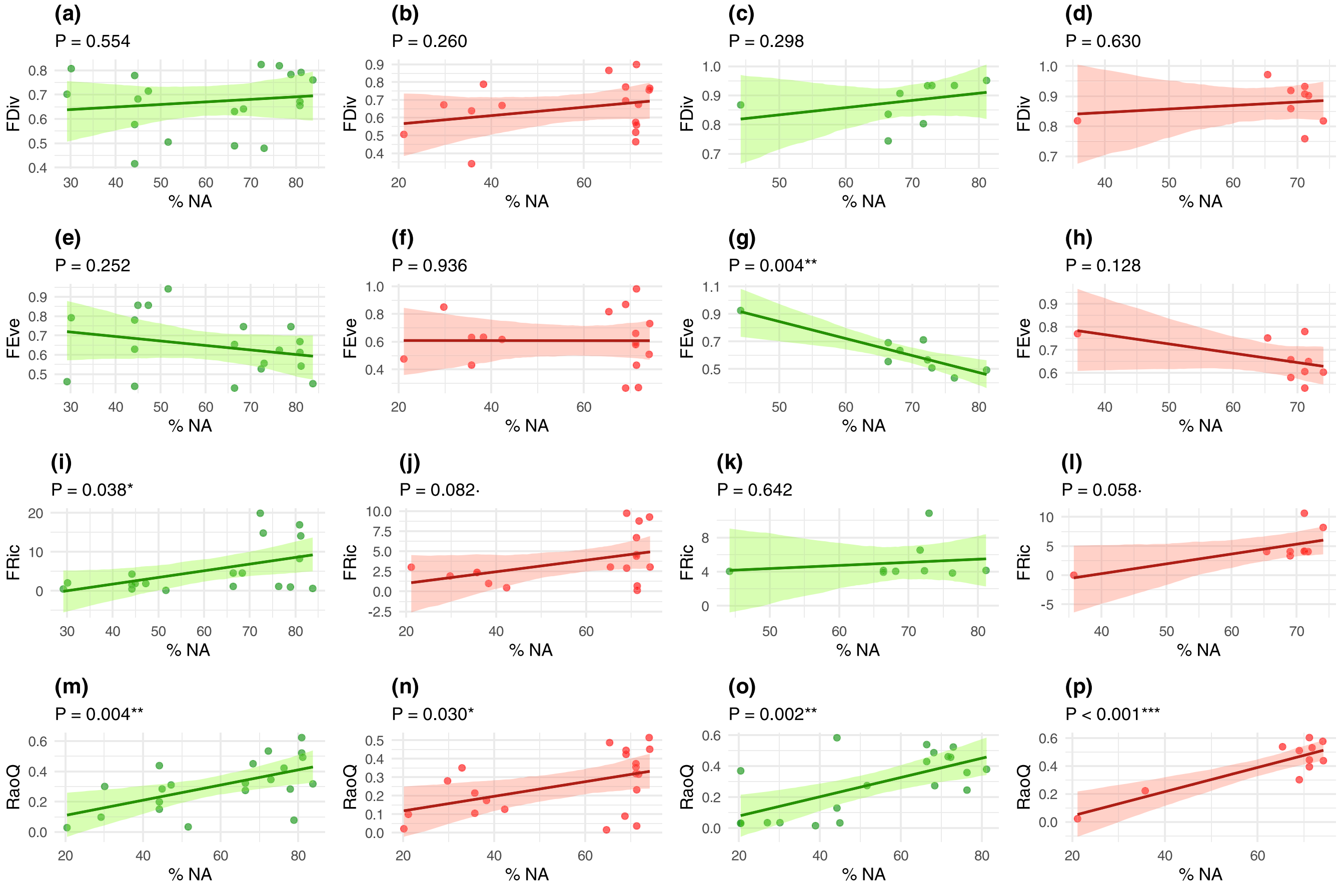


FIGURE 4 Relationships of functional diversity indices (FDiv = functional divergence (a–d), FEve = functional evenness (e–h), Fric = functional richness (i–l), and RaoQ = Rao's quadratic entropy (m–p)) and the percentage of surrounding natural area (%NA) on male bees of apple (in green) and cherry (in red) crops in 2021 (left panels) and 2022 (right panels). Significance values were estimated using MCMCGLM models.

4.1 | Taxonomic diversity

On the one hand, species diversity (H') and species richness (S) increased with the proportion of natural areas, regardless of the crop, which agrees with our hypothesis. This effect could be caused by higher floral and nesting resources available around orchards in landscapes with a higher proportion of natural areas (H), as Watson et al. (2011) previously found in North American apple orchards. A similar effect of adjacent forests on bees has been observed in cucumber home gardens, with an increased yield (Garibaldi et al., 2015). The detected decrease in bee richness associated with reduced proportion of natural areas aligns with previous results on natural area isolation effects on pollinator richness (Garibaldi et al., 2011). By contrast, we found that evenness decreased with the proportion of surrounding natural areas, which might be due to the low number of bee species in landscapes with a low proportion of natural areas (L). The most dominant species of wild bee in all three categories was *Lasioglossum* sp., but it is possible that we collected more than one species. However, due to the difficulty of differentiating species in this genus, we decided to leave them at the genus level. We also found that the Andrenid bee *Acamptopoeum submetallicum* was the second most abundant species in all natural area categories. Like others in this study, this species nests in soil, which means they could potentially nest inside orchards. This idea is supported by other studies in which *A. submetallicum* was the most abundant species collected within strawberry crops, where these bees usually build their nests (López-Aliste et al., 2021).

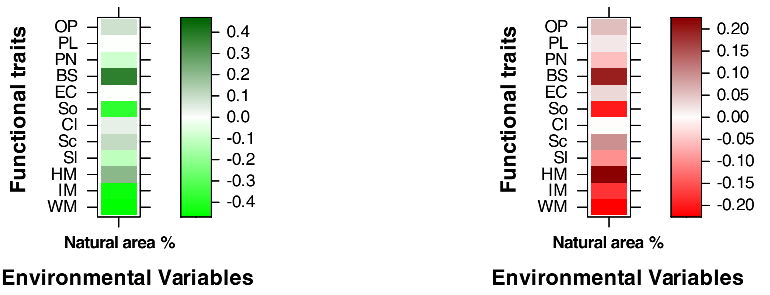
Even though we excluded *A. mellifera* from our analyses, it is important to point out that, by displacing other bees, the high abundance of this managed species could generate a high interspecific competition, as has been reported in other ecosystems (e.g. MacInnis et al., 2023; Renner et al., 2021; Su et al., 2022). With these results, we detected a more diverse but less even community with more dominant species in landscapes with a higher proportion of natural areas (H) for both crops. At the same time, in landscapes with a low proportion of natural areas (L), we observed a less rich and diverse community but with a more even representation of each species present in the community.

4.2 | Functional diversity

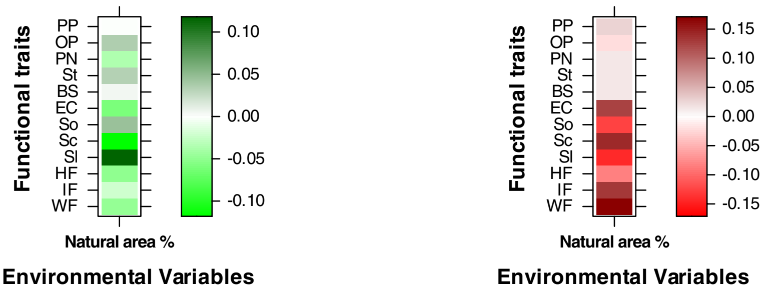
Regarding functional diversity indices, our results found marked differences in responses between sexes regarding trait diversity, as

(a) Male bees in Apple crops (2021) (b) Male bees in Cherry crops (2021)

(c) Male bees in Apple crops (2022) (d) Male bees in Cherry crops (2022)



(e) Female bees in Apple crops (2021) (f) Female bees in Cherry crops (2021)



(g) Female bees in Apple crops (2022) (h) Female bees in Cherry crops (2022)

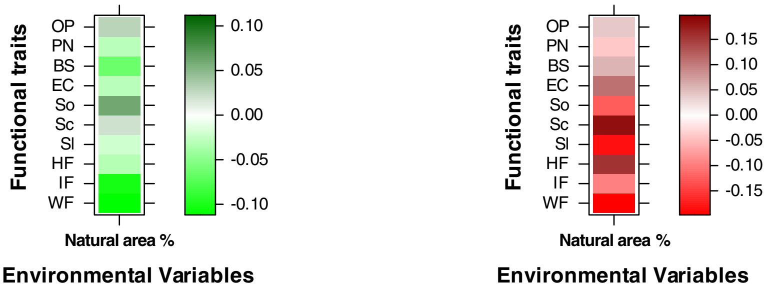


FIGURE 5 Relative influence of the percentage of surrounding natural area on bee functional traits per sampling year, crop and bee sex. Female morphological traits: Wing size = WF, Intertegular distance = IF, Hairiness = HF; Male morphological traits: Wing size = WM, Intertegular distance = IM, Hairiness = HM; Behavioural and life-history traits: [Sociality] Solitary = Sl, Social = Sc, Cleptoparasitic = Cl, [Nesting substrates] Soil = So, Existing cavities = EC, Branches and stems = BS, Stems = St, [Resource used] Pollen and nectar = PN, Pollen and nectar plus leaves = PL, Oil pollen and nectar = OP and Pollen and nectar plus petals = PP. (a–d) Correspond to male bee traits, and (e–h) correspond to female bee traits.

shown primarily by the RaoQ and FRic indices, which indicate the importance of distinguishing the ecological traits that male and female bees present. Interestingly, our results suggest that a low natural areas percentage generates functional homogenization on male bee functional diversity shown by the RaoQ data in both crop types and both years (Figure 4), on the contrary, female RaoQ values were not significantly affected. This contrast between male and female functional diversity may relate to behavioural differences between sexes. For example, female bees usually sleep in their nests while males seek refuge in cavities, leaves, stems or flowers overnight. Thus, natural areas may provide more of these elements used as resting sites. To understand this difference, adding other variables related to natural area configuration may be needed. On the other hand, functional richness was positively affected by neighbouring natural areas; this suggests that natural areas harness a greater range and variety of traits, especially for female bees, although FRic in male bees was also affected, but in a more subtle manner (see Figure 3).

The stronger and more consistent response of RaoQ compared to other functional diversity indices may be related to the fact that RaoQ quantifies the mean pairwise functional dissimilarity among individuals weighted by their abundances, making it particularly sensitive to functional homogenization (Botta-Dukát, 2005). In contrast, FRic measures only the outer boundaries of trait space (the convex hull volume) and remains unchanged as long as species with extreme trait values persist, regardless of changes in internal community structure. Similarly, FDiv and FEve capture distributional properties that may not shift dramatically during early stages of community filtering (Mouchet et al., 2010). Our finding that RaoQ consistently responded to natural area reduction in male bees suggests that decreased natural habitat leads to communities dominated by functionally similar males, even when the overall trait space appears relatively stable. This pattern likely reflects that natural areas provide diverse microhabitats (e.g. cavities, stems and flowers) used by male bees for overnight refuge, and as these habitats decrease, only males with traits suited to the remaining limited options persist. These results highlight the importance of using complementary functional diversity metrics, as relying solely on volume-based indices like FRic may underestimate the extent of functional homogenization occurring in agricultural landscapes. Considering the association of each trait to natural area percentage in the fourth-corner analysis, we observed sex-specific and temporarily variable associations. These results are similar to other studies like Bartomeus et al. (2018) that found inconsistencies in predicting trait to land-use responses. This variability may be explained by intensive practices, which can influence pollinator functional diversity (Roquer-Beni et al., 2021), or also by seasonal changes in the natural areas such as the availability of flower resources, known to affect bee traits like floral handling behaviour (Nagano et al., 2023).

Interestingly, all bee species found were polylectic, meaning they visit a wide range of flowering plant species. Also, most species found are solitary species except the native bumblebee (*Bombus dahlbomii*) and the two exotic species, *B. terrestris* and *B. ruderatus*, which are eusocial species that construct their nests in cavities (Flores-Prado, 2021, 2023). We also found one species that presents a kleptoparasite behaviour, *Epiclopus gayi*. Further, it is important to mention that *E. gayi* was collected only in (H) orchards, except for one individual in landscapes with a low proportion of natural areas (L) and one of its host bees: *Centris nigerrima* (Vivallo, 2014). However, *C. nigerrima* was found in all natural area categories. Both species belong to the same bee community. The fact that *E. gayi* was collected predominantly in the orchards containing the highest percentage of natural areas may indicate that it is more sensitive to the loss of native vegetation than its bee host (Packer & Graham, 2020).

There is a gap in understanding of how male and female bees separately contribute to pollination. For example, a study by Canto-Aguilar and Parra-Tabla (2000) in Mexico found that both sexes in *Peponapis limitaris* (Apidae) were more efficient pollinators than *A. mellifera*. On the other hand, female *Andrena emeishanica* (Andrenidae) in China have been seen to transfer less pollen than males of the same species, but males have lower visit rates than females (Tang et al., 2019). Furthermore, Kendall et al. (2019) showed that intertegular distance (one of the most used body size proxies in bees) varies, and this is attributable to sexual dimorphism. Therefore, these previous studies demonstrate that male and female bees can be functionally different when it comes to pollination, which is important when studying bee functional ecology. Unfortunately, in Chile, there is a lack of information on wild bee life-history traits and ecological information, which is limited by the lack of expert bee taxonomists (for instance, we had to exclude many specimens because we were unable to identify them to the species level) limiting our ability to integrate functional ecology and decision-making, but our study goes some way to closing this gap.

In conclusion, the proportion of natural area is important in shaping wild bee communities in commercial crops. We observed that wild bee taxonomic diversity shows a clear response to natural areas in the Southern hemisphere's Mediterranean region; specifically, highlighting that maintaining a minimum of natural surroundings is required to promote species diversity. On the other hand, functional diversity exhibited a more complex response, being affected by different environmental filters and crop management approaches. We also demonstrate that future studies should consider sex-dimorphism as it is a significant factor explaining how trait diversity behaves. Finally, both taxonomic and functional diversity must be considered when making land management decisions to achieve the dual goals of species conservation and to maintain the delivery of functions such as pollination. Yet we show that the optimal approach may differ depending on the desired response. Nonetheless, ecological intensification and conservation of natural areas are promising alternatives to secure the ecosystem service that bees and other pollinators provide and safeguard the unique biodiversity these areas host.

AUTHOR CONTRIBUTIONS

Juan L. Celis-Diez and Francisco E. Fontúrbel conceived the study; Juan L. Celis-Diez, Francisco E. Fontúrbel, Michael P. D. Garratt and Luis F. Flores-Prado designed the methodology; Manuel López-Aliste, Camila B. García, Pablo Díaz-Siefer and Fernanda Montero-Silva collected the data; Manuel López-Aliste, Angela M. Vargas-Daza, Juan F. Betancurt-Grisales and Francisco E. Fontúrbel analysed the data; Manuel López-Aliste and Francisco E. Fontúrbel led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Original data associated with this manuscript are available from the figshare digital repository: https://doi.org/10.6084/m9.figshare.28886678 (López-Aliste et al., 2026).

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REFERENCES

Arbetman, M. P., Meeus, I., Morales, C. L., Aizen, M. A., & Smagghe, G. (2013). Alien parasite hitchhikes to Patagonia on invasive bumblebee. *Biological Invasions*, *15*(3), 489–494. https://doi.org/10.1007/s10530-012-0311-0

Bartomeus, I., Cariveau, D. P., Harrison, T., & Winfree, R. (2018). On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. *Oikos*, *127*(2), 306–315. https://doi.org/10.1111/oik.04507

Bartomeus, I., Park, M. G., Gibbs, J., Danforth, B. N., Lakso, A. N., & Winfree, R. (2013). Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecology Letters*, *16*(11), 1331–1338. https://doi.org/10.1111/ele.12170

Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(16), 9383–9387. https://doi.org/10.1073/pnas.1633576100

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., & Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. *Science*, *313*(5785), 351–354. https://doi.org/10.1126/science.1127863

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H., & White, J. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, *16*(5), 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Brondizio, E., Settele, J., Díaz, S., & Ngo, H. (2019). *Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services*. IPBES Secretariat.

Cane, J. H. (1987). Estimation of bee size using intertegular span (Apoidea). *Journal of the Kansas Entomological Society*, *60*(1), 145–147.

Canto-Aguilar, M. A., & Parra-Tabla, V. (2000). Importance of conserving alternative pollinators: Assessing the pollination efficiency of the squash bee, in *Cucurbita moschata* (Cucurbitaceae). *Journal of Insect Conservation*, *4*(3), 203–210. https://doi.org/10.1023/A:1009685422587

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Clarke, K. R. (1993). Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology*, *18*, 117–143.

CONAF. (2020). *Sistema de informacion territorial – CONAF*. Retrieved from November 02, 2025, https://sit.conaf.cl/

Coutinho, J. G. E., Hipólito, J., Santos, R. L. S., Moreira, E. F., Boscolo, D., & Viana, B. F. (2021). Landscape structure is a major driver of bee functional diversity in crops. *Frontiers in Ecology and Evolution*, *9*, 624835. https://doi.org/10.3389/fevo.2021.624835

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., … Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, *5*(10), eaax0121. https://doi.org/10.1126/sciadv.aax0121

Dicks, L. V., Breeze, T. D., Ngo, H. T., Senapathi, D., An, J., Aizen, M. A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L. A., Gemmill-Herren, B., Howlett, B. G., Imperatriz-Fonseca, V. L., Johnson, S. D., Kovács-Hostyánszki, A., Kwon, Y. J., Lattorff, H. M. G., Lungharwo, T., Seymour, C. L., … Potts, S. G. (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature Ecology & Evolution*, *5*(10), 1462. https://doi.org/10.1038/s41559-021-01554-5

Dray, S., & Dufour, A. B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*(4), 1–20.

Dray, S., & Legendre, P. (2008). Testing the species traits-environment relationships: The fourth-corner problem revisited. *Ecology*, *89*(12), 3400–3412. https://doi.org/10.1890/08-0349.1

Eeraerts, M. (2022). Increasing wild bee richness and abundance on sequentially flowering cultivars of a pollinator-dependent crop. *Agriculture, Ecosystems & Environment*, *325*, 107745. https://doi.org/10.1016/j.agee.2021.107745

Eeraerts, M., Vanderhaegen, R., Smagghe, G., & Meeus, I. (2020). Pollination efficiency and foraging behaviour of honey bees and non-Apis bees to sweet cherry. *Agricultural and Forest Entomology*, *22*(1), 75–82. https://doi.org/10.1111/afe.12363

Flores-Prado, L. (2021). Sociabilidad en Insectos. In L. A. Ebensperger & A. Labra (Eds.), *Comportamiento social de la fauna nativa de Chile* (pp. 153–218). Ediciones Universidad Católica de Chile.

Flores-Prado, L. (2023). Nidificación en abejas nativas. In L. Flores-Prado (Ed.), *Abejas en Chile: Desde su biología hacia su conservación* (pp. 76–101). Ediciones Fremen.

Földesi, R., Howlett, B. G., Grass, I., & Batáry, P. (2021). Larger pollinators deposit more pollen on stigmas across multiple plant species-A meta-analysis. *Journal of Applied Ecology*, *58*(4), 699–707. https://doi.org/10.1111/1365-2664.13798

Fontúrbel, F. E., Betancurt-Grisales, J. F., Vargas-Daza, A. M., & Castaño-Villa, G. J. (2022). Effects of habitat degradation on bird functional diversity: A field test in the Valdivian rainforest. *Forest Ecology and*

Management, *522*, 120466. https://doi.org/10.1016/j.foreco.2022.120466

Frank, J., Martin, S., & Volkmar, W. (2016). Intra-specific body size determines pollination effectiveness. *Basic and Applied Ecology*, *17*(8), 714–719. https://doi.org/10.1016/j.baae.2016.07.004

Galetto, L., Aizen, M. A., Arizmendi, M. D., Freitas, B. M., Garibaldi, L. A., Giannini, T. C., Lopes, A., Do Espírito Santo, M. M., Maués, M. M., Nates Parra, G., & Rodríguez, J. I. (2022). Risks and opportunities associated with pollinators' conservation and management of pollination services in Latin America. *Ecología Austral*, *32*, 55–76. https://doi.org/10.25260/EA.22.32.1.0.1790

Garibaldi, L. A., Bartomeus, I., Bommarco, R., Klein, A. M., Cunningham, S. A., Aizen, M. A., Boreux, V., Garratt, M. P. D., Carvalheiro, L. G., Kremen, C., Morales, C. L., Schüepp, C., Chacoff, N. P., Freitas, B. M., Gagic, V., Holzschuh, A., Klatt, B. K., Krewenka, K. M., Krishnan, S., … Woyciechowski, M. (2015). Trait matching of flower visitors and crops predicts fruit set better than trait diversity. *Journal of Applied Ecology*, *52*(6), 1436–1444. https://doi.org/10.1111/1365-2664.12530

Garibaldi, L. A., Carvalheiro, L. G., Leonhardt, S. D., Aizen, M. A., Blaauw, B. R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A. M., Kremen, C., Morandin, L., Scheper, J., & Winfree, R. (2014). From research to action: Enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment*, *12*(8), 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., Szentgyörgyi, H., … Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, *14*(10), 1062–1072. https://doi.org/10.1111/j.1461-0248.2011.01669.x

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N. P., Dudenhöffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., … Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, *339*(6127), 1608–1611. https://doi.org/10.1126/science.1230200

Garratt, M. P. D., O'Connor, R. S., Carvell, C., Fountain, M. T., Breeze, T. D., Pywell, R., Redhead, J. W., Kinneen, L., Mitschunas, N., Truslove, L., Xavier E Silva, C., Jenner, N., Ashdown, C., Brittain, C., McKerchar, M., Butcher, C., Edwards, M., Nowakowski, M., Sutton, P., & Potts, S. G. (2023). Addressing pollination deficits in orchard crops through habitat management for wild pollinators. *Ecological Applications*, *33*(1), e2743. https://doi.org/10.1002/eap.2743

Gathmann, A., & Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, *71*(5), 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Gould, J. (2015). Meet our prime pollinators. *Nature*, *521*(7552), S48–S49. https://doi.org/10.1038/521S48a

Goulnik, J., Plantureux, S., Van Reeth, C., Baude, M., Mesbahi, G., & Michelot-Antalik, A. (2020). Facial area and hairiness of pollinators visiting semi-natural grassland wild plants predict their facial pollen load. *Ecological Entomology*, *45*(6), 1296–1306. https://doi.org/10.1111/een.12913

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957. https://doi.org/10.1126/science.1255957

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589–596. https://doi.org/10.1007/s00442-007-0752-9

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(1), 1–22. https://doi.org/10.18637/jss.v033.i02

Hoehn, P., Tscharntke, T., Tylianakis, J. M., & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B-Biological Sciences*, *275*(1648), 2283–2291. https://doi.org/10.1098/rspb.2008.0405

Hsieh, H. Y., Ma, K. H., & Chao, A. (2024). *iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 3.0.1*. http://chao.stat.nthu.edu.tw/wordpress/software-download/

Hutchinson, L. A., Oliver, T. H., Breeze, T. D., O'Connor, R. S., Potts, S. G., Roberts, S. P. M., & Garratt, M. P. D. (2022). Inventorying and monitoring crop pollinating bees: Evaluating the effectiveness of common sampling methods. *Insect Conservation and Diversity*, *15*(3), 299–311. https://doi.org/10.1111/icad.12557

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kendall, L. K., Rader, R., Gagic, V., Cariveau, D. P., Albrecht, M., Baldock, K. C. R., Freitas, B. M., Hall, M., Holzschuh, A., Molina, F. P., Morten, J. M., Pereira, J. S., Portman, Z. M., Roberts, S. P. M., Rodriguez, J., Russo, L., Sutter, L., Vereecken, N. J., & Bartomeus, I. (2019). Pollinator size and its consequences: Robust estimates of body size in pollinating insects. *Ecology and Evolution*, *9*(4), 1702–1714. https://doi.org/10.1002/ece3.4835

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., … Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, *16*(5), 584–599. https://doi.org/10.1111/ele.12082

Kindt, R., & Coe, R. (2005). *Tree diversity analysis: A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre.

Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), 299–305. https://doi.org/10.1890/08-2244.1

Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0–12.3*.

Legendre, P., & Legendre, L. (2012). *Numerical ecology*. Elsevier.

López-Aliste, M., Flores-Prado, L., Ruz, L., Sepúlveda, Y., Rodríguez, S., Saraiva, A. M., & Fontúrbel, F. E. (2021). Wild bees of Chile: A database on taxonomy, sociality, and ecology. *Ecology*, *102*(8), e03377. https://doi.org/10.1002/ecy.3377

López-Aliste, M., García, C. B., Díaz-Siefer, P., Montero-Silva, F., Vargas, A. M., Betancurt-Grisales, J. F., Garratt, M. P. D., Flores-Prado, L., Celis-Diez, J. L., & Fonturbel, F. (2026). Data from: Differential effects of agricultural expansion on wild bee taxonomic and functional diversity. *Figshare Digital Repository*. https://doi.org/10.6084/m9.figshare.28886678

Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience*, *56*(4), 311–323. https://doi.org/10.1641/0006-3568(2006)56[311:Tevoes]2.0.Co;2

MacInnis, G., Normandin, E., & Ziter, C. D. (2023). Decline in wild bee species richness associated with honey bee (*Apis mellifera* L.) abundance in an urban ecosystem. *PeerJ*, *11*, e14699. https://doi.org/10.7717/peerj.14699

Mason, N. W. H., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, *111*(1), 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Mateos-Fierro, Z., Garratt, M. P. D., Fountain, M. T., Ashbrook, K., & Westbury, D. B. (2022). Wild bees are less abundant but show better pollination behaviour for sweet cherry than managed pollinators. *Journal of Applied Entomology*, *146*(4), 361–371. https://doi.org/10.1111/jen.12984

Morales, C. L., Arbetman, M. P., Cameron, S. A., & Aizen, M. A. (2013). Rapid ecological replacement of a native bumble bee by invasive species. *Frontiers in Ecology and the Environment*, *11*(10), 529–534. https://doi.org/10.1890/120321

Mouchet, M. A., Villéger, S., Mason, N. W., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, *24*(4), 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Nagano, Y., Wabiko, N., & Yokoi, T. (2023). Female solitary bees flexibly change foraging behaviour according to their floral resource requirements and foraging experiences. *The Science of Nature*, *110*(4), 37. https://doi.org/10.1007/s00114-023-01864-7

ODEPA fruit registre. (2021). *Catastro frutícola 2020*. Oficina de Estudios y Políticas Agrarias.

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Borman, T., Carvalho, G., Chirico, M., De Caceres, M., … Weedon, J. (2013). *vegan: Community ecology package*. *R package version 2.0–10*. http://CRAN.R-project.org/package=vegan

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*, 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Osterman, J., Mateos-Fierro, Z., Siopa, C., Castro, H., Castro, S., & Eeraerts, M. (2024). The impact of pollination requirements, pollinators, landscape and management practices on pollination in sweet and sour cherry: A systematic review. *Agriculture Ecosystems & Environment*, *374*, 109163. https://doi.org/10.1016/j.agee.2024.109163

Ostwald, M. M., Gonzalez, V. H., Chang, C. R., Vitale, N., Lucia, M., & Seltmann, K. C. (2024). Toward a functional trait approach to bee ecology. *Ecology and Evolution*, *14*(10), e70465. https://doi.org/10.1002/ece3.70465

Outhwaite, C. L., McCann, P., & Newbold, T. (2022). Agriculture and climate change are reshaping insect biodiversity worldwide. *Nature*, *605*(7908), 97–102. https://doi.org/10.1038/s41586-022-04644-x

Packer, L., & Graham, L. (2020). Four new species of Isepeolini (Hymenoptera; Apidae) from northern Chile. *BMC Zoology*, *5*(1), art3. https://doi.org/10.1186/s40850-020-00052-8

Plischuk, S., Martín-Hernández, R., Prieto, L., Lucía, M., Botías, C., Meana, A., Abrahamovich, A. H., Lange, C., & Higes, M. (2009). South American native bumblebees (Hymenoptera: Apidae) infected by *Nosema ceranae* (microsporidia), an emerging pathogen of honeybees (*Apis mellifera*). *Environmental Microbiology Reports*, *1*(2), 131–135. https://doi.org/10.1111/j.1758-2229.2009.00018.x

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. https://doi.org/10.1038/nature20588

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. *Nature Communications*, *10*, art1018. https://doi.org/10.1038/s41467-019-08974-9

R Development Core Team. (2022). *R: A language and environment for statistical computing, reference index version 4.2.0*. Foundation for Statistical Computing.

Rader, R., Bartomeus, I., Tylianakis, J. M., & Laliberté, E. (2014). The winners and losers of land use intensification: Pollinator community disassembly is non-random and alters functional diversity. *Diversity and Distributions*, *20*(8), 908–917. https://doi.org/10.1111/ddi.12221

Rees, G. N., Baldwin, D. S., Watson, G. O., Perryman, S., & Nielsen, D. L. (2004). Ordination and significance testing of microbial community composition derived from terminal restriction fragment length polymorphisms: Application of multivariate statistics. *Antonie van Leeuwenhoek International Journal of General and Molecular Microbiology*, *86*(4), 339–347. https://doi.org/10.1007/s10482-004-0498-x

Renner, S. S., Graf, M. S., Hentschel, Z., Krause, H., & Fleischmann, A. (2021). High honeybee abundances reduce wild bee abundances on flowers in the city of Munich. *Oecologia*, *195*(3), 825–831. https://doi.org/10.1007/s00442-021-04862-6

Roquer-Beni, L., Alins, G., Arnan, X., Boreux, V., García, D., Hambäck, P. A., Happe, A.-. K., Klein, A.-. M., Miñarro, M., Mody, K., Porcel, M., Rodrigo, A., Samnegård, U., Tasin, M., & Bosch, J. (2021). Management-dependent effects of pollinator functional diversity on apple pollination services: A response–effect trait approach. *Journal of Applied Ecology*, *58*(12), 2843–2853. https://doi.org/10.1111/1365-2664.14022

Russo, L., Park, M. G., Blitzer, E. J., & Danforth, B. N. (2017). Flower handling behavior and abundance determine the relative contribution of pollinators to seed set in apple orchards. *Agriculture Ecosystems & Environment*, *246*, 102–108. https://doi.org/10.1016/j.agee.2017.05.033

Soto, E. F., Pozo, R. A., Díaz-Siefer, P., Celis-Diez, J. L., & Fontúrbel, F. E. (2023). Vertebrate diversity in productive landscapes in Mediterranean Chile: The role of neighboring natural vegetation. *Global Ecology and Conservation*, *45*, e02508. https://doi.org/10.1016/j.gecco.2023.e02508

Stavert, J. R., Liñán-Cembrano, G., Beggs, J. R., Howlett, B. G., Pattemore, D. E., & Bartomeus, I. (2016). Hairiness: The missing link between pollinators and pollination. *PeerJ*, *4*, e2779. https://doi.org/10.7717/peerj.2779

Su, R. J., Dai, W. F., Yang, Y. L., Su, R., Dai, W., Yang, Y., Wang, X., Gao, R., He, M., Zhao, C., & Mu, J. (2022). Introduced honey bees increase host plant abundance but decrease native bumble bee species richness and abundance. *Ecosphere*, *13*(6), e4085. https://doi.org/10.1002/ecs2.4085

Tang, J., Quan, Q. M., Chen, J. Z., Wu, T., & Huang, S. Q. (2019). Pollinator effectiveness and importance between female and male mining bee (*Andrena*). *Biology Letters*, *15*(10), 20190479. https://doi.org/10.1098/rsbl.2019.0479

Velásquez-Trujillo, V., Betancurt-Grisales, J. F., Vargas-Daza, A. M., Lara, C. E., Rivera-Páez, F. A., Fontúrbel, F. E., & Castaño-Villa, G. J. (2021). Bird functional diversity in agroecosystems and secondary forests of the tropical Andes. *Diversity*, *13*(10), 493. https://doi.org/10.3390/d13100493

Vieli, L., Murúa, M. M., Flores-Prado, L., Carvallo, G. O., Valdivia, C. E., Muschett, G., López-Aliste, M., Andía, C., Jofré-Pérez, C., & Fontúrbel, F. E. (2021). Local actions to tackle a global problem: A multidimensional assessment of the pollination crisis in Chile. *Diversity*, *13*(11), 571. https://doi.org/10.3390/d13110571

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Vivallo, F. (2014). Taxonomic revision of the cleptoparasitic bee genus *Epiclopus* Spinola, 1851 (Hymenoptera: Apidae: Ericrocidini). *Zootaxa*, *3857*(1), 41–70. https://doi.org/10.11646/zootaxa.3857.1.2

Wan, N.-F., Fu, L., Dainese, M., Kiær, L. P., Hu, Y. Q., Xin, F., Goulson, D., Woodcock, B. A., Vanbergen, A. J., Spurgeon, D. J., Shen, S., & Scherber, C. (2025). Pesticides have negative effects on non-target organisms. *Nature Communications*, *16*(1), 1360. https://doi.org/10.1038/s41467-025-56732-x

Watson, J. C., Wolf, A. T., & Ascher, J. S. (2011). Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. *Environmental Entomology*, *40*(3), 621–632. https://doi.org/10.1603/En10231

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer.

Woodcock, B. A., Garratt, M. P. D., Powney, G. D., Shaw, R. F., Osborne, J. L., Soroka, J., Lindström, S. A. M., Stanley, D., Ouvrard, P., Edwards, M. E., Jauker, F., McCracken, M., Zou, Y., Potts, S. G., Rundlöf, M., Noriega, J. A., Greenop, A., Smith, H. G., Bommarco, R., … Pywell, R. F. (2019). Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nature Communications*, *10*(1), 1481. https://doi.org/10.1038/s41467-019-09393-6

Zattara, E. E., & Aizen, M. A. (2021). Worldwide occurrence records suggest a global decline in bee species richness. *One Earth*, *4*(1), 114–123. https://doi.org/10.1016/j.oneear.2020.12.005

Zhao, Y. Y., Feng, D. L., Yu, L., Zhao, Y., Feng, D., Wang, X., Chen, Y., Bai, Y., Hernández, H. J., Galleguillos, M., Estades, C., Biging, G. S., Radke, J. D., & Gong, P. (2016). Detailed dynamic land cover mapping of Chile: Accuracy improvement by integrating multi-temporal data. *Remote Sensing of Environment*, *183*, 170–185. https://doi.org/10.1016/j.rse.2016.05.016

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Pan trap arrangement in the field, showing how white, yellow and blue containers were placed among fruiting trees to capture floral visitors.

Figure S2. Examples of wild bees photographed using a photo-stacking system to obtain high-quality images.

Table S1. List of qualitative traits obtained from the literature, detailing the levels and abbreviations used for each trait category (nesting substrate, floral resources used and sociality).

Table S2. List of bee species collected during the 2-year field study.

Figure S3. Rarefaction-based diversity estimations for wild bee species in 2021.

Figure S4. Rarefaction-based diversity estimations for wild bee species in 2021 for (a) apple and (b) cherry orchards.

Figure S5. Rarefaction-based diversity estimations for wild bee species in 2022.

Figure S6. Rarefaction-based diversity estimations for wild bee species in 2022 for (a) apple and (b) cherry orchards.

Table S3. Individual species contribution to wild bee composition differences (based on a SIMPER test) between L and H in sweet cherry orchards in 2021.

Table S4. Individual species contribution to wild bee composition differences (based on a SIMPER test) between L and H in apple orchards in 2021.

Table S5. Individual species contribution to wild bee composition differences (based on a SIMPER test) between L and H in sweet cherry orchards in 2022.

Table S6. Individual species contribution to wild bee composition differences (based on a SIMPER test) between L and H in apple orchards in 2022.

Table S7. Relationships of functional diversity indeces (FDiv = functional divergence, FEve = functional evenness, FRic = functional richness, and RaoQ = Rao's quadratic index) with natural area percentage by bee sex and crop type for both sampling years.

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