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RESEARCH ARTICLE

Maintaining habitat diversity at small scales benefits wild bees and pollination services in mountain apple orchards

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Abstract

1. Landscape context influences wild bee abundance and diversity, alongside pollination-related services. Growing evidence supports the positive effects of landscape heterogeneity on bee diversity and fruit production for pollination-dependent crops in flatlands. However, little remains known about these relationships in mountainous environments where the landscape matrix surrounding crops is often more complex than in lowlands.
2. We conducted our study in apple orchards in South Tyrol, an Alpine region in Italy, using pan-traps, direct observations of visitation frequency and a pollinator exclusion experiment. We investigated the scale-dependent effects of landscape heterogeneity and other parameters on wild bee assemblages and the related pollination service they provide at five spatial scales (radius 100–2000 m).
3. We found that landscape heterogeneity positively affected the abundance and richness of wild bees, with the strongest effect at 500 m. We calculated a multidiversity index, reflecting the land-use intensity based on the species richness of vascular plants, grasshoppers, butterflies, birds and bats. We identified a positive relationship between this multidiversity index and wild bee richness. Additionally, we found that visitation rate of wild bees was negatively affected by crop cover and that abundance of honeybees did not influence wild bee visitation rate or reproductive success. Finally, reproductive success was positively related to semi-natural habitat cover.
4. Landscape heterogeneity should be maintained in apple orchards to continue to reap the benefits of vital pollination-related services. Diversification strategies should be implemented to promote habitat diversity at small scales, even in regions with more than 80% of (semi-)natural habitats.

KEYWORDS
bee diversity, fruit set, landscape heterogeneity, mountain farming, multidiversity index, pollination-dependent crops, scale dependence

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1 | INTRODUCTION

More than half of food crops worldwide require zoophilous pollination to develop fruits and seeds or to improve yield (Klein et al., 2007). However, for pollination-dependent crops, growers rely mainly on managed honeybees (*Apis mellifera* Linnaeus, 1758) (Garibaldi et al., 2013). Wild bees which visit fruit orchards and other cultivated crops are generally more efficient pollinators than honeybees (Garibaldi et al., 2013; Holzschuh et al., 2012; Macinnis & Forrest, 2019; Mallinger & Gratton, 2015). They provide free pollination services, reducing crop productivity vulnerability (Garibaldi et al., 2011). However, wild bees are threatened by agricultural intensification due to the degradation of the agro-natural landscape and the growing use of agrochemical compounds (Kremen et al., 2002). In particular, loss or degradation of semi-natural habitats (SNH) in farming landscapes is a major driver for pollinator decline worldwide (Ipbes, 2016).

In heterogeneous landscapes, greater crop alternation and semi-natural elements such as hedgerows, trees and grasslands sustain the presence of wild pollinators over time (Grass et al., 2016; Kremen et al., 2002) by providing nesting habitats and alternative foraging resources to transient mass-flowering crops (Andersson et al., 2014; Martins et al., 2015; Persson & Smith, 2011). They can also buffer the detrimental effects of pesticide residues (Andrione et al., 2016; Park et al., 2015; Samuelson et al., 2016; Williams et al., 2015). Hence, farming landscapes with a higher degree of SNH are generally associated with increased abundance and richness of wild bee pollinators (Kennedy et al., 2013), enhanced pollination service to crops (Garibaldi et al., 2011) and, in turn, increased crop production (Lautenbach et al., 2012).

Landscape composition and land-use intensity can significantly influence local biodiversity (Felipe-Lucia et al., 2020), and intensive agriculture has a greater impact than management type on pollinator service provision (Martins et al., 2015; Sprayberry et al., 2013). According to Allan et al. (2014), a measure of biodiversity of the whole ecosystem can represent a good indicator of habitat quality and integrity, reflecting the effects of land-use intensity. For this purpose, the authors develop a multidiversity index that integrates the richness of species of various groups of organisms.

Growing evidence supports that the capacity of agricultural landscapes to maintain biodiversity is pivotal in achieving balanced functionality and, thus, providing ecosystem services (Dainese et al., 2019; Tilman et al., 2014). Therefore, the structure of the landscape surrounding agricultural fields plays an important role in supporting pollinator communities and pollination services. Empirical evidence is derived mainly from flatlands characterised by large fields and surrounded by scattered SNH (e.g. Martin et al., 2019). In contrast, mountain farming systems have relatively smaller plots of cultivated land, usually concentrated in valleys, surrounded by a mosaic of forests and meadows arranged along the mountainside. In this context, the positive effect of landscape characteristics on wild bees visiting crops may be less evident compared to more simplified agro-ecosystems due to the occurrence of habitats with higher biodiversity, and therefore, greater potential for spillover of pollinators from non-crop habitats to crops (Tscharntke et al., 2012). Additionally, pollinator response to landscape complexity is expected to be conditional on scale. (Chaplin-Kramer et al., 2011; Martin et al., 2019).

We conducted our study in a mountain region with up to 80% cover of natural and semi-natural habitats to investigate the scale-dependent effects of landscape context on wild bee assemblages and related pollination services they provide in a mountain region. In particular, we selected intensively cultivated apple orchards distributed along a valley-range landscape using a gradient from apple-dominated to a more heterogeneous matrix (Figure 1). We examined the abundance and diversity of wild bees in apple orchards, their visitation rate to apple flowers and the effects of pollinators on apple fruit set using an exclusion experiment.

We hypothesised that:

1. the abundance and diversity of wild bees along with pollination-related services increase with (i) landscape heterogeneity and (ii) SNH cover, and decrease with (iii) crop cover and (iv) honeybee abundance;
2. landscape heterogeneity, crop cover or SNH cover, despite explaining complementary processes, have a scale-dependent impact on wild bees and pollination services; and
3. a synthetic index of total ecosystem biodiversity reflecting the effects of landscape structure and land-use intensity can predict wild bee assemblages and their pollination services in apple orchards (e.g. multidiversity index).

2 | MATERIALS AND METHODS

2.1 | Study area

In South Tyrol (Central Alps, Italy), apple production is an integral component of agriculture. With 18,000 hectares of farmland, this region supports one of the largest orchard areas in Europe, supplying half of the Italian apple market and up to 10% of the European one (ISTAT, 2019). Farms are typically small, with an average field size per landowner of 2.5 ha, often extending over multiple plots of land. The region is also characterised by a high coverage of natural habitats and SNH (82.3%) (Anderle et al., 2022) surrounding apple orchards in the valleys. However, in recent decades, the landscape has been dramatically homogenised in the valleys bottom, creating large areas covered by apple monoculture. Some apple orchards surrounded by a more heterogeneous matrix, composed of finely interspersed SNH, are still present on the valley-range scale (100 to 500 m from the valley centre). On larger spatial scales (moving 1–2 km from the bottom valley to the mountainsides), the cover of SNH increases considerably.

2.2 | Study design

From the pool of apple orchards monitored within the framework of the project “Biodiversity Monitoring South Tyrol” (Hilpold

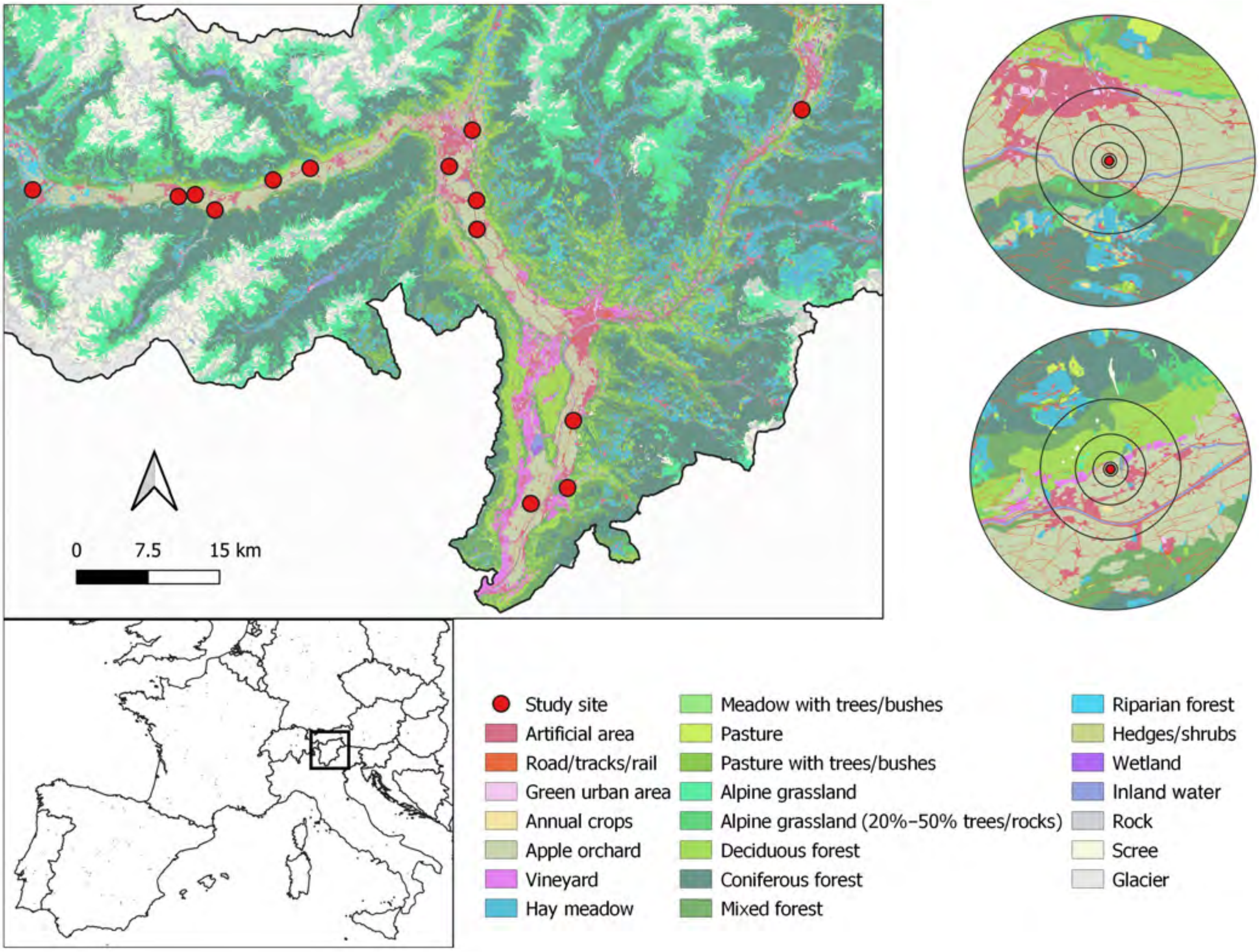

FIGURE 1 Section of the autonomous province of South Tyrol in Italy with the study area and sites. On the right, two study sites show land cover mapping. Each buffer represents a different spatial extent from the centre of the apple orchard (100, 250, 500, 1000, 2000 m). Moving toward larger scales, the land covered with semi-natural habitats (SNH) reaches similar proportions among locations. In this example, the top right site has a proportion of SNH of 0% at 250 m and 47% at 2000 m. For the one below, the proportion of SNH at the same scales is 28% and 56%, respectively.

et al., 2023) ($n = 20$, monitored in 2019 and 2020), we selected 14 apple orchards distributed along a gradient of apple orchard cover in the landscape (using a buffer of 500 m around each site) (Figure 1 and Appendix S2; Appendix S1 for coordinates of locations and information on the crop production system). At this scale, the proportion of apple orchards ranged from 15% to 92%. This gradient was strongly negatively correlated with the SNH cover ($r = -0.73$). The mean distance between the apple orchards was 8.1 ± 9.5 km (mean ± standard deviation [SD]), with a minimum of 1.8 km. A polygon map based on regional land use maps (Anderle et al., 2022) was used to calculate landscape parameters based on 21 land use categories (Appendix S2) in ArcGIS 10.8.1 (ESRI, 2011) and R Statistical Software v. 3.3.0 (RStudio Team, 2020). Landscape parameters were calculated at five different radii from the centre of the fields: 100, 250, 500, 1000 and 2000 m, representing a nested set of spatial scales. Our study defines landscape scales with a radius from 100 to 500 m as ‘small scale’ and those with a radius from 1000 to 2000 m as ‘large scale’. We derived a landscape heterogeneity index at each spatial scale using the Shannon diversity of all the land cover types considered (Forman, 1995). SNH encompassed grasslands, meadows, pastures, wetlands, forests, hedges and shrubs. The first four land cover groups were defined as open SNH, and the remaining three were defined as closed SNH. Crop cover included annual crops, vineyards and orchards (Appendix S2). For the proportion of SNH and crop cover, we aggregated areas (ha) covered by these categories and then quantified the proportion for each spatial scale.

The multidiversity index was used as a proxy for land-use intensity (Allan et al., 2014) based on species richness measures collected in the same orchards by the “Biodiversity Monitoring South Tyrol” in 2019 and 2020 (BMS, 2023). The species richness measures were the number of species of vascular plants, grasshoppers, butterflies, birds and bats. We rescaled the data (minimum–maximum normalisation) within each taxonomic group and obtained a standardised range between 0 and 1. Normalisation prevented us from assigning greater importance to species-rich groups (i.e. vascular plants). We then aggregated by summing the rescaled values of each taxonomic group per site.

2.3 | Pollinator sampling

Data were collected during the apple-tree blossoming period (14 April–3 June 2021). At each site, we placed nine UV-bright white pan-traps to primarily attract wild bees who visit apple flowers (500mL plastic saucer pots from Geli GmbH with an internal diameter of 14.5cm, coloured with a white "Sparvar Leuchtfarbe" from Spray-Color GmbH). These traps were arranged along three adjacent rows of trees in the centre of the orchards. We carried out three rounds of sampling: beginning, full and end of mass flowering (Appendix S1 for details).

Trap catches were used to link the diversity of bee species (species richness, Shannon index and Simpson index) with landscape parameters and the multidiversity index. Shannon and Simpson indices were used to discern potential disparities between indices with different sensitivity to rare species. The limited workforce and the brief apple-tree blossoming period prevented us from conducting transect walks, the preferred method to observe which insect species provide pollination services to crops (Gibbs et al., 2017; O'Connor et al., 2019). Instead, we used visitation rate to characterise the pollination provided to apple flowers at the group level (wild bee or honeybee).

2.4 | Visitation rate

The visitation rate of honeybees and wild bees was expressed considering the overall number of visits per 100 flowers during 1hour, as proposed by Garibaldi et al. (2020). In each orchard, four apple trees were selected from the rows where pan-traps were placed (Appendix S1 for details). For each tree, we counted all visible flowers and recorded all pollinators visiting apple flowers for 5min (a total of 20min per site). For the second and final round of observations, 13 of the initially selected trees were no longer in flower, so new apple trees were chosen to quantify the insect visitation rate. For this reason, we calculated an average value per site.

2.5 | Pollination services

We conducted a pollinator exclusion experiment on three trees per orchard to estimate pollination services. The trees were chosen among those in pan-trap rows. For each tree, we covered one branch with fine mesh net to exclude insect pollination and selected one free branch as control (Appendix S1 for details). The nets were placed when the flowers were closed but distinguishable for counting ("pink bud" phenological stage). We counted the initial number of open flowers and the number of developed green fruits (fruit size up to 20mm). We separately calculated the fruit set as the ratio between the number of fruits and the initial number of flowers for open and closed branches. For each tree, we derived a standardised index of plant reproductive success, analogous to a response ratio (RR; Hedges et al., 1999), as the natural logarithm of the ratio between the fruit set for the open branch and the closed branch, as follows:

$$\mathrm{RR}_{\text{fruit set}} = \ln\left(\frac{\mathrm{Nfruits}_{\text{open}} / \mathrm{Nflowers}_{\text{open}}}{\mathrm{Nfruits}_{\text{bagged}} / \mathrm{Nflowers}_{\text{bagged}}}\right)$$

We used this ratio to determine the effect size over the fruit set. Positive values of reproductive success indicate a higher fruit set in open branches than in bagged ones.

2.6 | Data analysis

Data files analysed during the current study are available on Zenodo (Zanini, 2024). Statistical analyses were performed in Rstudio 4.1.1 with a significance level of $p < 0.05$. We built a series of models to test the effect of seven independent variables (landscape heterogeneity, crop cover, SNH cover, open SNH cover, closed SNH cover, multidiversity index and honeybee abundance) on eight dependent variables (richness and abundance of wild bees; Shannon and Simpson indices based on the diversity of wild bees; visitation rate of wild bees and honeybees; and reproductive success). We analysed each variable separately to account for the collinearity of independent variables (Appendix S3–A). Similarly, we separately analysed the five nested spatial scales (radius from 100 to 2000m). Regarding pollination services, we tested the effect of wild bee richness, abundance, visitation rate and Shannon and Simpson indices based on the diversity of wild bees on reproductive success. Furthermore, we assessed whether the fruit set statistically differed between the open pollination and pollinator exclusion treatment by applying the non-parametric Mann–Whitney *U* test.

The statistical models were built accounting for the different sampling designs and data distribution. Wild bee species richness was analysed using generalised linear mixed-effects models (GLMMs) with Poisson distribution using the R package "lme4" (Bates et al., 2015) and site ID as a random factor. Wild bee abundance (log-transformed) and reproductive success were analysed using linear mixed-effects models (LMMs) with normal distribution and site ID as a random factor. We quantified one value per site for Shannon and Simpson indices of wild bee diversity and the log-transformed visitation rate and used simple linear models with normal distribution. Given the sampling intensity, calculating these variables per site per sampling round would lack representative values. To compare the different independent variables and spatial scales, we standardised fixed predictors to a mean of 0 and a difference of 1, using the "standardise" function within the "arm" R package. (Gelman et al., 2013). The results were plotted using the "visreg", "sjPlot" and "ggplot2" R packages (Breheny & Burchett, 2017; Lüdecke, 2018; Wickham, 2016), while model residuals were checked for uniformity with the “DHARMa” R package (Hartig & Hartig, 2017). Other model requirements (such as a posterior predictive check, overdispersion, homogeneity of variance, normality of the residuals and random effects) were evaluated using the ‘performance’ R package (Lüdecke et al., 2021). Models were then compared using the R^2 (adjusted). For GLMMs, we used the variance explained by the fixed term of the model (marginal R^2, R2m) as a measure of R^2 (Nakagawa & Schielzeth, 2013).

To account for the differing number of pan-traps per site and, therefore, sampling effort, we calculated the incidence frequencies of wild bee species per site based on the rarefaction technique. We interpolated the data to the lowest number of traps collected at a site (18 traps) using the “iNEXT” R package (Hsieh et al., 2016). Next, we examined whether the relationships would change sign or whether the model estimates would enhance model fit (R^2 adj.) compared to the linear models that did not undergo the rarefaction process.

3 | RESULTS

3.1 | Effects of local and landscape factors on the diversity and abundance of wild bees

In total, 3230 bees were caught in pan-traps (2438 honeybees and 792 wild bees), and 55 species of wild bees were identified (Appendix S4). The most captured genera were *Andrena* (70%) and *Lasioglossum* (20%), with 17 *Andrena* species and 14 *Lasioglossum* species (31% and 25% of the total species richness). The average number ± SD of bees caught per pan-trap was 9.6 ± 9.9 (7.2 ± 8.5 for honeybees and 2.3 ± 3.7 for wild bees), while the mean number of wild bee species considering all sites together was 11.9 ± 5.6.

We summarised the results, presenting them for the ‘small scale’ (radius from 100 to 500 m) and the ‘large scale’ (radius from 1000 to 2000 m; Table 1). Wild bee species richness was negatively associated with crop cover and positively with landscape heterogeneity (Figure 2). The strength of landscape effects was greater at small spatial scales than at larger spatial scales (e.g. the magnitude of the effects tended to increase from 100 to 500 m and decrease from 500 to 2000 m; Appendix S5-1).

Wild bee abundance was negatively related to crop cover and positively to landscape heterogeneity. The strongest relationships were found at smaller scales, but the model fit (R^2) showed less pronounced differences between scales (Table 1, Appendix S5-1). Considering SNH cover, we found a significant positive association with both species richness and abundance of wild bees only on large scales. These variables were not associated with open SNH, whereas they were with closed SNH, especially at large scales (Table 1; Appendix S5-1).

To assess the impact of the loss of pan-traps on the examined relationships and model performance, we conducted a comparative analysis between models using both the non-rarefied and rarefied datasets. Since the latter accounted for the sampling effort at the site level, we aggregated the non-rarefied data to the site level too. Our findings revealed consistent results between the rarefied and non-rarefied datasets, indicating that the loss of pan-traps did not significantly change our outcomes. Notably, the linear regression models exhibited substantial improvements in explanatory power across the landscape scales when compared to mixed-effects models (Appendix S6).

Shannon and Simpson diversity indices were not significantly related to landscape variables except for the Shannon index and landscape heterogeneity at 500 m. However, the same indices recalculated after rarefaction showed significant positive relationships with landscape heterogeneity and a negative relationship with crop cover with a general improvement of model fit at all spatial scales, particularly at small scales (Appendix S6-3). Additionally, SNH cover was linked to the Shannon index, but only at large scales and not with the Simpson index. Similarly, none of the indices were significantly related to open SNH, whilst closed SNH was a good predictor, especially for the Shannon index at large scales (Appendix S6-3).

Wild bee diversity (species richness, Shannon and Simpson index) and abundance were not influenced by honeybee abundance from pan-traps in any of the models, even after rarefaction (Table 2, Appendices S6-2 and S6-4). Instead, they showed a positive relation with the multidiversity index (Figures 2 and 3; Table 2, Appendices S6-2 and S6-4). This index and landscape heterogeneity exhibited a strong positive association at each scale, underscoring the potential influence of landscape heterogeneity on local biodiversity across varying spatial scales (Appendix S3-B).

3.2 | Effects of local and landscape factors on flower visitation rate

The visitation rate of wild bees was not influenced by landscape heterogeneity, while it was negatively affected by crop cover at 500 and 1000 m spatial scales. Instead, SNH cover was a good predictor of the visitation rate of wild bees at both small and large scales (except for the 100 m scale; Figure 4; Appendix S5-1). The cover of open SNH did not explain the visitation rate for any of the pollinator groups studied. On the contrary, closed SNH positively influenced small and large scales for wild bees (Appendix S5-1).

We found no significant relationship between wild bee abundance and their visitation rate, but we did find a positive relationship between honeybee abundance and their visitation rate (Appendix S5-3). On average, honeybees visited apple flowers 33 times more frequently than wild bees. However, the abundance of honeybees did not significantly affect the flower visitation rate of wild bees. Similarly, the multidiversity index did not influence wild bee visitation rate (Table 2).

3.3 | Effects of local and landscape factors on pollination services

The fruit set was significantly lower for branches with pollinator exclusion ($F_{1,82} = 14.54$, $p < 0.001$; Figure 5). Due to management

TABLE 1 All model estimates can be found in Appendix S5-1.

	Landscape scales			
	Small scale (100, 250, 500 m)		Large scale (1000, 2000 m)	
	Estimate	R^2	Estimate	R^2
Species richness				
Crop cover	− (3)	[0.28–0.42]	− (2)	[0.31–0.34]
Landscape heterogeneity	+ (3)	[0.37–0.54]	+ (2)	[0.32–0.43]
SNH cover	ns (3)	/	+ (2)	[0.26–0.31]
Open SNH	ns (3)	/	ns (2)	/
Close SNH	+2; ns (1)	[0.27–0.32]	+ (2)	[0.33–0.46]
log (Abundance + 1)				
Crop cover	− (3)	[0.18–0.31]	− (2)	[0.19–0.25]
Landscape heterogeneity	+ (3)	[0.25–0.39]	+ (2)	[0.19–0.27]
SNH cover	ns (3)	/	+ (2)	[0.21]
Open SNH	ns (3)	/	ns (2)	/
Close SNH	+2; ns (1)	[0.28–0.29]	+ (2)	[0.30–0.32]
log (Visitation rate + 1) wild bees				
Crop cover	− (1); ns (2)	[0.31]	− (1); ns (1)	[0.26]
Landscape heterogeneity	ns (3)	/	ns (2)	/
SNH cover	+ (2); ns (1)	[0.50–0.62]	+ (2)	[0.25–0.46]
Open SNH	ns (3)	/	ns (2)	/
Close SNH	+2; ns (1)	[0.34–0.41]	+ (2)	[0.32–0.37]
Reproductive success				
Crop cover	ns (3)	/	ns (2)	/
Landscape heterogeneity	ns (3)	/	ns (2)	/
SNH cover	+ (1); ns (2)	[0.23]	ns (2)	/
Open SNH	ns (3)	/	ns (2)	/
Close SNH	ns (3)	/	ns (2)	/

Note: Here, we report under 'estimate' the sign of relationships with the number of significant and non-significant models under small and large spatial scales. Under "R^2", we present the range of the goodness of fit of the models.

practices that reduce the number of flowers and fruits in the initial stage and natural pruning of the trees, we observed that on average 12% of the initial flowers remained on open branches, while only 3% persisted on bagged branches.

We found no significant relationships between reproductive success and landscape heterogeneity, crop cover and open/closed SNH cover at any spatial scale (Table 1). However, it was weakly but positively related to SNH cover at 500 m (Appendix S5-1). Additionally, we found a positive influence of both wild bee Shannon and Simpson diversity indices on reproductive success (Appendix S5-2).

4 | DISCUSSION

In this study, we aimed to test three hypotheses regarding the effects of landscape factors on wild bee assemblages and pollination services to apple orchards located in a mountain region. Our findings provide new insights, however, the outcomes only partially back the hypotheses. Our results strongly support the hypothesis that wild bee abundance and diversity are positively associated with landscape heterogeneity, SNH cover and multidiversity index. Additionally, we found wild bee abundance and diversity negatively related to crop cover. These relationships are scale-dependent as the impact of the three landscape indices (multidiversity is non-dimensional) varies with scale. However, the evidence concerning the relationships between these landscape factors and pollination services is less conclusive. We found that the proportion of SNH has a positive effect on wild bee visitation rate and reproductive success, whereas landscape heterogeneity and multidiversity index show no discernible influence. In contrast to our hypothesis, we detected no direct negative impact of honeybee presence on wild bee diversity, abundance, or visitation rate. In subsequent sections, these aspects are discussed further.

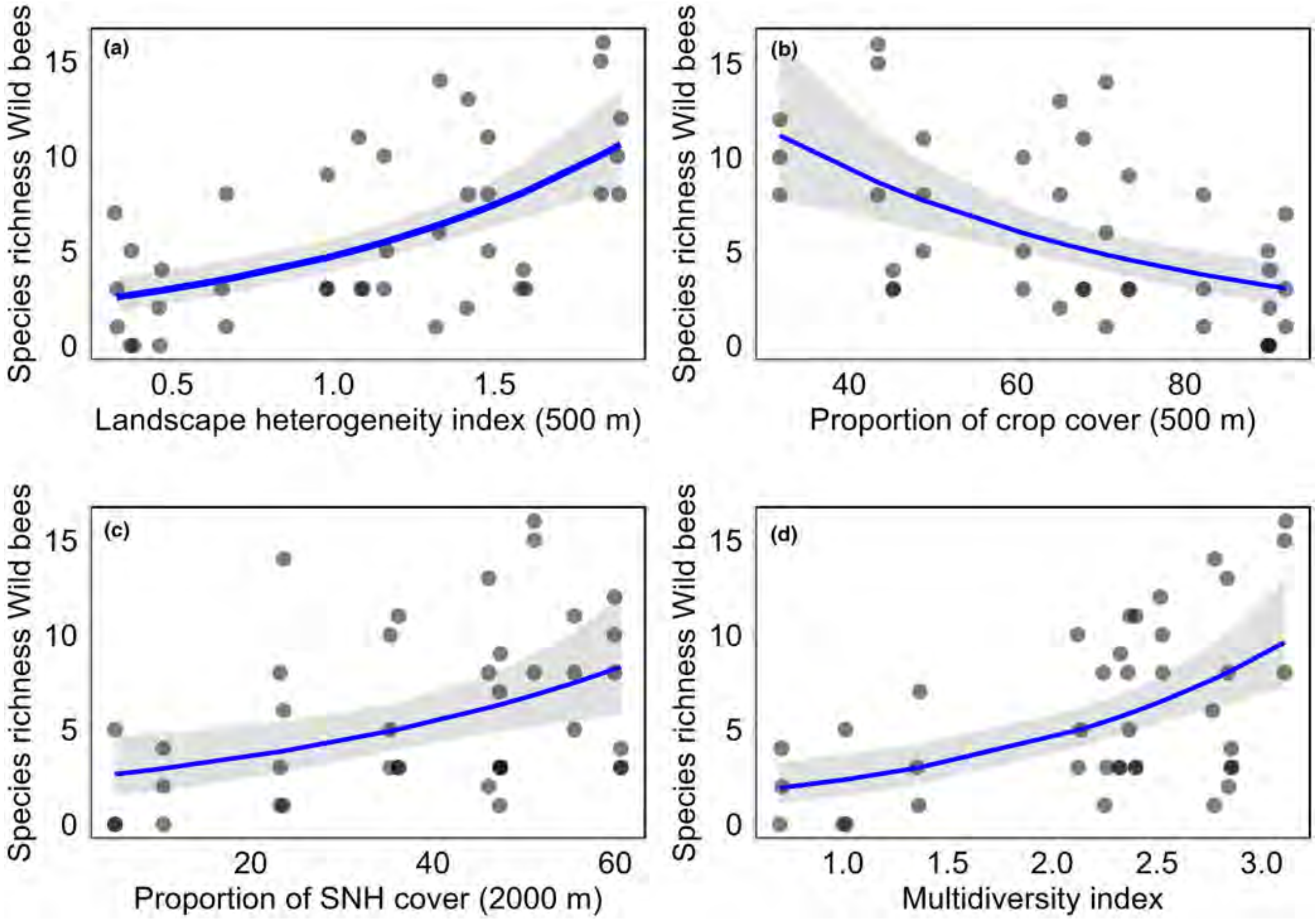

FIGURE 2 Plots showing the relationships between wild bee species richness and (a) landscape heterogeneity, (b) proportion of crop cover, (c) proportion of semi-natural habitats cover and (d) multidiversity index. The fitted lines and 0.95 confidence intervals are estimates from GLMMs. For landscape parameters (a–c), we reported the spatial scale (radius from the centre of the apple orchards) with the best marginal R^2.

TABLE 2 Model estimates of wild bee species richness and abundance, visitation rate, and reproductive success in relation to the multidiversity index and the number of honeybees.

	Estimate	R^2
Species richness		
Multidiversity index	0.96*** [0.53–1.40]	0.51
N honeybees	ns	/
log (Abundance + 0.1)		
Multidiversity index	2.03** [1.03–3.03]	0.32
N honeybees	ns	/
log (Visitation rate + 1) wild bees		
Multidiversity index	ns	/
N honeybees	ns	/
Reproductive success		
Multidiversity index	ns	/
N honeybees	ns	/

Note: Confidence intervals are reported in brackets, and significance levels are indicated as follows: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$. We used GLMMs with Poisson distribution for species richness; under “R2”, we reported the marginal R^2. We present model estimates from linear models with normal distribution and adjusted R^2 for the visitation rate, while for abundance and reproductive success, we used LMM models.

4.1 | Effects of landscape scales and landscape heterogeneity

While research has shown that habitat coverage and diversity in farmlands support wild bee populations (Kennedy et al., 2013; Pufal et al., 2017), studies conducted in mountain regions are lacking despite their typically higher complexity than flat regions. Concurrently, there is growing evidence that these positive effects are scale-dependent as they are bound to drivers acting at local and landscape scales. (Dainese et al., 2015; Hedges et al., 1999; Ricketts et al., 2008) This includes the seasonality of floral resources and flower richness (Blaauw et al., 2014; Scheper et al., 2013) as well as the foraging distances that pollinators can cover (Danner et al., 2016; Wood et al., 2015). Other common approaches, such as distance to nature or forest edge, have proven reliable predictors of pollinator presence and pollination services but cannot show scale dependencies (Bailey et al., 2014; Garibaldi et al., 2011). The positive relationships between landscape heterogeneity and wild bee assemblages that we observed highlight the importance of having a heterogeneous landscape matrix both at small and large spatial scales.

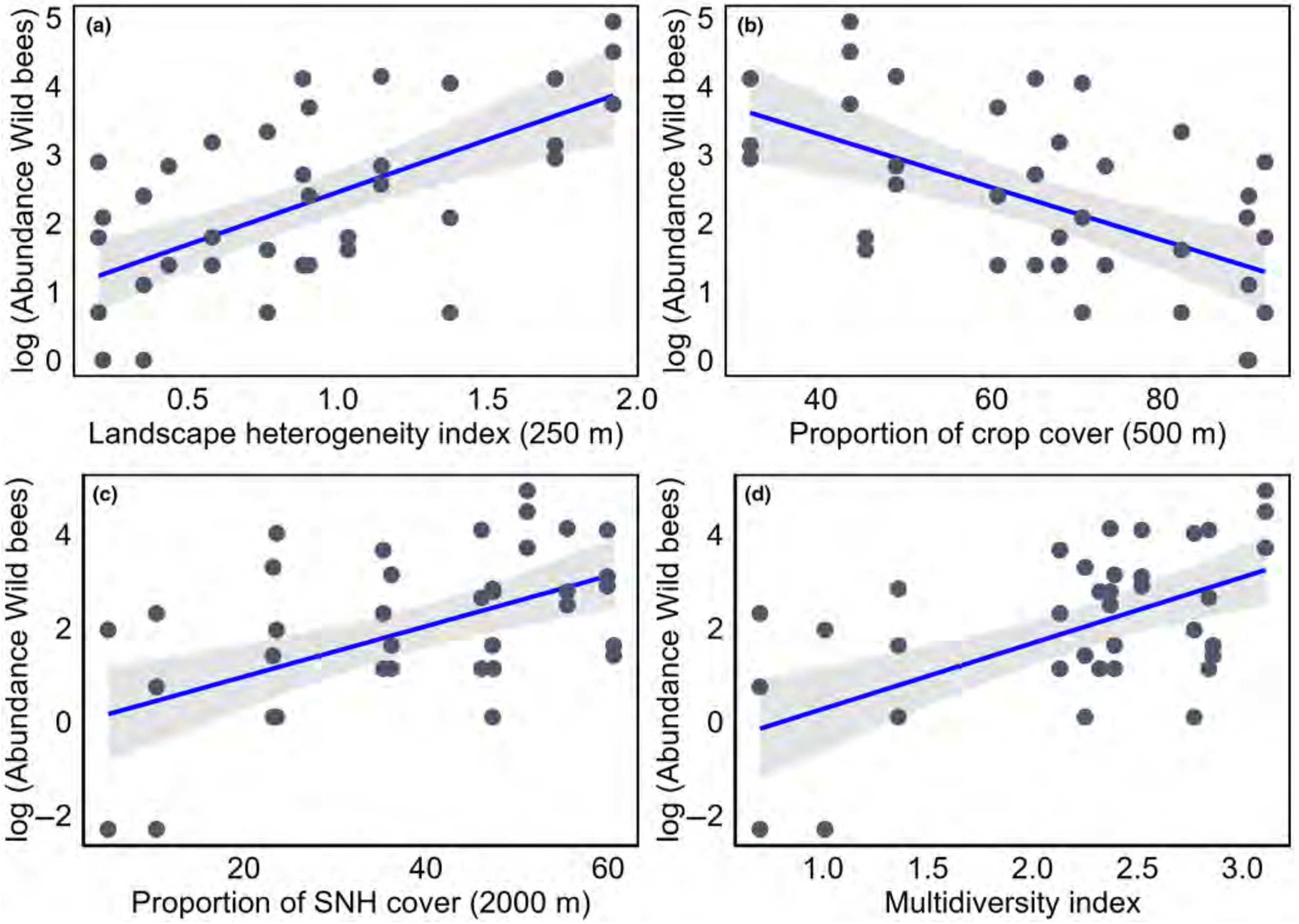

FIGURE 3 Plots showing the relationships between the abundance of wild bees and (a) landscape heterogeneity, (b) proportion of crop cover, (c) proportion of semi-natural habitats cover and (d) multidiversity index. The fitted lines and 0.95 confidence intervals are LMM estimates. For landscape parameters (a–c), we report the spatial scale (radius from the centre of the apple orchards) with the best marginal R^2.

Contrary to our expectations, landscape heterogeneity had no influence on the visitation rate of wild bees and reproductive success. A heterogeneous matrix in the landscape may offer suitable nesting sites and diverse foraging resources, contributing to the abundance and bee diversity. However, this does not imply that more wild bees will visit apple flowers. Despite our efforts to attract primarily wild bees that would potentially feed on apple flowers, our white pan-traps also captured oligotrophic species that do not typically feed on *Rosaceae*. This likely explains the absence of a significant relationship between the abundance of wild bees and their visitation rate.

Landscape parameters that showed a greater influence on pollination services are SNH cover and, to a lesser extent, crop cover.

4.2 | Effects of SNH and crop cover

The landscape heterogeneity index indirectly measures landscape diversity and considers non-natural land cover types such as green urban areas. Using SNH cover as a proxy of landscape complexity, artificial habitats were instead excluded (Bartual et al., 2019; Schirmel et al., 2018). The abundance and diversity of wild bees were positively influenced by SNH cover but only at a large scale. This result could be caused by low occurrence of these habitats on a small scale (only 4 of 14 sites had more than 10% cover of SNH), while at 2000 m, only one site had less than 10% of SNH. However, not all types of SNH meet the needs of generalist and specialist bee species. By distinguishing the SNH habitats in open and closed SNH, we found the richness of wild bee species was higher in apple fields surrounded by forests (closed SNH) than grasslands (open SNH). A similar result was reported in a study in Trentino, a region with comparable geographical characteristics to our study area (Marini et al., 2012).

Proportion of crop cover is often used as a measure of landscape simplification (Meehan et al., 2011; Tscharntke et al., 2005). Although crop cover was strongly negatively related to landscape heterogeneity, we kept both variables because the correlation decreased, moving toward large scales. Furthermore, most agricultural land constituting the ‘crop cover’ is cultivated with apple trees, thus a pollinator-attracting crop (Appendix S2). By running separate models, we could observe how these landscape parameters have influenced wild bees, honeybees and pollination services at multiple spatial scales. For example, crop cover was a better

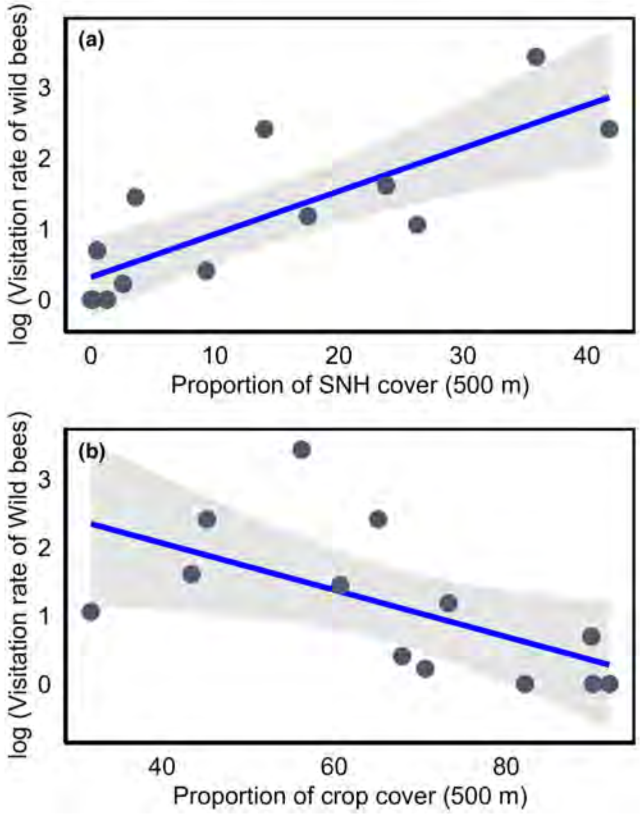

FIGURE 4 Plots showing the relationships between the visitation rate of wild bees and (a) the proportion of semi-natural habitats cover, (b) the proportion of crop cover. The fitted lines and the 0.95 confidence intervals are linear model estimates run with data at the site level. We report the spatial scale with the best-adjusted R^2.

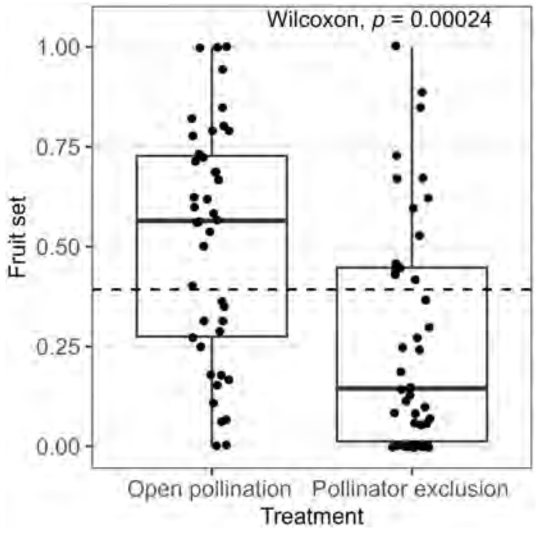

FIGURE 5 Box plot showing fruit set in open pollination and pollinator exclusion treatments. Solid black lines indicate the median values of 0.57 in open pollination and 0.15 in pollinator exclusion. The *p*-value is shown in the upper right corner of the graph.

predictor than landscape heterogeneity for visitation rate (although SNH cover was the best at all scales). We believe that season and, in this case, the mass flowering of apple trees changed wild bees' presence and foraging patterns (Bänsch et al., 2020). In our study, wild bees are strongly influenced by landscape heterogeneity. We expect that wild bees will be increasingly drawn to SNH after the apple-tree blossom, representing the available foraging resource at that time, as found by previous research (Lajos et al., 2021; Maurer et al., 2022).

4.3 | Effects of multidiversity index and honeybee abundance

Since one of the leading causes of biodiversity decline is habitat loss or degradation driven by land-use intensity (Hanski, 2011), we tested a multidiversity index that reflects the quality and integrity of the local habitats and surrounding landscapes (Dainese et al., 2015). We found that wild bee diversity covaries with the multidiversity index, suggesting that habitat quality and integrity may be another critical factor controlling wild bee assemblages. Similar results were also found in other crop systems. For instance, agricultural diversification practices and agri-environmental schemes can increase local biodiversity and positively influence related ecosystem services (Tamburini et al., 2020; Tschumi et al., 2016). However, multidiversity index did not predict wild bee pollination services. Fine-scale data on pollinator nesting resources and forage availability may offer more reliable insights to predict pollination provision (Lonsdorf et al., 2009).

Concerning honeybees, our pan-traps captured a relatively high number of them. Other studies have shown that honeybees can affect wild bees in terms of pathogen transmission, behaviour during pollination, and competition for forage (Iwasaki & Hogendoorn, 2022). In our study, honeybee abundance had no effect on the diversity or abundance of wild bees. There is increasing evidence that competitive exclusion between managed and wild bees appears variable over time and is reported to be negligible or absent when foraging resources are copious, such as during mass flowering of crops (Wignall et al., 2020). Crop cover was negatively related to honeybees and wild bee density, potentially indicating a dilution effect, as Holzschuh et al. (2016) also observed. Our analyses do not exclude that competition for floral resources could occur during other season periods (González-Varo & Vilà, 2017; Ropars et al., 2022). Another consideration is that we placed the pan-traps away from the orchard's edges to maximise the chances of capturing species that visit apple flowers, likely selecting wild bee species unaffected by high honeybee abundance. Despite the high number of honeybees in the studied orchards, there is no evidence that their visitation rate or abundance interfered with that of wild bees.

We found no link between reproductive success and the visitation rate of the pollinator groups studied. Additionally, wild bee species richness, honeybee abundance and landscape variables (except SNH cover at 500 m) were unrelated to reproductive success. This is possibly due to fewer visits by wild bees to apple flowers compared to honeybees and the ubiquitous presence of high densities of honeybees in our study sites. Földesi et al. (2016) also reported a similar outcome in apple orchards.

Numerous publications found evidence that wild bee species richness rather than honeybee abundance is positively related to fruit and seed set (Blitzer et al., 2016; Garibaldi et al., 2013; Mallinger & Gratton, 2015). We observed a weak but analogous trend between reproductive success (derived from fruit set) and Shannon and Simpson indices. Finally, Ramírez and Davenport (2013) reported that insect-mediated apple pollination is crucial for fruit set, which our results support through observation of the fruit set in the pollinator exclusion experiment and reproductive success.

5 | CONCLUSIONS

Our results confirm that a heterogeneous landscape structure is essential to maintain the richness of wild bee species and related pollination services. The presence of SNH is necessary to increase landscape heterogeneity, even on a small scale, regardless of the naturalness of the region. Our case study in a mountainous region shows that the heterogeneity of the landscape on a large scale (1000–2000 m) is not enough to benefit from pollination services provided by pollinators other than honeybees. Croplands with higher habitat diversity on a smaller scale (100–500 m) host a higher abundance and diversity of wild bees and, therefore, could potentially enhance fruit set. Overall, the positive impact of these landscape factors is consistent with findings in flatlands but tends to be more influenced by scale-dependent effects (Martins et al., 2018; Neira et al., 2024; Park et al., 2015). We emphasise the need for context-specific insights to contribute to understanding bee ecology and pollination services.

Wild bees that visit crops only account for a small fraction of pollinating insects' diversity. Conservation of these wild bees alone (2% of wild pollinators, according to Ipbes (2019)) cannot curb global pollinator decline (Kleijn et al., 2015). However, raising awareness of this issue in agricultural landscapes, where economic interests can combine with biodiversity conservation measures, represents a first step toward the implementation of an 'ecological intensification' (Kleijn et al., 2019) with a reduction in field sizes without loss of crop yields (Magrach et al., 2022). This work constitutes an initial point to develop tailored guidelines for local policies, fostering future initiatives to conserve and improve the current state. From a management perspective, maintaining landscape heterogeneity in mountain farming systems is crucial for sustaining biodiversity (not just pollinators) and enhancing the resilience of crop production, which benefits from the associated ecosystem services.

AUTHOR CONTRIBUTIONS

Sebastiano Zanini conceived and designed the study, performed the experiment, collected data in the field, analysed the data, prepared figures and tables, and authored the manuscript drafts. Matteo Dainese conceived and designed the experiments, supervised the data analysis and reviewed the drafts of the article. Timo Kopf identified wild bees at the species level. Georg Leitinger reviewed the drafts. Ulrike Tappeiner contributed to the study design and reviewed drafts. All authors critically contributed to the drafts and gave their final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data files analysed during the current study are available on Zenodo https://doi.org/10.5281/zenodo.10046644 (Zanini, 2024).

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SUPPORTING INFORMATION

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

Appendix S1. Table S1. Coordinates in (EPSG:4326 WGS84) of the studied apple orchards.

Appendix S2. Table S2-A. Proportions of land cover data calculated for each land use class at the studied distances (radii) from the centre of the apple orchards.

Table S2-B. Land cover proportions calculated at the studied distances (radii) from the centre of the apple orchards.

Appendix S3. Figure S3-A. Correlation matrix.

Table S3-B. The correlation values between the multidiversity index and the landscape heterogeneity index at the studied scales (radius from the centre of the apple orchards).

Appendix S4. Table S4. List of wild bee species collected with white pan-traps.

Appendix S5. Table S5-1. Model estimates at different landscape scales for the richness and abundance of wild bee species, the visitation rate, and reproductive success.

Table S5-2. Model estimates (LMM models) for the reproductive success.

Table S5-3. Model estimates of the relationships between wild bee abundance and wild bee visitation rate and between honeybee abundance and honeybee visitation rate.

Table S6-1. Model estimates at different landscape scales for wild bee species richness.

Table S6-2. Model estimates for wild bee species richness in relation to the multidiversity index and the honeybee abundance.

Table S6-3. Model estimates at different landscape scales for Shannon and Simpson's indices calculated over our species richness data.

Table S6-4. Model estimates for wild bee Shannon and Simpson diversity in relation to the multidiversity index and the number of honeybees.

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