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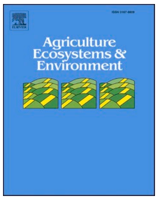

Disentangling biodiversity and temperature effects on bees and pollination services in mountain agroecosystems

Sebastiano Zanini [a,b], Matteo Dainese [c,*], Lisa Obwegs [a,b], Elia Guariento [b], Timo Kopf [d], Matteo Anderle [b], Georg Leitinger [a], Ulrike Tappeiner [a,b]

[a] *Department of Ecology, Universität Innsbruck, Innsbruck, Austria*
[b] *Institute for Alpine Environment, Eurac Research, Bolzano, Italy*
[c] *Department of Biotechnology, University of Verona, Verona, Italy*
[d] *Freelance Biologist, Innsbruck, Austria*

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ABSTRACT

Pollinating insects are declining globally due to habitat loss, agricultural intensification, and climate change. Wild bee loss threatens the delivery of pollination services essential for agriculture and ecosystem stability. Our study examined how multidiversity, reflecting the richness of four functional groups and indirectly indicating land-use intensity, together with temperature as a climatic proxy, shapes wild bee diversity and pollination services in mountainous agroecosystems. We selected 24 farmland sites in South Tyrol (NE Italy) spanning independent gradients of multidiversity and temperature. We used pan traps to quantify wild bee species richness and abundance of wild and managed bees. Additionally, we performed a phytometer experiment using radish and strawberry model plants to assess wild bee visitation and the resulting seed and fruit production. Our results showed that wild bee diversity and visitation rates increased with multidiversity, reflecting the strong influence of land-use intensity. In contrast, temperature had limited direct effect on wild bee diversity, partly because floral resources were not a limiting factor. Visitation rates varied with multidiversity: honeybee visitation rates dominated in low-diversity landscapes, while wild bee visitations peaked in more diversified landscapes. The pollinator exclusion experiment on strawberries revealed that higher temperatures reduced fruit weight more in the absence of insect pollination, suggesting an interaction between climate and pollination provision. Overall, our results findings highlight the complex interplay betweenbiotic and abiotic factors shaping wild bee communities and pollination. They also suggest that preserving biodiversity in agricultural landscapes could help buffer climate change impacts and support more resilient agroecosystems.

1. Introduction

Mountain environments are sensitive ecosystems that play crucial roles in sustaining biodiversity and essential ecological functions. A critical ecosystem service is insect-mediated pollination, which contributes to ecological stability by preserving plant genetic diversity and stabilising food webs while supporting agricultural production (Dainese et al., 2019). Global biodiversity loss driven by human activities increasingly undermines these ecosystem services (Díaz et al., 2019; Felipe-Lucia et al., 2020; Lau et al., 2023). Declines in wild bee populations, largely attributable to agricultural intensification and habitat loss, are especially concerning (Kennedy et al., 2013). Whilst honeybees (*Apis mellifera* Linnaeus, 1758) are maintained through beekeeping practices, wild bees are a diverse array of species with varied ecological roles and habitat requirements. Therefore, preserving disturbance-sensitive wild bee species is more challenging (Winfree, 2010). Many of these species experience increased pressures due to scarcity of nesting sites, reduced floral resources, and loss of (semi-) natural habitats (SNH) (Grass et al., 2016; Martins et al., 2015; Persson and Smith, 2011).

Mountain environments can serve as valuable natural laboratories to study how environmental gradients shape ecological and evolutionary processes (Dainese et al., 2024). Due to their steep elevation changes over short distances, mountains naturally encompass a range of climatic conditions and land-use intensities, making them ideal systems to disentangle the effects of environmental change (Williams and Newbold,

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* Corresponding author.
E-mail address: matteo.dainese@univr.it (M. Dainese).

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2020). Variations in temperature and precipitation along the elevation gradient, directly and indirectly, shape biodiversity patterns and agricultural practices, thereby driving adaptive responses in biotic communities and land use systems (Guo et al., 2018). Typically, species richness peaks at mid-elevations, coinciding with more extensive farming practices (Jiménez-Olivencia et al., 2021). At higher elevations, where climatic conditions become more extreme and less stable, diversity tends to decline due to increased environmental stress and reduced habitat suitability. A similar pattern is observed for wild bees (Minachilis et al., 2020; Perillo et al., 2017), although their diversity is also shaped by local factors such as habitat turnover (over the long term) and seasonality (over the short term) (Aguirre and Junker, 2024; Laiolo et al., 2018).

The interplay of elevation, land use, and climate makes it challenging to disentangle the effects of human-induced pressures on wild bees and their pollination services in mountain regions. Assessing land-use intensity in these highly dynamic environments presents significant challenges (Lenoir et al., 2017). While indirect measures such as landscape composition or diversity indices are commonly used to estimate land-use intensity, they can be susceptible to bias and scale-dependent limitations (Hayden et al., 2024; Martin et al., 2016; Torresani et al., 2024). Bioindicators provide an alternative approach (Rodrigues and Brooks, 2007), but their selection requires careful consideration of local conditions (Anderle et al., 2024; Eglington et al., 2012). Synthetic multi-taxon biodiversity indices, such as the multidiversity index proposed by Allan et al. (2014), generally show a strong negative correlation with land-use intensity (Allan et al., 2014). This index has been successfully applied in various studies and serves as a robust, though indirect, indicator of habitat quality and ecosystem integrity in agroecosystems (Guariento et al., 2024; Soliveres et al., 2016; Zanini et al., 2024).

Previous research has examined how animal pollinators respond to land use and climate on a global scale (Millard et al., 2021; Outhwaite et al., 2022). However, existing research has largely been conducted in lowland areas (e.g. Ganuza et al., 2022) or targeted at specific wild bee genera (Christman et al., 2022; Sponsler et al., 2022). Given increasing human pressures on mountain agroecosystems, there is an urgent need to disentangle the distinct impacts of land use and climate on wild and managed bees, as well as on the pollination services they provide (Ipbes, 2016; Potts et al., 2010).

Our study examined how multidiversity, defined here as the richness of four functional groups (birds, butterflies, grasshoppers, and vascular plants) and used as an indirect indicator of land-use intensity, together with mean annual temperature (MAT) as a proxy for climatic conditions, shapes wild bee diversity and pollination services in mountainous agroecosystems. To disentangle these drivers, we selected two independent, orthogonal gradients, in which multidiversity and MAT were not correlated. Specifically, we designed a multidiversity gradient, reflecting habitat quality and land-use intensity with minimal variation in MAT, and a temperature gradient with minimal variation in multidiversity. We used pan traps to quantify bee diversity and abundance and conducted a phytometer experiment with two model plant species to measure pollination services. Based on these gradients, we hypothesise that:

(i) Wild bee abundance and species richness vary along the two gradients (multidiversity and temperature), peaking where multidiversity is high and climatic conditions are favourable.
(ii) Differences in wild bee assemblages across these gradients influence visitation rates, as more abundant and diverse bee communities increase the likelihood of flower visitation.
(iii) Pollination success, measured by seed or fruit production, is shaped by both gradients. It is expected to increase along the multidiversity gradient (where greater bee diversity and abundance enhance visitation rates), but decrease under warmer conditions, as higher temperatures can stress plants and reduce yield.
(iv) Honeybee distribution is not influenced by these gradients, but rather by the density of floral resources and local management practices.

2. Methods

2.1. Study design and site selection

We selected study sites from a set of 204 locations monitored by the 'Biodiversity Monitoring South Tyrol' (BMS) between 2019 and 2021 (Hilpold et al., 2023). We initially examined 68 sites in the 'Etschtal' valley and close to Bozen/Bolzano to limit the distance between sites and minimise variation in the local weather conditions during fieldwork (further site information in Appendix S1). From this pool of sites, we focused on farmland habitats, which act as central interfaces between natural and managed landscapes where pollination is essential for both agricultural productivity and ecosystem functioning (Dainese et al., 2019). We included 34 sites spanning diverse agricultural land uses, such as apple orchards, crop fields, hay meadows, orchard meadows, pastures, and vineyards (Appendix S1).

For each site, we calculated a multidiversity index (Allan et al., 2014) based on the species richness of four taxonomic groups monitored by the BMS: birds, butterflies, grasshoppers, and vascular plants (Appendix S4). Species richness was rescaled using min-max normalisation within each taxonomic group, yielding values between 0 and 1. This normalisation approach ensured that species-rich groups (e.g. vascular plants) did not receive disproportionate weighting. These standardised values were summed across the four groups to generate the multidiversity index for each site.

MAT values for each site were quantified using the model developed by Tscholl et al. (2022), which was specifically designed for the study region (Appendix S1). Since temperature along elevation in the Eastern Central Alps is inversely related to precipitation (Körner, 2021), MAT was used as a major climatic variable.

MAT and the multidiversity index were strongly negatively correlated (r = -0.73). To disentangle this correlation (Appendix S2), we plotted MAT and multidiversity index values for the 34 sites in an XY plot to identify two subsets ($n = 12$ each) representing two uncorrelated gradients: (i) a multidiversity gradient, with minimal variation in MAT (r = -0.26), and (ii) a temperature gradient, with minimal variation in multidiversity (r = 0.08) (Appendix S3). The selection of potentially suitable sites was achieved by visual inspection and correlation analyses. The mean nearest-neighbour distance among sites was 4.5 ± 1.8 km.

In the multidiversity gradient, the multidiversity index ranged from 0.2 to 1.85, MAT from 13.34°C to 11.66°C, and elevations between 209 and 448 m a.s.l. In the temperature gradient, MAT ranged from 5.82°C to 10.67°C, elevation 743 and 1536 m a.s.l., and the multidiversity index from 2.03 to 2.98 (Appendix S1).

2.2. Landscape variables

In our study, SNH cover was calculated within a 1000 m radius around each field, following the approach described by Zanini et al. (2024) (Appendices S4, S6). Semi-natural habitats (SNH) are known to influence bee diversity and abundance by providing both nesting sites and floral resources throughout the season (Bishop et al., 2024; Grass et al., 2016; Kremen et al., 2002). SNH types, including meadows, forests, and hedgerows, have been shaped over centuries by agro-pastoral practices and support high levels of biodiversity, including pollinators (Boetzl et al., 2021; Kratschmer et al., 2024). In our dataset, SNH cover was strongly correlated with the multidiversity index ($r = 0.82$). We also calculated open SNH cover, a subset of SNH comprising habitats highly suitable for pollinator foraging, such as meadows, grasslands, pastures, and wetlands (Appendix S6), which also showed a strong correlation with the multidiversity index (*r* = 0.67; Appendix S3).

2.3. Bee sampling

For bee sampling, we used six UV-reflective pan traps (500 ml plastic saucer pots with a 14.5 cm interior diameter) per site, placed at vegetation height. The pan traps were divided into two triplets, each with a white, a blue, and a yellow trap placed 5 m apart, where triplets were separated by at least 10 m. Additionally, traps were placed at least 10 m from field edges. Sampling was repeated three times from May to July 2022, at intervals of about 29 ± 5 days. Each trap was exposed for 24 h, filled with water and a colourless, unscented detergent to reduce surface tension (a tablespoon of detergent for 5 L of water). Collected insects were stored in 75 % ethanol, wild bees were identified to species level, and honeybees were counted.

To estimate the average density of floral resources per site surrounding the pan traps, we conducted flower unit counts following an adaptation of the methodology proposed by the EU SPRING project (Potts et al., 2021). We counted flower units (individual flowers, flower heads, umbels, or spikes) in two 2 × 2 m plots per site: one around the study plants and one 15 m away. Only fresh, open flowers were counted. In the case of flower-rich sites, a 50 × 50 cm section of the plot was sampled, and the value was extrapolated to the entire plot.

2.4. Pollination services and exclusion experiment

We assessed pollinator visitation rates and plant production (seed and fruit resulting from pollination success) using two model plants, radish (*Raphanus sativus*) and strawberry (*Fragaria vesca*). These two species have been used previously as phytometers to study the effects of pollinator activity on plant reproduction success (Castle et al., 2019; Dainese et al., 2017) and are traditionally grown in the study region.

Plants were subjected to two treatments: (i) pollinator exclusion, achieved by covering the potted plants with a fine transparent polyethylene mesh (mesh 1 × 1 mm), and (ii) free pollination, with plants left uncovered. Each site had three replicates of each treatment per plant type, giving a total of 12 plants per site (6 radishes and 6 strawberries, split evenly between the two treatments). Radish plants had no developed flowers at the start of the experiment, whereas strawberry plants with open flowers and swollen buds were trimmed to remove pre-pollinated blooms and to facilitate acclimation in the new environment (more details in Appendix S4)

2.4.1. Visitation rate

We measured pollinator visits (wild bees and honeybees) at two dates per plant type and per site between May and July 2022. Observations were conducted between 09:00 and 17:00 under dry conditions, no rainfall, temperatures between 15°C and 32°C, and wind speeds no higher than four on the Beaufort scale. The minimum interval between rounds was five days.

For each 15-minute survey, we counted only insects touching the studied plants' anthers. Two sessions were conducted for each plant type per site. The cumulative number of visits from both sessions per plant type was taken as a measure of the visitation rate. The second round of observations could not be completed in four sites due to plant damage (strawberries at two sites and radishes at the other two).

2.4.2. Plant production

Strawberries were harvested between May and July 2022, when at least 75 % of the fruit surface was light red to red, to minimise fruit loss from pests or predation (Hodgkiss et al., 2018). The harvested fruits were stored in a cooled, polyester-insulated container to prevent deterioration. On the same day, each strawberry was weighed using a high-precision analytical balance with a glass chamber, after removing the pedicel and calyx.

Radish siliquae (fruits) were harvested at the end of the season. We moved the pots to a nursery at plant senescence to reduce predation risk. Once all traces of green tissue had disappeared, the siliquae were harvested and dried for 48 h at 80°C. Using a high-precision balance, we determined the following parameters: (i) total number of siliquae per plant, (ii) total dry weight of siliquae (containing seeds), (iii) number of seeds in the siliquae, (iv) total seed weight, and (v) seed set (ratio of seeds per siliquae). Radish plants experienced considerable mortality and seed predation in the temperature gradient, causing considerable sample-size imbalances. We, therefore, present radish-related results only for the multidiversity gradient.

2.5. Data analysis

Statistical analyses were performed the R software version 4.3.2 (R Core Team, 2020). We adopted the "language of evidence" approach (Muff et al., 2022), which replaces binary significance thresholds (significant/non-significant) with a continuous scale ranging from little or no evidence to very strong evidence. Before running our models, we assessed spatial autocorrelation by performing a Mantel test comparing spatial distances and environmental dissimilarities among study sites. The test indicated no evidence of spatial autocorrelation (r = 0.06, p = 0.253, based on 999 permutations).

To evaluate the distinct roles of biodiversity and climate, we analysed the multidiversity and temperature gradients separately. We developed three sets of models to examine their effects on bee assemblages and pollination services. First, we examined the effects of the multidiversity index or MAT, on wild bee species richness, wild bee abundance, and honeybee abundance. Second, we tested the interaction between the number of flowers per phytometer plant (strawberry or radish) and multidiversity index or MAT on wild bee and honeybee visitation rates. Finally, we tested the interaction between pollination treatments and multidiversity index or MAT on plant productivity (fruit or seed production).

For the multidiversity gradient, we also examined additional predictors independently due to their high collinearity with the multidiversity index (Appendix S3): SNH cover, open SNH cover, and flower density (Appendix S5.1 and S5.2). We further evaluated the effects of SNH cover and open SNH cover on visitation rates of wild and managed bees, as well as the influence of honeybee visitation on wild bee visitation (Appendix S5.3 and S5.4).

For wild bee species richness, we applied generalised linear mixed-effects models (GLMMs) with a Poisson distribution using the 'lme4' package (Bates et al., 2015), including "site code" as a random factor. If overdispersion was detected, we used a negative binomial generalised linear model (GLM). Wild bee and honeybee abundances were log-transformed and analysed with linear models aggregated at the site level, as location did not contribute to the variance and model assumptions were met. Log-transformed visitation rates were modelled using linear mixed-effects models (LMMs) and "site code" as a random factor. Fruit and seed production were first compared between free pollination and pollinator exclusion treatments using the non-parametric Kruskal-Wallis test to account for unequal sample sizes (Appendix S5.7–8). We then calculated Cliff's delta ($-1 \leq \delta \geq +1$), a non-parametric measure of effect size, to better assess the magnitude of biologically meaningful differences between treatments. Radish-productivity variables were log-transformed, whereas strawberry weight was square-root–transformed. We analysed both sets of variables with linear mixed-effects models (LMMs), including "site code" as a random effect. However, highly uneven sample sizes for radishes rendered these analyses inconsistent, especially in the temperature gradient. Consequently, we present only the analyses for the multidiversity gradient.

In all the models, fixed predictors were standardised to a mean = 0 and a SD = 1 using the function 'standardise' in the 'arm' package (Gelman et al., 2013). Visualisation was performed with the 'visreg', 'sjPlot', and 'ggplot2' packages (Breheny and Burchett, 2017; Lüdecke, 2018; Wickham, 2016), while model residuals were assessed for uniformity using the ‘DHARMa’ package (Hartig and Hartig, 2017). Additional model diagnostics were performed using the ‘performance’ package, including posterior predictive checks, overdispersion, variance homogeneity, residual normality, and random effects (Lüdecke et al., 2021). Model comparisons were based on adjusted R^2 for linear models, Nagelkerke’s R^2 for GLMs, and marginal R^2 for (G)LMMs (Nakagawa and Schielzeth, 2013).

3. Results

3.1. Species richness and abundance of wild bees

We collected 3521 bees, including 1000 honeybees and 2521 wild bees. In total, 135 wild bee species were identified (Zanini et al., 2025). We captured 1094 wild bees and 92 species along the multidiversity gradient, while 1427 wild bees and 99 species were captured along the temperature gradient. The honeybees were 303 and 697 individuals, respectively.

3.1.1. Multidiversity gradient

Our findings provide strong evidence that the multidiversity index is positively associated with wild bee species richness. This index was also positively associated with wild bee abundance and showed a weak association with flower density (Fig. 2 and Appendix S5.2). Honeybee abundance, in turn, was positively associated with the multidiversity index but not with flower density (Appendix S5.2). Because semi-natural habitat (SNH) cover—and particularly open SNH—can influence the presence of both wild and managed bees, we examined these two landscape metrics separately. Notably, flower density was strongly correlated with open SNH cover (r = 0.62). Both SNH and open SNH cover predicted wild bee species richness, whereas open SNH cover was a better predictor of wild bee abundance and SNH cover more effectively explained honeybee abundance (Appendix S5.1).

3.1.2. Temperature gradient

We found weak evidence of a positive effect of MAT on wild bee species richness, while their abundance was not related to MAT. Along the temperature gradient, flower density had only a weak influence on both wild bee richness and abundance (Fig. 2 and Appendix S5.2). The abundance of honeybees was not related to either MAT or flower density (Appendix S5.2).

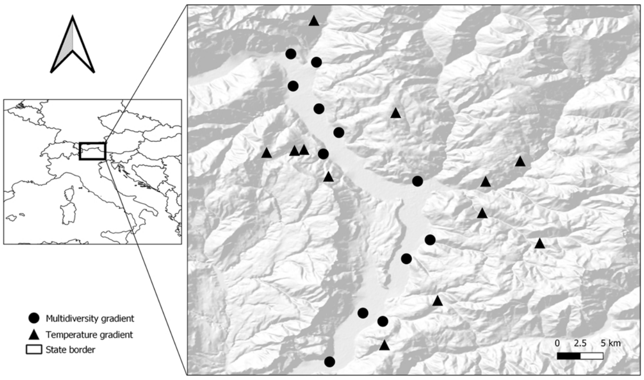

Fig. 1. Map of the study area showing the selected sampling sites along two distinct gradients. Sites in the multidiversity gradient exhibit minimal variation in mean annual temperature (MAT), while sites in the temperature gradient show minimal variation in multidiversity index values.

3.2. Visitation rate of wild bees

3.2.1. Multidiversity gradient

We found a significant interaction between flower number and the multidiversity index in shaping wild bee and honeybee visitation rates for radish plants. Wild bee visitation rates peaked in areas with both a high multidiversity index and a high number of open radish flowers (Fig. 3a; see Appendix S5.3 for models estimates). In contrast, honeybee visitation rates were highest in areas with low multidiversity but similarly high flower availability (Fig. 3b). Wild bee visitation rate was positively associated with open SNH cover and flower availability, whereas honeybee visitation rate showed positive associations with SNH cover and flower availability (Appendix S5.3). In strawberry plants, we found no evidence that either flower number or multidiversity index influenced visitation rates of wild bees and honeybees (Appendix S5.4).

3.2.2. Temperature Gradient

We found no evidence that MAT influenced wild bee or honeybee visitation rates on either radish or strawberry plants. There was only weak evidence of a positive relationship between the number of open flowers in radish and the honeybee visitation rate.

3.3. Plant production

We found strong evidence that free-pollinated plants had higher yields than those under pollinator exclusion (Table 1). In both gradients, bagged strawberry plants produced more fruits, but the mean strawberry weight was higher in freely pollinated plants in both gradients (Appendix S5.7 - 8).

3.3.1. Multidiversity gradient

We tested the interaction between the multidiversity index and pollination treatment on fruit or seed production. For radish, there was no evidence of an interaction; however, both the multidiversity index and pollination treatment had separate effects on seed and fruit production, with varying strengths of association (model estimates in Appendix S5.5). For strawberries, only the pollination treatment affected fruit weight (Fig. 4a; Appendix S5.6).

3.3.2. Temperature gradient

We found weak evidence of an interaction between MAT and pollination in strawberry (Appendix S5.6). As shown in Fig. 4, increasing temperatures did not strongly affect fruit weight in freely pollinated plants. However, in the pollinator exclusion treatment, strawberry weight appeared to be negatively impacted by the increase in MAT (model estimates in Appendix S5.6).

4. Discussion

In this study, we tested four hypotheses regarding the distinct effects of multi-taxon diversity (as a proxy for land-use intensity) and temperature on wild bee assemblages and pollination services in mountainous agroecosystems. Our results strongly support the hypothesis (H1), which states that wild bee abundance and diversity are positively associated with the multidiversity index, but only marginally support the relationship between wild bee abundance and MAT. Similar relationships were observed for wild bee visitation rate (H2). Additionally, we found that for the visitation rate of radish flowers, honeybee-dominated pollination occurred in simplified landscapes (where the multidiversity index is low), whereas wild bee visitation rate peaked in areas with high multidiversity. In both cases, visitation rates increased with floral resources availability. In partial contrast to our third hypothesis (H3), we detected no direct effect of multidiversity on pollination success, but, as expected, temperature negatively affected yield. We found evidence that honeybee abundance and their visitation rate were not influenced by MAT in the temperature gradient, but we found

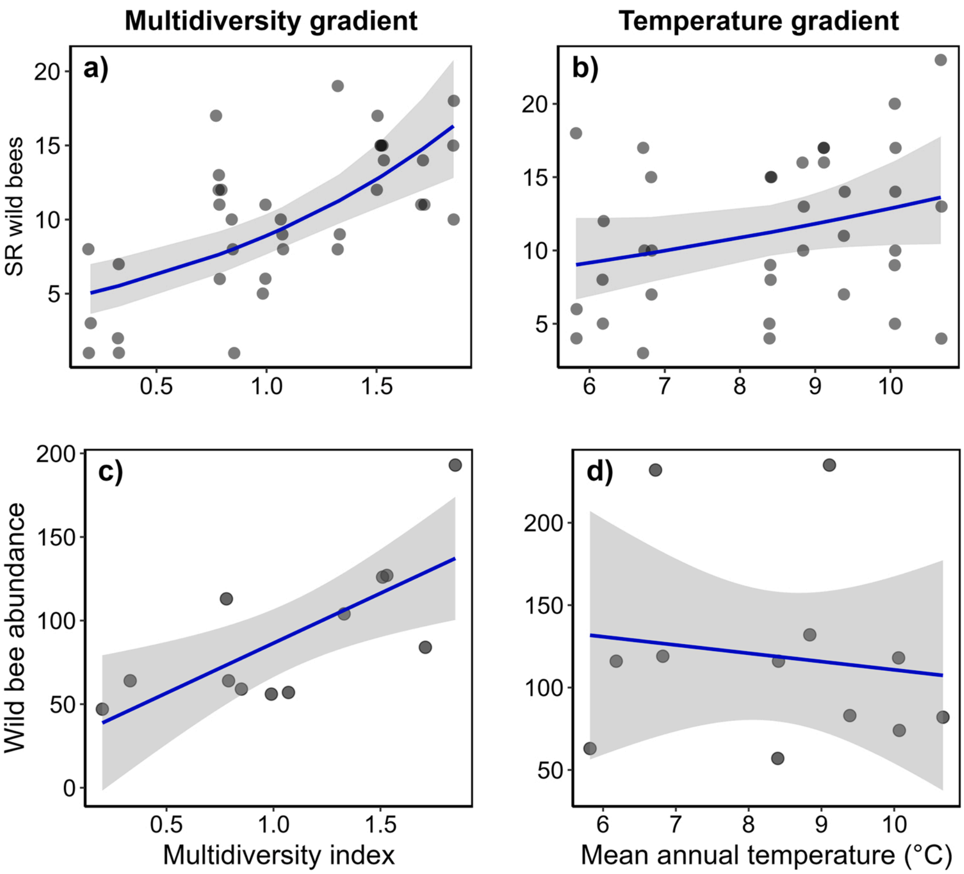

Fig. 2. Relationships between (a, c) wild bee species richness (SR wild bees) and (b, d) wild bee abundance along the multidiversity index (left panels) and mean annual temperature (MAT; right panels). These relationships correspond to the two independent environmental gradients analysed in the study. Model estimates and statistical details are provided in Appendix S5.2.

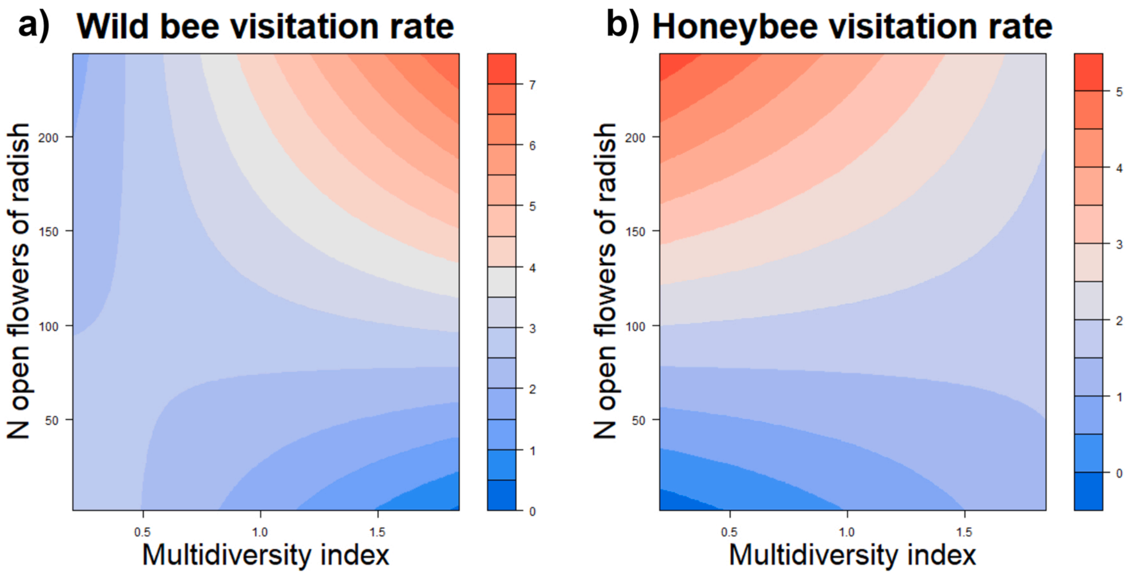

Fig. 3. Plots illustrating the relationships between the visitation rate of (a) wild bees and (b) honeybees with the multidiversity index and the number of open flowers on radish. Colour bars adjacent to each plot indicate the visitation rate. Plots are based on linear mixed-effects model (LMM) estimates.

contrasting results in the multidiversity gradient (H4). These aspects are discussed in more detail in subsequent sections.

4.1. Wild bee species richness and abundance of wild and managed bees

While we do not directly measure land-use intensity, we used the multidiversity index, based on the species richness of four taxonomic groups, as an integrative ecological indicator that reflects the

Table 1
Mean value, standard error of the mean, and sample size (mean ± SEM, N) are shown for each gradient and treatment. Cliff's delta ($-1 \leq \delta \leq +1$), a non-parametric measure of effect size, is also provided. Effect size categories follow: negligible → $|\delta| < 0.147$; small → $0.147 \leq |\delta| < 0.33$; moderate → $0.33 \leq |\delta| < 0.474$; large → $|\delta| \geq 0.474$.

Model plant	Variable	Multidiversity gradient			Temperature gradient		
		free pollination (mean ± SEM, *N*)	pollinator exclusion (mean ± SEM, *N*)	Cliff's δ	free pollination (mean ± SEM, *N*)	pollinator exclusion (mean ± SEM, *N*)	chi-square
strawberry	weight (g)	6.48 ± 0.41 (*n* = 94)	5.41 ± 0.31 (*n* = 184)	0.20 (small effect)	11.97 ± 0.70 (*n* = 77)	5.90 ± 0.32 (*n* = 162)	0.62 (large effect)
radish	N seed	118.22 ± 29.66 (*n* = 18)	9.82 ± 2.96 (*n* = 11)	0.64 (large effect)	N/A	N/A	N/A
	weight seed (g)	0.74 ± 0.18 (*n* = 18)	0.04 ± 0.01 (*n* = 11)	0.72 (large effect)	N/A	N/A	N/A
	N siliquae	42.50 ± 9.14 (*n* = 18)	8.09 ± 1.90 (*n* = 11)	0.63 (large effect)	N/A	N/A	N/A
	weight siliquae (g)	3.67 ± 0.87 (*n* = 18)	0.47 ± 0.13 (*n* = 11)	0.66 (large effect)	N/A	N/A	N/A
	seed set (N seed/N siliqua)	2.21 ± 0.26 (*n* = 18)	1.02 ± 0.25 (*n* = 11)	0.59 (large effect)	N/A	N/A	N/A

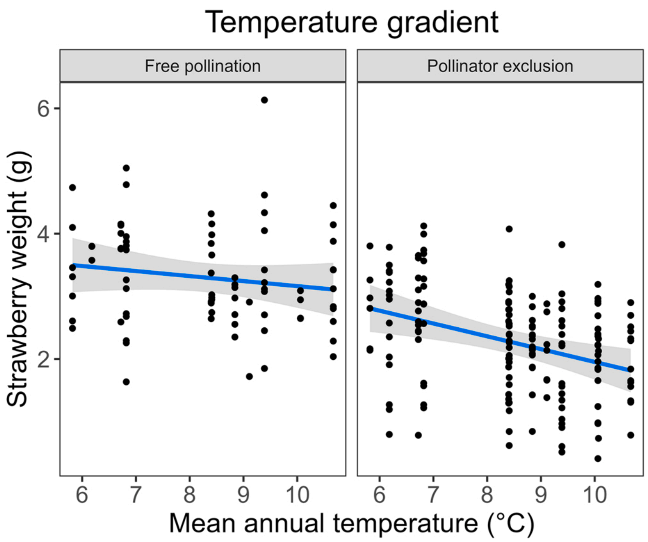

Fig. 4. Plot depicting the relationships between strawberry fruit weight and mean annual temperature (MAT) within the temperature gradient, differentiated by pollination treatment (free pollination vs. pollinator exclusion). The plot is based on linear mixed-effects model (LMM) estimates.

cumulative effects of land-use intensity and habitat quality (Allan et al., 2014, 2015; Allart et al., 2024; Hendrickx et al., 2007; Wen et al., 2020). In agreement with Hypothesis 1, wild bee species richness and abundance were positively associated with the multidiversity index (Fig. 2). This index proved to be an effective predictor of wild bee diversity in agroecosystems and was also strongly correlated with SNH cover (Appendix S5.1). These results are consistent with previous studies demonstrating the positive effects of SNH on pollinator diversity (Kremen et al., 2002; Maurer et al., 2022; Zanini et al., 2024). Contrary to our expectations (H4), honeybees were also more abundant in higher-multidiversity areas, suggesting their ability to thrive in varied environments and species-rich communities (Moritz et al., 2005). Overall, the positive relationships between the multidiversity index and wild bee species richness and the abundance of wild and managed bees suggest that higher ecosystem diversity and lower land-use intensity support a higher number of species and larger populations (Guariento et al., 2024; Kleijn et al., 2011). These findings have important implications for ecosystem services, as greater pollinator diversity and abundance can enhance pollination efficiency and crop production (Dainese, Martin, Aizen, Albrecht, Steffan-Dewenter, et al., 2019; Klein et al., 2007).

The observed increase in honeybee abundance with multidiversity may also be influenced by seasonal scarcity of floral resources (Danner et al., 2016; Steffan-Dewenter and Kuhn, 2003), as fields with lower surrounding floral availability tend to be less attractive to foraging bees (Verrier et al., 2024). Although our on-site measurements of flower density did not show a clear relationship with honeybee abundance, flower density was strongly correlated with open SNH cover around the study sites. This suggests that the association with multidiversity may instead be mediated by SNH availability and large-scale floral resource distribution (Danner et al., 2016; González-Varo and Vilà, 2017).

Along the temperature gradient, we found only weak evidence of a positive effect of MAT on wild bee species richness and no evidence of an association with their abundance (Fig. 2). This suggests that while temperature may have some influence on species richness, other factors such as landscape features and floral resources are likely to play a more significant role in shaping wild bee abundance. Floral resource availability (flower density) in the plots was associated with a lower wild bee abundance. This phenomenon is often observed using pan traps because of their intrinsic sampling bias: in fields with abundant blooms, pan traps may attract fewer bees (Westerberg et al., 2021). Indeed, sites in the temperature gradient had, on average, about twice the floral density of those in the multidiversity gradient, suggesting that resources were not a limiting factor. This confirms that we tested the direct effect of temperature, separating it from other confounding factors such as land-use intensity (since high multidiversity was fixed across all sites during site selection) and resource availability. In contrast, sites in the multidiversity gradient differed in habitat quality, ecosystem diversity, and flower density, explaining a positive association with wild bees. In these areas, the availability of floral resources attracted more wild bees and increased their presence. As hypothesised (H4), honeybee abundance did not respond to MAT or floral density in the temperature gradient. Overall, floral resources in the temperature gradient were likely a non-limiting factor, allowing for effective capture of climate variation. At the same time, although the range of MAT was relatively wide (see Methods), the study did not cover the full elevational range of wild bee habitats in the Alps, which may help explain the observed stability in wild and managed bee abundance across all sites.

4.2. *Visitation rate of wild bees*

Consistent with Hypothesis 2, we found that along the multidiversity gradient, wild bee visitation to radish plants was driven by both the multidiversity index and the number of open radish flowers (Appendix S5.3). Specifically, the visitation rate for wild bees peaked where ecosystem diversity and plant flower resources were highest. In contrast, honeybee visitation was highest where the number of radish flowers was high but the multidiversity index was low (Fig. 3). This dynamic may reflect differences in habitat preferences and foraging behaviours between wild bees and honeybees (Rollin et al., 2013; Wood et al., 2018), and is consistent with studies showing that land-use intensification and landscape homogenisation not only reduce habitat diversity, but also lead to declines in wild pollinator populations (Rader et al., 2014; Weiner et al., 2014). In such simplified landscapes, the pollination service is mainly provided by managed honeybees. In contrast, where multidiversity index is higher, we see a strong increase in pollination services delivered by wild bees. For instance, a previous study reported that honeybees visited flowers in intensively cultivated apple orchards on average 33 times more frequently than wild bees (Zanini et al., 2024). In contrast, as the proportion of SNH cover increases and land use becomes more extensive, wild bee visitation rates rise accordingly (Herbertsson et al., 2016).

Fig. 3 illustrates a pattern that, at first glance, appears to contradict the pan trap results discussed earlier, which indicated that honeybee abundance increases with greater multidiversity. However, it's essential to differentiate between the patterns observed through passive sampling and those derived from direct observations of visitation, which tend to be more localized. In sites with low multidiversity, we observed that when a high density of flowers was experimentally introduced (as seen with the radish phytometers), honeybee visitation rates increased, which was anticipated. However, under similar floral conditions, high visitation by wild bees was only noted at sites with high multidiversity. Our study indicated that sites with low multidiversity also had a lower coverage of semi-natural habitats (SNH), suggesting simplified landscapes where the demand for pollination services is primarily fulfilled by honeybees. In fact, analyzing the interaction between radish flower availability and SNH cover showed a positive correlation with honeybee visitation (see Appendix S5.2). This relationship reflects the connection observed between SNH cover and honeybee abundance, helping to clarify the apparent inconsistency between visitation rates and pan trap results.

Our results showed no direct negative relationship between wild and managed bee visitation rates (Appendix S5.3). However, competitive interactions may arise in areas with higher honeybee density (Cane, 2024; Iwasaki and Hogendoorn, 2022; Wignall et al., 2020), even though their presence is unrelated to natural occurrences of wild bees (Angelella et al., 2021; Davis et al., 2025)), or according to season (González-Varo and Vilà, (2017); Ropars et al., (2022). In the temperature gradient, where multidiversity values were high across sites, neither wild bee nor honeybee visitation on radish was related to MAT.

In contrast to radish, strawberry showed no clear effects from either gradient, suggesting that other factors, likely related to plant-specific traits or local conditions, might have influenced pollinator behaviour. This aligns with other studies emphasising the multifaceted nature of pollination dynamics, where factors such as plant-pollinator interactions and resource availability play pivotal roles (Potts et al., 2010; Rollin et al., 2013). A possible explanation for the specific case of strawberry flowers is that their floral scent and composition can be influenced by temperature, affecting bees' olfactory perception of the flowers, making them more difficult to spot or less attractive (Cordeiro and Dötterl, 2023). Additionally, our plant selection may have unintentionally favoured certain pollinators: mainly generalist species within a particular body-size range. During direct observations, we never observed bumblebees or wild bees bigger than honeybees visiting strawberry flowers. Overall, predicting visitation rates was challenging. For example, the number of open strawberry flowers was consistently low in both gradients (mean of 2.1 ± 1.5 for the temperature gradient and 1.4 ± 0.9 for the multidiversity gradient), compared to radish (mean of 46.7 ± 37.2 for the temperature gradient and 70.2 ± 61.1 for the multidiversity gradient). This limited flower availability likely contributed to the lack of significant associations between our variables of interest.

4.3. Plant yield

Insect pollination (H3) clearly enhanced the reproductive success of both radishes and strawberries (Table 1; Fig. 4), consistent with numerous previous studies (Bartomeus et al., 2014; Klein et al., 2007). While we could not directly link visitation rates to yield, the patterns in Fig. 4 suggest a potential 'insurance effect' of biodiversity (Yachi and Loreau, 1999), also known as the 'portfolio effect' (Lázaro et al., 2022). This principle posits that high biodiversity in ecological communities can stabilise ecosystem functioning under environmental stress such as warming (Pires et al., 2018). In our study, freely pollinated strawberry plants appeared less impacted by higher temperatures than plants in the pollinator exclusion treatment. Since sites in the temperature gradient were generally located in areas with high multidiversity, our findings support the idea that biodiversity can buffer the negative effects of warming (Outhwaite et al., 2022). Diverse wild bee communities, in particular, can maintain pollination services despite species fluctuations caused by agricultural management or climate stress (Hong et al., 2022; Kühsel and Blüthgen, 2015). However, further studies are needed to assess whether this buffering effect extends to other crop species.

The 'insurance effect' may also operate across spatial scales for mobile organisms like pollinators. In heterogeneous landscapes, species can move across habitats, sustaining ecosystem functions despite local extinctions caused by environmental pressures (Loreau et al., 2003; Wang and Loreau, 2016). Notably, our findings that wild bee diversity and overall bee abundance were higher at high-multidiversity sites support the idea that these ecosystems may promote greater ecosystem functioning. Such communities benefit from reduced competition for resources in flower-rich habitats, which can help buffer the impacts of agricultural land-use and climate stress (de Mazancourt et al., 2013).

Regarding the multidiversity gradient, neither strawberries nor radishes showed an interaction between pollination treatment and multidiversity index, although both predictors independently influenced seed and fruit production. Some studies report a decline in fruit set at high pollinator densities (Macinnis and Forrest, 2019) and suggest that stigma receptivity also plays a crucial role, as saturation or damage caused by frequent visits can reduce fruit set (Rollin and Garibaldi, 2019).

We used white, breathable mesh to exclude pollinators while minimizing any potential microclimatic artifacts. However, we did not measure the temperature underneath the netting. While minor warming effects cannot be ruled out, they were likely consistent across all sites and therefore unlikely to skew the temperature gradient observed between the sites.

4.4. Conclusion

Our findings indicate that multidiversity, as an indirect proxy for land-use intensity, exerted a stronger influence on wild bee communities and their pollination services than temperature. Along the temperature gradient, climatic effects became relevant primarily through interactions with other factors, such as floral resource availability and pollination provision. These insights are particularly important under climate change, where projected warming is expected to intensify pressures on pollinators. Although our elevational gradient was narrower than that of the Italian Alps, similar patterns have been observed elsewhere (Ganuza et al., 2022; Papanikolaou et al., 2017). More broadly, research highlights the importance of resilient, functionally redundant, and biodiverse ecosystems in buffering temperature stress under global warming (Bouvier et al., 2012; Mori et al., 2021; Shin et al., 2022). As climate change progresses, maintaining networks of biodiversity-rich habitats will be crucial in agroecosystems, particularly if rising temperatures exacerbate pollinator declines in combination with land-use pressures (Pires et al., 2018; Williams and Newbold, 2020). It is important to note that our study was conducted over a single year, which was characterized by above-average temperatures in South

Tyrol. While this condition was consistent across the study sites and does not affect the internal validity of our findings, it highlights that short-term studies may capture only a snapshot of climate–land use interactions. Therefore, long-term and multi-year monitoring will be essential to fully understand how pollinator communities and the services they provide respond to the combined pressures of warming and land-use intensity.

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CRediT authorship contribution statement

Sebastiano Zanini: Writing – original draft, Methodology, Investigation, Data curation. **Matteo Dainese:** Writing – review & editing, Supervision, Conceptualization. **Lisa Obwegs:** Writing – review & editing. **Elia Guariento:** Writing – review & editing. **Timo Kopf:** Writing – review & editing, Methodology. **Matteo Anderle:** Writing – review & editing. **Georg Leitinger:** Writing – review & editing, Funding acquisition. **Ulrike Tappeiner:** Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109945.

Data availability

Data will be made available on request.

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