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Spatial mismatch between wild bee diversity hotspots and protected areas

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Keywords: anthophila, biodiversity facet, community-based conservation, elevation gradient, protected area, Switzerland, urbanization

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/cobi.14082.

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Article Impact statement: Distributions of hotspots of wild bee alpha and ß diversity differ by elevation and overlap with existing protected areas.

Abstract

Wild bees are critical for multiple ecosystem functions but are currently threatened. Understanding the determinants of the spatial distribution of wild bee diversity is a major research gap for their conservation. Here, we model wild bee α and ß taxonomic and functional diversity in Switzerland to (i) uncover countrywide diversity patterns and determine the extent to which they provide complementary information, (ii) assess the importance of the different drivers structuring wild bee diversity, (iii) identify hotspots of wild bee diversity, and (iv) determine the overlap between diversity hotspots and the network of protected areas. We use site-level occurrence and trait data from 547 wild bee species across 3343 plots and calculate community attributes, including taxonomic diversity metrics, community mean trait values, and functional diversity metrics. We model their distribution using predictors describing gradients of climate, resource availability (vegetation), and anthropogenic influence (i.e. land-use types and beekeeping intensity). Wild bee diversity changes along gradients of climate and resource availability, with high-elevation areas having lower functional and taxonomic α-diversity and xeric areas harbouring more diverse bee communities. Functional and taxonomic ß-diversities diverge from this pattern, with high elevations hosting unique species and trait combinations. The proportion of diversity hotspots included in protected areas depends on the biodiversity facet, but most diversity hotspots occur in unprotected land. Climate and resource availability gradients drive spatial patterns of wild bee diversity, resulting in lower overall diversity at higher elevations, but

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simultaneously greater taxonomic and functional uniqueness. This spatial mismatch among distinct biodiversity facets and the existing degree of overlap with protected areas challenges wild bee conservation, especially in the face of global change, and calls for better integrating unprotected land. The application of spatial predictive models represent a valuable tool to aid the future development of protected areas and achieve wild bee conservation goals.

1. Introduction

Wild bees are of great ecological, economic, and social importance (Potts et al., 2016) but are threatened by ongoing global change (Goulson et al., 2015). Drivers of wild bee declines have long been noted (Goulson et al., 2015) and existing evidence has shown that some species have suffered extirpations and contractions of their distribution ranges (Cameron et al., 2011). In turn, this has led to a loss of species and a potential erosion of functional diversity (Pradervand et al., 2014), challenging the resilience of wild bee communities to future changes (Lavorel et al., 2013). Therefore, efficient protection of wild bee taxonomic and functional diversity is urgently needed. However, knowledge on wild bee diversity is severely constrained, due to existing taxonomic bottlenecks and a lack of comprehensive datasets on wild bee occurrence and trait measurements (Nieto et al., 2014, but see Woodcock et al., 2014; Polce et al., 2018). This limitation also applies in Europe, one of the most studied continents. Europe hosts around 10% of the world bee diversity (ca. 2000 species; Nieto et al., 2014) but over 56% of the species reported are considered data deficient (Nieto et al., 2014). Overall, these shortages in data hamper the development of conservation

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planning (Guisan et al., 2013; Di Marco et al., 2017), as an understanding of the drivers shaping diversity patterns and the spatial distribution of diversity is required to designate protected areas for wild bee conservation (Chowdhury et al., 2022).

Biodiversity is a multi-faceted concept that should inform conservation planning (Devictor et al., 2010; Villalta et al., 2022). Taxonomic metrics, such as species richness and species diversity, are widely used to evaluate the importance of different drivers of wild bee diversity, including land-use change (Ekroos et al., 2020), disturbance (Winfree et al., 2009), pollution (Moroń et al., 2012) and climate (Bystriakova et al., 2018). Approaches based on functional traits, that is, the phenotypic attributes of an individual that determine its fitness (Violle et al., 2007), are increasingly being used in combination with taxonomic metrics. They help us to better understand the variation in species assemblages along ecological gradients (Coutinho et al., 2021) and to predict the consequences for ecosystem functions and services (e.g. Fründ et al., 2013). Comprehensive national bee monitoring and functional trait datasets are becoming available (e.g. Woodcock et al., 2014; Fournier et al., 2020) for specific regions, enabling us to study functional trait gradients at higher resolutions. Phylogenetic diversity, a metric of the shared evolutionary history among species (Faith, 1992), represents another biodiversity facet. Unfortunately, a comprehensive phylogeny for bees is still lacking (Hedkte et al., 2013). Similarly, decomposing diversity into its α and ß components provides complementary information. Local α-diversity typically provides a measurement of diversity (i.e. taxonomic, functional, phylogenetic) at the spatial scale where studies are conducted (Socolar et al., 2016). Conversely, ß-diversity represents a measurement of the compositional differences between local species assemblages. It is often

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an important metric to understand diversity change due to, e.g. environmental gradients, and to study biodiversity loss and homogenisation (Socolar et al., 2016). Among other applications, ß-diversity can help uncover areas harbouring unique species assemblages. Thus, the combination of α and ß taxonomic and functional diversity represents an important metric to understand diversity change and inform conservation planning (Socolar et al., 2016).

The determinants of wild bee diversity have been previously explored. Nonetheless, existing work has limitations regarding spatial coverage, the diversity facets included, the environmental predictors tested, and the completeness of bee diversity data. Recent analyses at the global scale have confirmed the bimodal latitudinal bee richness gradient proposed by Michener (1979). Specifically, climate and resource availability (i.e. vegetation communities) have arisen as the main drivers of bee diversity worldwide (Bystriakova et al., 2018; Orr et al., 2021) and regionally (Dzekashu et al., 2022; Sponsler et al., 2022). Moreover, anthropogenic stress in the form of land-use change has been shown to negatively impact wild bee α- and ß-diversity for Palearctic bees at the continental (Bystriakova et al., 2018) and smaller scales (e.g. Moroń et al., 2012; De Palma et al., 2017). For instance, highly intensified agricultural and urban areas tend to reduce wild bee diversity by selecting species with specific traits that allow them to persist and thrive in those environments, hence decreasing both α- and ß-diversity (Collado et al., 2019; Fournier et al., 2020; Villatla et al., 2022). However, urban areas may harbour a greater wild bee diversity than highly intensified agricultural areas (Baldock 2020), and maintain higher ß-diversity values (Fournier et al., 2020; Villalta et al., 2022). Finally, anthropogenic stress through the influence of managed

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pollinators (e.g. honeybees), which might compete with wild bees, has rarely been tested at large spatial scales, but evidence has shown a gradual replacement of wild bees by honeybees across the Mediterranean Basin region (Herrera, 2020). Nonetheless, how the determinants of bee distribution act at smaller spatial scales (e.g. countrywide) and the consequences for wild bee diversity remain largely unknown, limiting our knowledge of wild bee ecology and our capacity to manage and conserve their biodiversity.

Switzerland hosts a relatively high bee diversity compared with other European countries, exhibits large gradients in climate and land-use intensity, and is therefore a good location to study bee distribution patterns. Bee richness in Switzerland is estimated at 633 species (Ascher & Pickering, 2020), 45% of which are threatened (Federal Office for the Environment FOEN, 1994). National surveys of bees have a good spatial coverage, which enables spatial modelling approaches at relatively high resolutions (e.g. Vitasse et al., 2021). The quality and quantity of these data are unparalleled in Europe, as few other countries have long-term surveys of bee occurrence and none cover such sharp environmental gradients. Switzerland has developed a network of protected areas aimed at the conservation of the country's biodiversity. Nonetheless, as in other countries, protected areas have mostly been designed for plants and vertebrates. Their effectiveness for insect conservation is largely unknown (Chowdhury et al., 2022). For instance, how the protected areas cover the geographic range of wild bees and their diversity hotspotshas not yet been assessed

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Here, we studied bee diversity spatial patterns by mapping the distribution of taxonomic and functional attributes of bee communities from a unique dataset containing records of 547 wild bee species in Switzerland at an unprecedented spatial resolution. We modelled wild bee taxonomic and functional diversity using sets of predictors that represent gradients of climate, resource availability (i.e. vegetation communities), and anthropogenic stress (i.e. land-use composition and beekeeping intensity). We aimed to (i) uncover countrywide taxonomic and functional α- and ß-diversity patterns and determine the extent to which they provide complementary information, (ii) assess the importance of the different drivers structuring wild bee α and ß taxonomic and functional diversity, (iii) identify hotspots of α and ß taxonomic and functional diversity, and (iv) quantify the degree of overlap between diversity hotspots and the network of Swiss protected areas.

2. METHODS

2.1 Study location

This study was carried out in Switzerland, central Europe. Switzerland is a country with pronounced elevation gradients , a broad range of climatic conditions and a variety of land-use types. Thus, sharp environmental and land-use gradients are characteristic of Swiss landscapes, making them ideal for studying the drivers of spatial patterns in community-level taxonomic and functional diversity.

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2.2. Bee occurrence, trait values and community metrics

Occurrence data were provided by the Swiss Biological Records Centre (http://www.cscf.ch, data accessed on 12 April 2020). These data originate from community-level surveys performed in 100 m by 100 m plots in 2015-2020, in the context of a project focused on updating the red list of the Swiss bees (Müller & Praz, in press, see also Text S1). In total, 6200 plots were surveyed. All quadrats were sampled several times per year by seasoned specialists in bee taxonomy. The number of sampling campaigns per year vary as a function of elevation where higher elevation plots were sampled fewer times because of the shorter vegetation period. Most of our data was taken in a standardised way. Nevertheless, a minority of the samples come from diverse projects that, in some cases, used different methodologies, that we included to get a maximal cover of the territory. To minimise the risk of varying sampling intensity and ensure the comparability of all our samples, we removed all plots with less than 5 species to avoid including under-sampled localities (2730 plots). We also removed the plots within the 2 % higher quantiles of species richness to avoid potential over-sampling (128 plots). At the end, we used data from 3343 plots, containing 52092 records, that is, wild bee species occurrences (mean±sd=15.58±9.81 wild bee species per plot) and a total of 547 wild bee species (Table S1). The used database includes more than 98% of the species predicted to be present in Switzerland based on species accumulation curves (Fig. S1). All data used in this study were projected on the same 100 m by 100 m grid covering all of Switzerland (see Fig. S2 for methodological framework). The entire dataset can be accessed on GBIF (Praz et al. 2022).

We selected eight functionally relevant traits from the European trait database (compiler: Stuart Roberts; pollinator loss module of the EU- FP6 ALARM project, version: 01.2017),

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for which sufficient data were available (Fournier et al., 2020). Specifically, we used the following traits and definitions: (1) intertegular distance (ITD), (2) feeding specialisation; (3) tongue length, (4) beginning of the adult flying period (hereafter phenology start), (5) duration of the flying period (hereafter phenology duration), (6) nesting mode (hereafter belowground), (7) parasitic behaviour (hereafter cleptoparasite), (8) sociality (hereafter solitary). Details on the traits can be found in Text S2 and Table 1.

We derived several α-diversity metrics using the data described above. For taxonomic α-diversity, we calculated the species richness (S) and the Shannon diversity index (H'). For functional α-diversity metrics, we first standardised all trait values by subtracting the mean and dividing by the standard deviation, to ensure that they had the same unit. We then calculated the community-weighted mean value (CWM) of each trait, which can be used to identify major patterns in trait variation within wild bee communities (Woodcock et al., 2014). Moreover, we calculated three complementary indices of functional diversity: functional richness, evenness and dispersion following Fontana et al. (2016) and Laliberté and Legendre (2010). We further calculated ß-diversity metrics in terms of the local community contribution to taxonomic and functional ß-diversity (LCBD) using the approach of Legendre and Cáceres (2013). This approach provides the ecological uniqueness (e.g. taxonomic and functional) of the sites in terms of community composition. Large LCBD values indicate sites that have unusual species combinations and/or strongly different species compositions in comparison to other sites with low LCBD values (Legendre 2014). For further information on the definitions and calculation of the metrics, see Text S3.

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2.3 Environmental predictors

2.3.1 Climate

To infer climate gradients, we considered the main trends in climatic conditions across Switzerland using the 19 Bioclim variables of the CHELSA database set at 1x1 km resolution (Karger et al., 2017), which provide information about biologically relevant aspects of climate for 1979–2013. Using these data, we first ran a PCA with 100,000 randomly sampled cells (Table S2). We then projected the remaining cells onto the PCA. The first four PCA axes represented the main trends in climate, i.e. temperature, precipitation, climate seasonality and temperature range (92% of the total variation, see also Table S2), and were selected for further analyses. Finally, the resulting maps were downscaled (from 1 km by 1 km cells to 100 m by 100 m cells) to match the resolution of the other datasets. See Text S4 for details on the PCA axes and Fig. S3 for maps corresponding to the PCA results.

2.3.2 Vegetation

To infer resource gradients, we mapped the major trends in vegetation across Switzerland using plant occurrence data from the biodiversity monitoring programme of Switzerland (BDM, InfoFlora). The BDM contains about 500 plots distributed regularly across Switzerland, which were surveyed between 2015 and 2019 (detailed information about plant survey: https://biodiversitymonitoring.ch/index.php/en/). In total, the dataset includes 1,727 species, representing about half of the Swiss flora.

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We first ran a PCA of the plant occurrence data, in order to reduce the dimensionality of the dataset and capture the main trends in vegetation structure and composition. We selected the first four PCA axes, representing 43% of the total variation in plant occurrence, for further analyses (PCA1 = 24%; PCA2 = 12%; PCA3 = 4%; PCA4 = 3%, Table S3). All other axes explained < 2% of the variation. We then modelled the distribution of the four PCA axes. This step was meant to avoid gaps in the datasets and to transfer the vegetation information onto the same grid as used for bees. Specifically, each plant PCA axis was modelled individually using the raw 19 CHELSA variables as descriptors (Text S5). The random forest algorithm was trained on 80% of the data and evaluated on the remaining 20%, stratified according to the response variable (function 'createDataPartition' in R package caret v. 6.0-86, Kuhn, 2008). Model training and parameter tuning were done using three times three-fold cross-validation (function 'train' in R package caret). The best model was chosen based on the root mean squared error (RMSE), mean absolute error (MAE) and R2 measured on the trained dataset.

The four plant PCA axes represent the main trends in plant community composition across Switzerland. The first PCA axis was highly correlated with climate (> 0.7) and thus excluded from the analyses. The other three PCA axes (PCA2–PCA4) represented gradients of plant communities: from those dominated by coniferous trees to other communities (named mid-elevation coniferous), from dry to wet vegetation (named dry–wet), and from woody to open plant communities (named forest). See Text S5 for details on the interpretation and Table S3 and Fig. S4 for results.

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2.3.4 Land use

We used land-use and land-cover (LULC) data from Swiss Area Statistics set at 100 x 100 m resolution (Fig. S5a, Altwegg & Weibel, 2015), collected in the period 2015 to 2018. For modelling, we focused on three of the four principal domains: urban, agricultural and forest (see Text S6 for additional details). We calculated the percentage of urban, agricultural and forest cells in 200, 500, 1000 and 2500 m radii around each raster cell centre (Fig. S6). In addition, we initially considered land-use intensity as an important driver of bee diversity using a country-scale land-use intensity map (Meier et al., 2020) based on habitat type and environmental data. Due to high collinearity with several predictors (Fig. S7), however, we ultimately did not use land-use intensity in the final analyses.

2.3.5 Beekeeping intensity

To assess beekeeping intensity, we used annual data on the spatial distribution of beekeeping locations and the number of hives in Switzerland, which were obtained from the cantonal veterinary offices. The considered period was 2012 to 2018. As exceptions, data were only available from the period 2012–2014 for the canton of Basel and from 2013–2018 for the canton of Vaud. The data from each veterinary office were checked separately, and only records of beekeeping locations with reliable coordinates were included. We then calculated the number of honeybee hives in 200, 500, 1000 and 2500 m radii around each 100 m by 100 m raster cell centre (Fig. S8).

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2.4 Elevation and protected areas

We used the digital elevation model of Switzerland (DHM25, see swisstopo, 2021) to obtain elevation values and to study the elevational patterns of the predictors (Fig. S9). Swiss protected areas include different types of spatial objects that vary in the degree of anthropogenic influence, with some of them subjected to strict levels of protection and cover around 27 % of the surface (Table S4). Hence, we classified the protected areas in two groups. First, we considered only those areas that are strictly protected (i.e. protected areas *sensu stricto*). These protected areas include only the biotopes of national importance (dry grasslands, fens, bogs, amphibian reproduction sites, floodplains), the Swiss National Park, Ramsar areas, forest reserves and private forest and nature reserves (i.e. owned by Pro Natura), which cover around 5.6% of the Swiss surface (Table S4, Delarze et al., 2016). Second, we considered protected areas with lower degrees of protection and variable land-use intensity and anthropogenic interference, referred as protected areas *sensu lato* (Table S4).These areas cover ca. 21 % of the Swiss surface. We also combined the two classes of protected areas in a single one (all protected areas).

2.5 Variable selection

We selected variables that had Pearson intercorrelations < 0.7 (Fig. S3, Dormann et al., 2013). For the variables that were calculated using 200, 500, 1000 and 2500 m buffers (i.e. beekeeping, land use and land-use intensity), we also ran preliminary analyses including all variables to assess which neighbourhood windows were the best descriptors of the various

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bee diversity metrics. We found that the variables calculated at 2500 m around the raster cell centre were the best predictors.

After the variable selection, we retained climate (4 PCA axes), vegetation (3 PCA axes), beehive density (number of beehives in a 2500 m radius), and land use (percentage of urban, agricultural and forest in a 2500 m radius) for further analyses. These variables represent gradients in climate, resource availability, habitat amount and disturbance, respectively. All variables were scaled and centred prior to analyses.

2.6 Statistical analyses

All analyses were conducted in the R environment v. 4.0.3 (R Core Team, 2020). All α and ß taxonomic and functional diversity metrics (species richness, Shannon diversity, TOP, TED, FDis, LCBD taxonomic, and LCBD functional), as well as the CWM of the eight studied traits, were modelled using the selected variables (see previous section). Model calibration, parameter tuning, and model performance and selection were done following the same steps as for the vegetation structure and composition (section 2.3.2). Three algorithms were tested: generalised linear models (GLM), neural networks (nnet, Venables & Ripley, 2002), and random forests (rf, Liaw & Wiener, 2002). Model performance on the test data was estimated with three metrics, that is, the root mean squared error (RMSE), the mean absolute error (MAE) and the R^2. Random forest analysis produced the best results for each diversity metric, having the lowest RMSE and MAE, and the highest R^2 (random forest R^2 was always > 0.9, see Table S5 for more detail) and was used to produce country-scale predictions of

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diversity patterns (Table S5, Figs S10–S11). The importance of each descriptor in the random forest models was estimated as the averaged difference across all trees (before and after permuting a variable) in root mean squared error (RMSE) computed on the out-of-bag data and normalised by the standard error (function 'varImp', package *caret*). In addition, we used partial dependence plots (PDP) to assess the changes in diversity metrics while limiting the influence of other descriptors (Friedman, 2001; Greenwell, 2017). PDPs are especially useful for visualising the relationships discovered by complex machine learning algorithms such as random forests (Greenwell, 2017). In particular, PDPs help visualise the relationship between one specific predictor and the response variable while accounting for the average effect of all other predictors in the model.

We identified hotspots of wild bee α and ß taxonomic diversity and functional diversity using the predicted maps of the different diversity metrics. Specifically, we retained only those cells containing diversity values from the upper 10th percentile of their distribution.

3. Results

3.1 Wild bee spatial diversity patterns in Switzerland

We found countrywide patterns in wild bee taxonomic and functional diversity in Switzerland (Figs 1 & S13). Specifically, we found wild bee diversity metrics to be strongly structured along elevation gradients (Figs 1a–e & S1c–d), with taxonomic and functional α-diversity decreasing at higher elevations (> 2000 m a.s.l., Fig. S13a–e). Furthermore, community attributes showed high Pearson's correlations, not only between species richness and

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Shannon diversity (r = 0.86, Fig. 2h), but also between species richness and functional richness (TOP, r = 0.83). While trait evenness (TED) generally declined with elevation, there was also a local maximum at ca. 1300 m a.s.l. (Fig. S13e). The predicted CWM of the eight selected traits also showed important shifts with increasing elevation (Figs S12 & S14). Specifically, high-elevation wild bee communities had a lower proportion of belowground-nesting, cleptoparasitic and solitary bee species (Fig. S14a, b, f). Additionally, the proportion of short-tongued species (Fig. S14g) and the proportion of generalist species decreased (Fig. S14c), while body size increased (Fig. S14d). Taxonomic LCBD and functional LCBD, which provided an indication of the ecological uniqueness of the cells, were correlated (r = 0.63) and negatively associated with α-diversity metrics, such as richness (r = -0.71), Shannon diversity (r = -0.83) and FDis (r = -0.80). We found that taxonomic and functional uniqueness increased with elevation, resulting in a negative correlation with taxonomic and functional richness, with the pattern being stronger for taxonomic than for functional LCBD (Fig. 1f–g).

3.2 Drivers of wild bee diversity

We assessed the importance of each predictor individually from the four categories considered, that is, climate, vegetation, land use and beekeeping. Climatic variables, represented by the first four axes of the climate PCA, were always among those explaining the highest proportion of variance for all responses, followed generally by vegetation, land-use and beekeeping metrics (Figs 2 & S15). Concerning climate, temperature range (PCA4, Table S2) explained a large proportion of the variation in taxonomic and functional α-diversity metrics (Fig. 2a–e), whereas temperature and precipitation gradients explained a

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large part of the variation in the taxonomic and functional LCBD ß-diversity (Fig. 2f–g, Table S2) and in most CWMs, including the proportion of belowground-nesting, cleptoparasitic and solitary bee species, ITD, phenology duration, and tongue length (Fig. S15). Higher temperature values (lower PCA scores) enhanced wild bee taxonomic diversity and functional richness (TOP, Fig. 3 - climate PC1), but the patterns were less clear for the remaining α and ß functional diversity metrics (Fig. 3- climate PC1), as well as for the CWM of the studied traits (Fig. S16). Xeric conditions boosted species and functional richness and Shannon diversity, as well as functional LCBD ß-diversity (Fig. 3- climate PC2), particularly in the lowlands of southwestern (canton of Wallis) and southeastern (canton of Graubünden) Switzerland. Finally, wild bee diversity metrics generally decreased in areas with higher temperature ranges (Fig. 3, climate PC4).

Wild bee diversity metrics and traits were structured along the three PCA axes depicting different gradients of vegetation change. First, changes in the plant communities based on their drought tolerance (PCA2, dry–wet, see also Table S3) influenced several wild bee diversity metrics. Increasingly drought-tolerant plant communities boosted wild bee species richness, functional richness (TOP), Shannon diversity and taxonomic ß-diversity, whereas functional evenness (TED) and dispersion (FDis) peaked at intermediate values. Furthermore, drylands had more solitary, small and belowground-nesting bees (Fig. S16). Second, changes from open vegetation to forest had a small effect on wild bee diversity metrics, with the exception of TED, which peaked at intermediate values. Finally, plant PCA2, representing plant communities in coniferous forest at mid-elevation (see Table S3) mostly affected TED and functional ß-diversity (Fig. 3).

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Wild bee diversity metrics were influenced differently by the three types of land use considered (i.e. agricultural, forest, urban, Figs 2 & S15). Wild bee species and functional richness were lowest in landscapes covered ca. 50% by agricultural areas (Fig. 3). Landscapes containing higher proportions of agricultural land were associated with reduced TED (Fig. 3) and taxonomic LCBD ß-diversity, as well as shorter tongues and a lower proportion of belowground-nesting and solitary wild bee species (Fig. S16). Wild bee species and functional richness (TOP) increased with larger proportions of forest in the landscape (Fig. 3). Conversely, Shannon diversity, TED and FDis peaked in landscapes with intermediate levels of forest (Fig. 3). Furthermore, in landscapes increasingly dominated by forest, wild bee communities had higher proportions of belowground-nesting and solitary species, as well as longer tongues (Fig. S16). Finally, increasingly urbanised landscapes enhanced wild bee species and TOP, but reduced Shannon diversity, TED and FDis (Fig. 3). Strikingly, the local community contributions to functional ß-diversity (LCBD functional) increased when landscapes became more urbanised (Fig. 3) suggesting original combinations of traits, whereas taxonomic LCBD remained largely unaffected (Fig. 3). Furthermore, urban areas triggered changes in trait values. For instance, the proportion of belowground-nesting bees and feeding specialisation decreased as urban area increased, while the proportion of cleptoparasitic and solitary bees and the phenology duration increased (Fig. S16).

Finally, beekeeping was the predictor explaining the lowest percentage of variance for all the responses modelled (Fig. 2), with some metrics being completely unaffected, such as FDis (Fig. 3) and phenology duration (Fig. S16). Nonetheless, species and functional richness and

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Shannon diversity increased with increasing beekeeping and then stabilised at high values (Fig. 3). Interestingly, TED, taxonomic ß-diversity and feeding specialisation decreased with larger numbers of beehives in the landscape (Figs 3 & S16).

3.3 Identification of hotspots

Predicted species richness, Shannon diversity, TOP, FDis and TED were larger in urban areas than in forest and agricultural areas (Fig. S17a–e), whereas taxonomic and functional LCBD were lower in urban areas (Fig. S17f–g). Nonetheless, because agricultural areas include high-elevation alpine meadows, which are typically species poor, we also compared wild bee diversity at low (197–1000 m a.s.l., Fig. 4), mid (1000–2000 m a.s.l., Fig. S19) and high (> 2000 m a.s.l., Fig. S20) elevations. At mid and high elevations, urban land use represents a very small proportion of the total land use (Figs S19–S20) and does not represent major settlements but other types of urban land use (see Text S6), which hampered comparisons. Further, at low elevations, we found that agricultural and urban areas have a similar species richness (Fig. 4 In addition, agricultural areas harbour larger Shannon diversity and functional dispersion (FDis) (Fig. 4), whereas urban areas have a higher wild bee species richness, TOP and TED. ß-diversity was also higher in urban areas (Fig. 4).

3.4 Protected areas

We assessed the representation of wild bee diversity facets and metrics in protected areas, considering different levels of protection. Protected areas followed elevation gradients. When considering protected areas *sensu lato*, we observed a clear positive elevational gradient (Fig.

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5b), whereas protected areas *sensu stricto* had a unimodal distribution along elevation (peaking at intermediate elevations of 1000–2000 m a.s.l., Fig. 5d).

The majority of α- and ß-diversity hotspots (cells with the upper 10% diversity values) were predicted in un-protected areas (Figure 5, see also Figure S25). This was particularly prominent for α-diversity metrics (species richness, Shannon diversity, functional richness and dispersion), typically found in the lowlands, with more than 75% of the hotspots predicted in unprotected land (Fig 5). In the case of ß-diversity hotspots, the overlap with protected areas was substantially higher (Figure 5a & g). For instance, nearly 50% of the taxonomic LCBD hotspots, typically found in highlands, were predicted in protected land (Fig. 5g).

The overlap between the hotspots of the different diversity facets of wild bee communities varied substantially depending on the degree of protection (Fig. 5). We found α-diversity hotspots to be better represented within the protected areas *sensu stricto* (Fig. 5c), with the proportion of protected cells containing the highest diversity metrics (e.g. 1-10% of the diversity gradient in Fig. 5c) larger than the national average (ca. 5.6 %). Conversely, ß-diversity hotspots were better represented within the protected areas *sensu lato* (Fig. 5a). We further compared the representation of diversity hotspots between protected areas *sensu lato* and *sensu stricto*. Hotspots of α-functional metrics were equally distributed in protected areas *sensu stricto* (~49 %, Figure 5g) and protected areas *sensu lato* (Figure 5g). However, for the remaining metrics, diversity hotspots were always found in higher proportions within

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protected areas *sensu lato,* specially for ß-diversity hotspots (Figure 5g). Finally, regarding the occurrences of the bee species in the community plots, seven species were only sampled in protected areas *sensu stricto* and nine species in protected areas *sensu lato* (Figure S25).

4. Discussion

Wild bee diversity metrics followed clear elevation gradients. Species richness, functional richness, Shannon diversity and functional divergence declined monotonically with elevation, taxonomic and functional ß-diversity increased with elevation, and functional evenness followed a hump-shaped relationship. Elevation gradients represent one of the most prominent ecological gradients, shifting species assemblages of plants (e.g. Pellissier et al., 2010) and other taxonomic groups, such as grasshoppers (Pitteloud et al., 2021) and bumblebees (Sponsler et al., 2022). Elevation gradients select for specific phenotypes, which generates multiple patterns, including mid-elevation peaks (hump shapes), monotonic declines and unimodal distributions, depending on the group and context (Rahbek, 1995). In any case, the number of wild bee species is typically lower in the highlands of mountain slopes, as changes in climatic variables, as well as a shortened phenological season and reduced productivity and resource availability, constraint species persistence (Rahbek, 1995).

Nonetheless, high-elevation communities tend to be ecologically unique, as they are composed of species that display specific adaptations to survive at high elevation, and consequently contribute disproportionately to large-scale taxonomic and functional ß-diversity (e.g. invertebrates, Fontana et al., 2020; lichens, Nanda et al., 2021). In the case of

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wild bee communities in temperate latitudes, high-elevation areas contain multiple wild bee species, including several high-elevation specialist bumblebee species, which have been studied in Switzerland (Pellissier et al., 2013). High-elevation bumblebees are highly sensitive to heat stress (Pellissier et al., 2013), which might extend to other high elevation bees. Hence, global warming threatens to trigger drastic declines of these taxa due to rising temperatures and, potentially, increased competition with migrating bees from lower elevation (Pradervand et al., 2014). Such a change has also been observed for plant communities (Vitasse et al., 2021) and herbivorous insects (e.g. grasshoppers, Descombes et al., 2021).

In agreement with the xeric hypothesis (Michener, 1979), wild bee diversity thrived in warm, xeric areas such as dry grasslands. At a global scale, wild bee diversity has been found to be highest in these climatic regions (e.g. in Mediterranean-type regions, Orr et al., 2021). Here, we demonstrate that it also applies to much smaller spatial scales in the Alps. Xeric areas might recreate the conditions where the clade originated in Gondwana (Michener, 1979), and bees may therefore possess adaptations to such environments (Michener, 1979). Xeric areas tend to have large plant species pools and promote specialised interactions (Minckley et al., 2000). In the Alps, dry grasslands are well-known biodiversity hotspots but are increasingly threatened by climate and land-use change (Boch et al., 2019a).

We found urban and agricultural land-uses to promote distinct diversity metrics. Specifically, while Shannon diversity and functional dispersion were higher in increasingly urbanised

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landscapes, species richness, functional richness and functional evenness were higher in increasingly agricultural landscapes. Furthermore, our results showed lower ß-diversity in cities than in forest and agricultural areas. This is in line with recent research showing that urban features (e.g. technological innovations, gardening techniques) tend to be similar among different cities (Alberti, 2015), thereby leading to a convergence and homogenisation in the selected phenotypes and species (Groffman et al., 2014). While cities can harbour diverse bee communities (Theodorou et al., 2020), they simultaneously exert a strong filter for certain traits (Fournier et al., 2020), and might even represent a subset of the species from agricultural areas (Banaszak-Cibicka & Żmihorski, 2020).

We did not find clear evidence that beekeeping negatively influences bee diversity, even though Switzerland has one of the highest hive densities in Europe, with around 4 hives/km^2 in 2019 (Charriere et al., 2018). This might be due to the elevational structure of beekeeping, which is far more intense at low elevations where bee richness is also highest. Beekeeping might be located in areas with high resource availability. Our data could not incorporate the temporal and spatial variability in urban beekeeping, including the movement of hives uphill during the summer season. In any case, wild bee declines might be lagged and gradual, thus requiring temporal data, as observed in the Mediterranean Basin (Herrera, 2020). This is concerning, as beekeeping is changing fast in Switzerland. For instance, urban beekeeping doubled in Swiss cities between 2012 and 2018 (Casanelles-Abella & Moretti, 2022).

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Our study comes with limitations. First, we did not model individual species occurrences but focused on community attributes. Although species distribution models (SDMs) provide species-specific responses to environmental gradients, they require a sufficient number of observations to be reliably applied (Guisan et al., 2013), which in our case would have excluded many rare species. Conversely, modelling community attributes makes full use of community data and helps to highlight general diversity trends. Nonetheless, wild bee SDMs are a necessary next step to further understand bee ecology and forecast changes in distribution ranges due to global change drivers (e.g. climate, land use), as has been done for a large number of taxa (Isaac et al., 2020). Second, we assessed resource availability gradients through vegetation patterns, as we could not use direct metrics of plant diversity or nectar/pollen productivity, both important drivers of bee diversity at different scales (Orr et al., 2021). Developing high-resolution countrywide maps of plant diversity and nectar/pollen productivity, including spontaneous and horticultural non-native plants, will be key to improving predictions of wild bee diversity and occurrence. Third, we did not explore wild bee phylogenetic metrics, which might have different patterns than functional and taxonomic diversities (Devictor et al., 2010), due to a lack of a comprehensive bee phylogeny (Hedtke et al., 2013). Fourth, we did not consider the extent of overlap among wild bee diversity, ecosystem functions (especially pollination), and nature contributions to people. Finally, we did not explore the spatial configuration and connectivity of protected areas, which might play a key role in bee biodiversity (Schüep & Hermann, 2011).

Our results call for the implementation of multiple-faceted approaches to inform biodiversity conservation planning and strategies. The spatial mismatch in the distribution of the different

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diversity facets and scales shows the necessity of considering multiple dimensions to study and protect biodiversity in all its complexity (Pollock et al., 2020). In that regard, protected areas *sensu stricto* and *sensu lato* provide complementary protection on different biodiversity dimensions. On the one hand, strictly protected areas, which have highly regulated anthropogenic intervention and that contain habitats with high plant richness (Delazare et al., 2016), serve as highly valuable habitat for bee α-diversity. On the other hand, protected areas *sensu lato*, which are mostly located in higher elevations, also represent an important infrastructure to protect bee ecological uniqueness, although they experience more anthropogenic influence.

Our study points out the role of unprotected land for wild bee conservation. Although α-diversity hotspots were well-represented in strictly protected areas, these areas cover a small surface and some of them are under stress due to global change (Boch et al., 2019a). For instance, in Switzerland the habitat quality of dry grasslands is decreasing at an alarming rate (Boch et al., 2019a). Furthermore, protected areas *sensu lato* are often found in high elevation, areas that are expected to suffer substantially from changing temperatures. Among other, high elevation areas may have modified plant assemblages and be colonised by lowland species, which will likely negatively affect high elevation specialist bees (Pradervand et al., 2014). Therefore, the existing network of unprotected ecological infrastructure (different natural, seminatural and novel habitats) found within anthropogenic landscapes (e.g. agricultural areas, cities) or in seminatural habitats represents a key element for further safeguarding wild bee diversity, particularly if properly integrated and planned within the strictly protected areas. Unprotected areas of value for wild bee conservation

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include a myriad of habitats, such as flower strips, urban gardens, and ruderal sites, and are often quite sensitive to global change drivers, such as land-use change, global warming and invasion. It will be important to quantify the specific contributions of this network of unprotected areas to wild bee diversity.

The Post-2020 Global Biodiversity Framework draft stressed the importance of protected and conservation areas to mitigate ongoing biodiversity loss and set an ambitious goal of protecting 30% of all land by 2030 (Convention for Biological Diversity, 2020). Nonetheless, without an evaluation on performance of protected areas these actions may ultimately have a limited impact on reducing biodiversity declines. Protecting insect diversity is challenging, because the spatial distribution of insect multi-facet diversity remains elusive for many groups (Chowdhury et al., 2022). In that regard, our study provides a practical case on the already stated importance of spatial predictive models to overcome the distributional gaps and contribute to informing the planning and evaluation of biodiversity conservation measures (Pollock et al., 2020). To achieve the global conservation goals, countrywide prioritisation of existing and future protected areas emerges as a major issue, due to the potential spatial mismatch among biodiversity facets and the uncertainty of the conservation value of some protected areas under future conditions. Solving these issues represents a pressing problem in the face of future global change.

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Data Availability

Data on the community metrics are available from ENVIDAT under the doi: https://doi.org/10.16904/envidat.337.

The raw species records data are protected by a code of conduct common to all Swiss national data centres. Those data can be ordered via infospecies (https://www.infospecies.ch/fr/donnees/) according to this deontology. The dataset is also available on GBIF.org (https://doi.org/10.15468/ksfmzj) at a 5km grid squares, according to nationally agreed ethical framework.

The bee trait database is managed and maintained by Stuart Roberts and enquiries and requests for data can be made to stuart.roberts@cantab.net. Trait data used in this paper will be made available in ENVIDAT once the full database from Stuart Roberts is published in Oracle for Research.

Data on the swissTLMRegio protected areas are available from https://opendata.swiss/en/dataset/swisstlmregio-schutzgebiete.

The DHM25 is available from https://www.swisstopo.admin.ch/en/geodata/height/dhm25.html#technische_details. Land-use data for Switzerland can be obtained by request from the Federal Office of Statistics FOS (www.bfs.admin.ch). Plant data are available from infospecies (https://www.infospecies.ch/fr/donnees/) as well. Data on beekeeping in Switzerland can be obtained from the Cantonal Offices with a confidentiality agreement.

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Acknowledgments

We acknowledge financial support from the DFG (FO 1420/1-1; project FunShift) and the WISNA programme from the German Federal Ministry of Education and Research to BF; JCA was supported by the Swiss National Science Foundation (project 31BD30_172467) within the programme ERA-Net BiodivERsA project "BioVEINS: Connectivity of green and blue infrastructures: living veins for biodiverse and healthy cities" (H2020 BiodivERsA32015104) and by the Swiss Federal Office for the Environment (FOEN) in the framework of the project "City4Bees" (contract no. 16.0101.PJ/S284-0366). We also acknowledge Göhner Stiftung for supporting this project (2019-2917/1.1). Finally, we thank Pro Natura for providing the maps on their forest and nature reserves. The bee dataset has been assembled with funding from the Federal Office for the Environment to info fauna (Neuchatel, Switzerland), within a project coordinated by C. Praz and A. Müller. We thank Kurt Bollmann for his input on Swiss protected areas.

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Table 1. Wild bee traits used in this study. For each trait, we provide the name used in the article, the type of trait, the unit for numeric traits, the categories for categorical traits, and a description. See also Text S2 for details.

Trait	Name used	Type	Unit	Categories	Description
Intertegular distance (ITD)		Numeric continuous	mm		The distance across a bee's thorax between the base of the wings, which relate to body size and mobility
Tongue length		Categorical		0: long tongue 1: short tongue	The community level of species that have short tongues. Indicates the diversity of floral morphologies, and consequently resources, a species can access
Nesting behaviour	Belowground	Categorical		0: aboveground 1: belowground	The community level of species that nest below ground
Cleptoparasite	Cleptoparasite	Categorical		0: non-cleptoparasite 1: cleptoparasite	The community level of species that are cleptoparasites
Sociality	Solitary	Categorical		0: primitive social, subsocial and eusocial	The community level of species that are social.

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			1: solitary	
Phenology start	Numeric discrete	Week	1–52	First week of a bee species' active period
Phenology end	Numeric discrete	Week	1–52	Last week of a bee species' active period
Feeding specialisation	Categorical		0: monolectic and oligolectic 1: polilectic	The community level of species that are polylectic. Indicates the dietary breath.

Figures

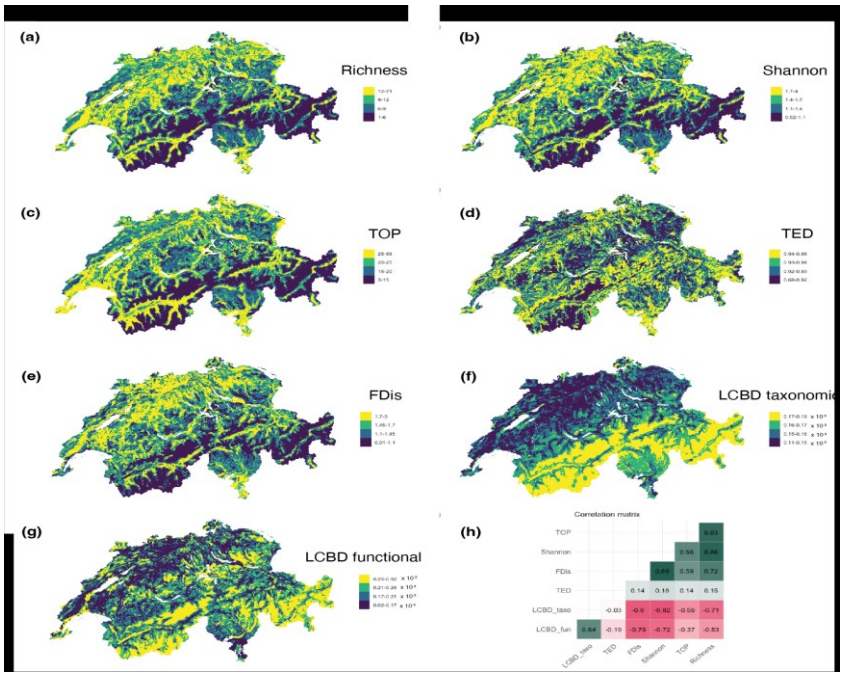

Figure 1. Wild bee diversity in Switzerland. Maps of taxonomic α-diversity metrics: (a) species richness and (b) Shannon diversity. Maps of functional α-diversity metrics: (c) functional richness expressed as trait onion peeling (TOP), (d) functional evenness expressed as trait evenness distribution (TED), and (e) functional dispersion (FDis). Maps of the local

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community contributions to (f) taxonomic and (g) functional ß-diversity (LCBD). The four values in all maps were obtained from the quantile values of 25%, 50% and 75% for each response separately, with yellow indicating higher values and dark purple indicating lower values. (h) Pearson correlation matrix (r) among the response variables, with red shades indicating positive correlations and blue indicating negative ones. Note that empty (white) regions within Switzerland correspond to water bodies (e.g. lakes, rivers). See Supplementary Material for maps of the community-weighted means of the considered traits (Fig. S12).

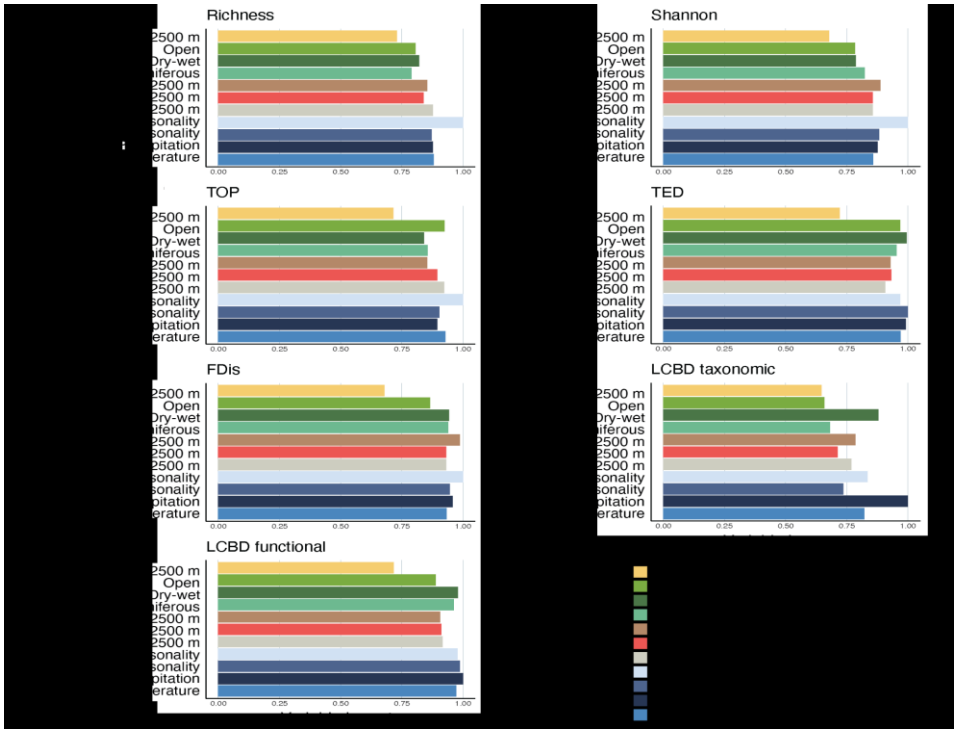

Figure 2. Importance of environmental descriptors as predictors of the studied α and ß taxonomic and functional community attributes of wild bees in Switzerland. Predictors were classified into four main categories: climate, vegetation, land use and beekeeping. Variable importance was estimated using the residual sum of squares from random forests models

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(Breiman, 2001). Longer bars indicate descriptors that are better predictors of community attributes. (a) Species richness; (b) Shannon diversity index; (c) trait onion peeling (TOP); (d) trait evenness distribution (TED); (e) functional dispersion (FDis); (f) local community contributions to taxonomic ß-diversity (LCBD taxonomic); (g) local community contributions to functional ß-diversity (LCBD functional). Note that all importance values were divided by the maximum value to obtain a comparable range from 0 to 1. Climate and vegetation variables represent the PCA axes (PCA 1–4 for climate and PCA 2–4 for vegetation, representing 17% of the variation; for details see Methods and Tables S3–S4).

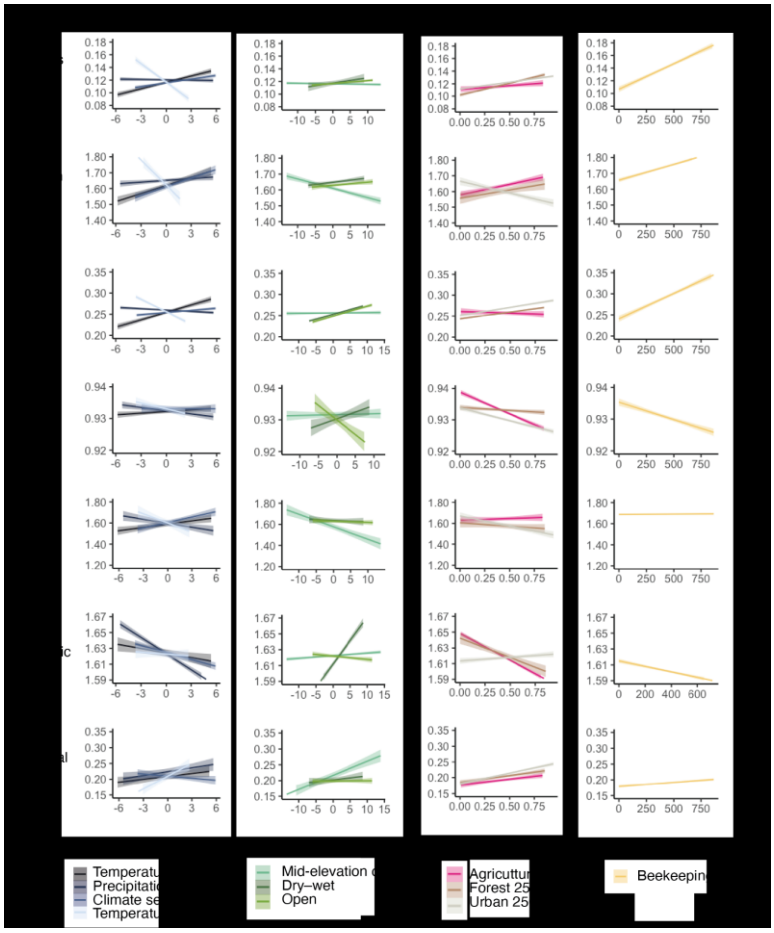

Figure 3. Predicted changes in α and ß taxonomic and functional metrics along multiple environmental gradients. The partial dependence plots summarise the marginal effect (i.e. the

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effect of each specific variable when the others are kept constant) of the predictors representing climate (x-axis = PCA axis scores), vegetation (x-axis = PCA axis scores), land use (x-axis = proportion of each land-use type in a 2500 m radius) and beekeeping intensity (x-axis = number of honeybee hives within a 2500 m radius) on the predicted values of wild bee α and ß taxonomic and functional metrics. The y-axis displays the range of predicted values of each response variable: (a) species richness, (b) Shannon diversity index, functional richness (trait onion peeling TOP), (d) functional evenness (trait evenness distribution TED), (e) functional dispersion (FDis), (f) the local community contributions to the taxonomic ß-diversity (LCBD taxonomic), and (g) the local community contributions to the functional ß-diversity (LCBD functional). Fitted lines and the 95% confidence interval (depicted with shaded bands) were obtained from linear models. Climate and vegetation variables represent the PCA axes (PCA 1–4 for climate, PCA 2–4 for vegetation; for details see Methods and Tables S3–S4). Information on α and ß taxonomic and functional diversity metrics can be found in the methods. Partial dependence plots on the community-weighted means of the studied traits can be found in Fig. S16.

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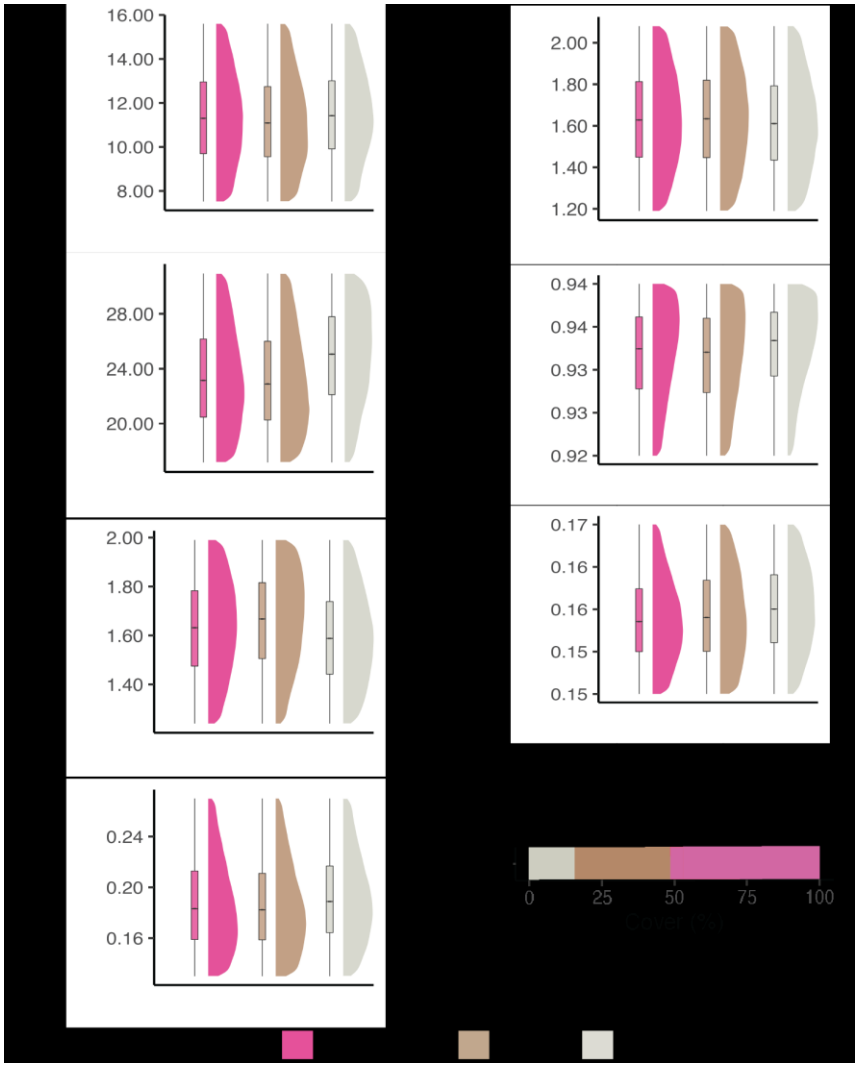

Figure 4. Flat violin plots and boxplots showing the differences in the α and ß taxonomic and functional metrics among the three main land-use types, agricultural, urban and forest, at low elevation (197–1000 m a.s.l.). Notches in the boxplots indicate the 95% confidence interval of the median. Flat violin plots were created using the *raincloud* package in R (Allen et al., 2019). (a) Species richness, (b) Shannon diversity index, (c) functional richness (trait onion peeling TOP), (d) functional evenness (trait evenness distribution TED), (e) functional dispersion (FDis), (f) local community contributions to taxonomic ß-diversity (LCBD taxonomic), and (g) local community contributions to functional ß-diversity (LCBD functional). Note that to facilitate the comparison of the boxplots, the figure shows the data

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between the 10th and the 90th percentiles. (h) Land-use composition (% cover) at low elevations. See Figs S18–S23 for additional plots of the α and ß taxonomic and functional diversity metrics and of the community-weighted means of the eight wild bee traits at low, mid and high elevation.

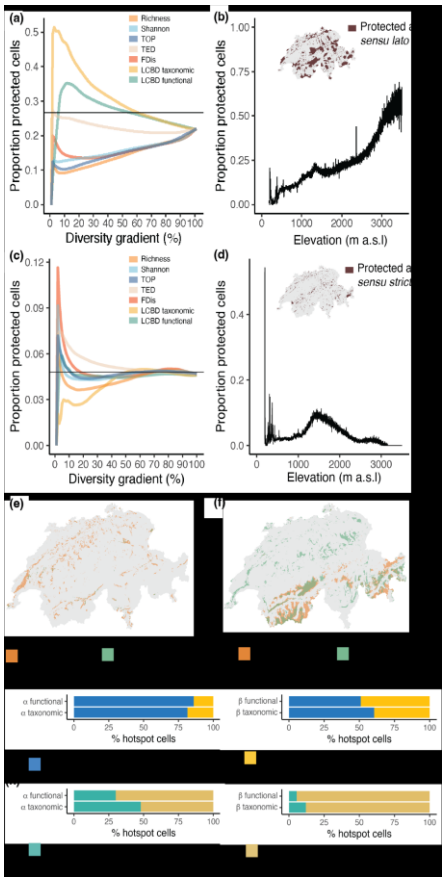

Figure 5. Wild bee diversity and protected areas. Proportion of taxonomic and functional diversities included in (a) the protected areas *sensu lato*, which. including areas with variable management intensity and anthropogenic influence and lower protective measures than protected areas *sensu stricto*, and (c) protected areas *sensu stricto*, i.e.t protected areas that include only those with strict protection measures (see also Table S4). For each diversity

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metric, we ranked each cell from the most to the least diverse using quantile values. The x-axis (diversity gradient in percentage) depicts a decreasing diversity gradient inversely related to the quantiles of the diversity metrics, with lower x-axis values indicating the most diverse cells. The y-axis depicts the cumulative proportion of cells belonging to protected areas. The horizontal black line indicates the proportion of protected cells in all of Switzerland (protected areas *sensu lato:* ca. 21% of the surface; protected areas *sensu stricto*: ca. 5.6% of the surface). (a) and (c) are based on Devictor et al. (2010). Taxonomic α-diversity metrics = species richness and Shannon diversity; functional α-diversity metrics = functional richness (trait onion peeling TOP), functional evenness (trait evenness distribution TED), and functional dispersion (FDis). Taxonomic ß-diversity metrics = local community contributions to taxonomic diversity (LCBD taxonomic); functional ß-diversity metrics = local community contributions to functional diversity (LCBD functional). Proportion of protected cells along an elevation gradient considering protected areas (b) *sensu lato* and (d) *sensu stricto*. The upper maps show the distribution of the protected areas in Switzerland (in grey). (e) Map of α taxonomic and α functional diversity hotspots and their overlap. Hotspot cells always contain the upper 10th percentile of the distribution of all α-diversity metrics. (f) Map of taxonomic and functional ß-diversity hotspots and their overlap. Hotspot cells always contain the upper 10th percentile of the distribution of all ß-diversity metrics. (g) Barplot showing the percentage of protected and unprotected cells that contain the upper 10th percentile of the distribution of all diversity metrics. Protected cells include both protected areas sensu stricto and sensu lato. (h) Within the protected cells in (g), barplot showing the percentage of strictly protected (i.e., sensu stricto) and broadly protected (i.e., sensu lato) cells containing the upper 10th percentile of the distribution of all diversity metrics.

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