Global taxonomic, functional, and phylogenetic diversity of bees in apple orchards

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ABSTRACT

An essential prerequisite to safeguard pollinator species is characterisation of the multifaceted diversity of crop pollinators and identification of the drivers of pollinator community changes across biogeographical gradients. The extent to which intensive agriculture is associated with the homogenisation of biological communities at large spatial scales remains poorly understood. In this study, we investigated diversity drivers for 644 bee species/morphospecies in 177 commercial apple orchards across 33 countries and four global biogeographical biomes. Our findings reveal significant taxonomic dissimilarity among biogeographical zones. Interestingly, despite this dissimilarity, species from different zones share similar higher-level phylogenetic groups and similar ecological and behavioural traits (i.e. functional traits), likely due to habitat filtering caused by perennial monoculture systems managed intensively for crop production. Honey bee species dominated orchard communities, while other managed/manageable and wild species were collected in lower numbers. Moreover, the presence of herbaceous, uncultivated open areas and organic management practices were associated with increased wild bee diversity. Overall, our study sheds light on the importance of large-scale analyses contributing to the emerging fields of functional and phylogenetic diversity, which can be related to ecosystem function to promote biodiversity as a key asset in agroecosystems in the face of global change pressures.

1. Introduction

Biogeography concerns the geographic distribution of species across space and time, and the biotic and abiotic factors that shape those patterns (Brown and Lomolino, 1998). As a discipline, it offers valuable insight into population trends, evolutionary history, extinction risk, and ecosystem services in a rapidly changing environment (Brown and Lomolino, 1998; Violle et al., 2014). Although the study of biogeography has been historically restricted to the distribution of species (i.e. taxonomic biogeography), more recent developments have included the evolutionary history of species (i.e. phylogenetic biogeography) and the spatial distribution of traits and ecosystem function (i.e. functional biogeography). Functional biogeography, in particular, bridges the gap between species-based biogeography and ecosystem functions, species interactions, and ecosystem services, which are fundamental processes from a conservation perspective (Violle et al., 2014). Over the last few decades, studies of biogeography have been centred around well-known organisms - especially plants and larger, charismatic vertebrate species such as mammals, birds, and amphibians (Bennie et al., 2014; Capinha et al., 2017; Farooq et al., 2020; Hochkirch et al., 2021; Olson et al., 2009; Pianka, 1966; Smith et al., 2020; Violle et al., 2014). However, to date, comparatively few biogeographical studies have focused on insects and even fewer on bees, despite bees being one of the most important groups of pollinators (Michener, 1979; Ollerton, 2017; Orr et al., 2021).

Alternatives to taxonomy-based metrics of diversity are particularly relevant for bees and the pollination services they provide to both (agro-)ecosystems and society, because functional and phylogenetic approaches are better predictors of ecosystem processes than taxonomy-based metrics (Blitzer et al., 2016; Grab et al., 2019; Roquer-Beni et al., 2021; Woodcock et al., 2019). This raises many hitherto unaddressed questions related to the role of bees as effective pollinators, especially for pollinator-dependent crops that are cultivated on a global scale. For example, our current understanding of global bee biogeography indicates that the Earth's evolutionary history, along with changing natural and anthropogenic, biotic (e.g. vegetation), and abiotic (e.g. climate) factors, have driven major taxonomic divergences among continents as well as high levels of continental endemism (Ascher and Pickering, 2022; Michener, 2007; Michener, 1979; Ollerton, 2017; Orr et al., 2021). However, the relevance of functional diversity of wild and native pollinators for crop production can be masked by the prevalent use of resource-competitive managed species deliberately introduced in agroecosystems to meet demands for pollination (Geslin et al., 2017).

Biogeography theory predicts that global insect-pollinated crops that have been cultivated, sometimes far outside their native range (Pilcher, 2012; Pollan, 2001), are pollinated by continentally and regionally variable pools of bee species (Michener, 1979; Winfree et al., 2018). The extent to which this involves communities of bees that are functionally and phylogenetically clustered (i.e. more functionally similar and evolutionarily related than expected by chance) is poorly understood. This phenomenon at the biodiversity-productivity nexus is further influenced by the idea that, unlike other groups of pollinators, bees

exhibit a rare bimodal latitudinal biodiversity gradient (Orr et al., 2021), with their species richness at its peak in xeric, temperate regions at mid-latitudes, then decreasing towards higher latitudes as well as lower latitudinal equatorial tropics (Michener, 2007; Michener, 1979; Orr et al., 2021).

One key pollinator-dependent crop that is presently distributed worldwide to become one of the most economically important fruit crops globally is apple (*Malus domestica* Borkh., *Rosaceae*) (FAO, 2022; Pollan, 2001). Apple trees generally are highly dependent on pollinators since most varieties exhibit high levels of self-incompatibility, a characteristic shared with many other orchard crops in the family Rosaceae, such as pear, plum, cherry, and almond (Burns and Stanley, 2022; Pardo and Borges, 2020; Wu et al., 2013). Apple blossoms are an important source of readily accessible floral rewards (pollen and nectar) that are potentially valuable to a wide taxonomic range of pollinators, particularly bees, which have been reported as important flower visitors (Garratt et al., 2014; Leclercq et al., 2022; Pardo and Borges, 2020; Prendergast et al., 2021; Weekers et al., 2022a) and which ensure high levels of cross-pollination required for commercial production (Garibaldi et al., 2013; Olhnuud et al., 2022; Pardo and Borges, 2020; Prendergast et al., 2021; Weekers et al., 2022b).

The extent to which wild bees are well represented in terms of abundance and species richness as flower visitors in commercial apple orchards can be jeopardised by at least two non-exclusive factors that have received little attention across large proportions of apple's current range, particularly at a global scale. First, it has been demonstrated that intensive agriculture is one of the major drivers of wild bee decline through its multifaceted impacts on nesting and floral resources, including the contamination of both with pesticides (Graham et al., 2022; Graham et al., 2021; Vanbergen et al., 2013; Wagner, 2020). Intensive agriculture also is typically associated with the homogenisation of biological communities (Clough et al., 2007; Gabriel et al., 2006; Karp et al., 2012). This generally manifests as strong phylogenetic and functional clustering and comparatively species-poor communities, resulting from a filtering process retaining species from the regional species pool with similar nesting habitats and often broad diet breadth (Ndiribe et al., 2013). Second, recent evidence points towards the negative impact of high densities of managed pollinators, particularly the western honey bee, *Apis mellifera* L., on the local diversity of wild bees and, therefore, also on the expected diversity of local crop pollinators (Angelella et al., 2021; Geslin et al., 2017; Iwasaki and Hogendoorn, 2022; Weekers et al., 2022b). Other bee species are also managed for crop production, e.g. *Apis cerana* F., *Bombus impatiens* C., *B. terrestris* L., *Osmia bicornis* L., *O. cornuta* L., *O. excavata* P., and *O. lignaria* S., but their ecological impacts on wild bees remain less investigated than for *A. mellifera* (Russo, 2016; Russo et al., 2021). This is another major, yet poorly understood, issue in a context in which wild pollinator diversity is known to improve seed set (Blitzer et al., 2016; Garibaldi et al., 2013; Grab et al., 2019; Roquer-Beni et al., 2021; Weekers et al., 2022a) and yields (Garibaldi et al., 2014) in many pollinator-dependent crops.

In this study, we aimed to address global- and local-level factors that influence the abundance and composition of wild bees in apple orchards. Using a standardised methodology, we surveyed the assemblages of bees in commercial apple orchards across six continents during the same year to address the following issues: (i) How do taxonomic (species composition), functional (diversity of ecological traits) and phylogenetic (shared evolutionary history) dissimilarities vary among sites across different spatial scales?; (ii) What is the influence of habitat characteristics, management, and surrounding land cover on wild bee diversity?; (iii) Do apple orchards worldwide share numerically dominant bee taxa, lineages, or functional groups in common?

2. Materials and methods

2.1. Study area and sampling method

During the apple blooming season in 2019 (except Bhutan in 2020), we surveyed 177 commercial apple orchards in 33 countries covering six continents (Fig. 1, see Fig. A.1. and Table A.1) following a strict and standardised protocol combining netting and pan trapping (Droege et al., 2010). Parts of this dataset have already been used in local or subcontinental studies to investigate the diversity of bees in apple orchards (Allen-Perkins et al., 2022; Dorji et al., 2022; Leclercq et al., 2022; Prendergast et al., 2021; Weekers et al., 2022b; Weekers et al., 2022a). Each site was sampled for three days (consecutive if weather permitting) during the peak blooming period. Netting collection incorporated surveying all bee specimens seen directly visiting the blossoms over two 90 min sessions (morning and afternoon) per day, while walking through orchard rows. Passive sampling consisted of deploying of painted pan traps at 9 h00 each day, in three trios (fluorescent yellow, fluorescent blue, and white) on cleared ground. The pan traps were filled with soapy water (Westphal et al., 2008) and were collected at 4 h00. All pan traps were painted at the Agroecology Lab (ULB, Belgium) then dispatched to each collaborator to ensure comparability of the results.

In the present study, we only considered bee species as they are the main pollinators of apple trees (Garratt et al., 2016; Pardo and Borges, 2020). Each bee specimen was identified by regional experts either to species or morphospecies level (except for the *Bombus terrestris* agg. complex, which is hereafter referred to as *B. terrestris* as it is the managed/manageable species among the complex) depending on the available knowledge and identification tools in the specific country; this sometimes required sending of material for expert identification. We aggregated together the records of *Andrena scotica* and *A. carantonica* (hereafter *A. scotica*) due to taxonomic uncertainties. Morphospecies designations were specific to each country. To test whether this decision had an effect of the computation of beta diversity (see Section 2.3.), we ran a separate analysis where we made a random selection, 100 times, of morphospecies names, whereby morphospecies of the same (sub)genus were treated as different species and, at other times, as the same species between countries.

We considered the following bee species as either managed or manageable: *Apis cerana*, *A. mellifera*, *Bombus impatiens*, *B. terrestris* (complex), *Osmia bicornis*, *O. cornuta*, *O. excavata*, and *O. lignaria*. However, our personal observations in situ during the field surveys suggest that non-*Apis* species were often not managed, and we assume that most specimens collected were wild, but could also result from past management. For example, we observed during field surveys that around 30 % of sites used *B. terrestris* colonies in the Iberian Peninsula and neither *B. impatiens* nor *O. lignaria* (only one specimen recorded) seemed to be managed by our collaborating orchardists in North America (see also Osterman et al. (2021)).

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2.2. Biogeographical zones

To investigate the global diversity of bees in apple orchards, we defined a 'biogeographical zone' as a biome (Mediterranean & Xeric, Temperate, Tropical & Subtropical, and Mountain) within a biogeographical realm (Afrotropic, Australasia, West Palearctic, Central Palearctic, East Palearctic, Indomalayan, Nearctic, and Neotropic). Biogeographical realms are divided based on geoelements and historic elements that characterise the evolutionary history of the organisms they host, while biomes are characterised by a climate and climax vegetation (Dinerstein et al., 2017; Olson et al., 2001; Udvardy, 1975). To compare biogeographical zones globally, we used the "Resolve Ecoregions 2017" dataset (Dinerstein et al., 2017) and intersected it
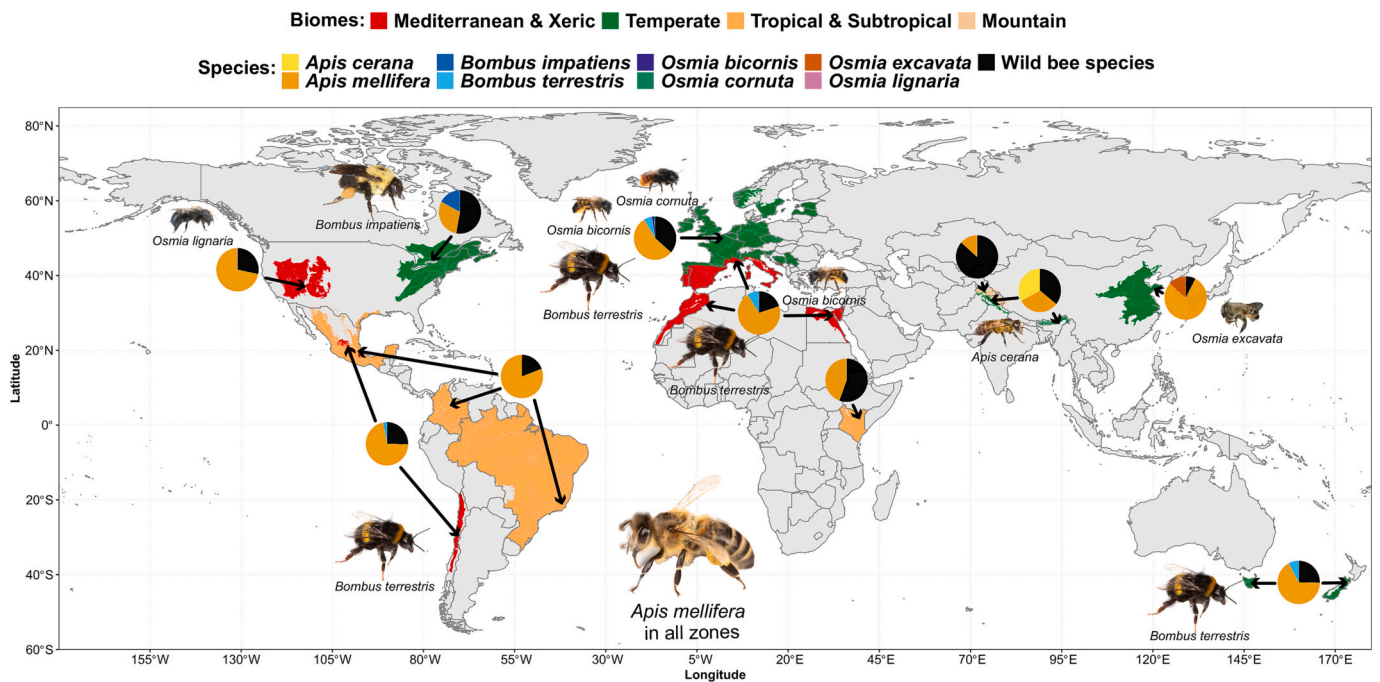
Fig. 1. Map of the sampled biogeographical zones showing the proportions of the various managed or manageable bee species. The biogeographical zones have been delineated by their range within the border of each country sampled. The pie charts show the proportion of both managed or manageable (colours) and wild bee species (black) for each zone (biomes within each realm). The bee images identify the dominant managed (non-*Apis mellifera*) species present in each zone. Photo of *B. impatiens* by © B. Gratwicke, photos of *B. terrestris*, *O. bicornis*, *O. cornuta*, and *A. mellifera* by ©N.J. Vereecken, photo of *A.cerana* by © Z. Soh, photo of *O. excavata* by ©C. Ritner, and photo of *O. lignaria* by © J. Wilson.

with the different site locations. Within these biogeographical zones, ecological regions (i.e. ecoregions) were identified based on faunal and community diversity patterns (Dinerstein et al., 2017; Holdridge, 1947; Olson et al., 2001; Whittaker, 1962). We did not use ecoregions per se because we wanted to compare similar 'habitats' (i.e. biomes) in different regions (i.e. realms); hence both approaches tend to cover similar information (Dinerstein et al., 2017; Olson et al., 2001). Ecoregion delineations have been successfully tested to show that they correspond to sharp community transitions at borders, rather than smooth transition gradients, although the intensity of transition varied across taxa (Smith et al., 2018).

For each site, we computed its related biome and realm and merged these two as one variable ("biogeographical zones") (see Fig. 1 and Table A.1). We merged the following biomes into larger "climate" biomes to ensure sufficient replicates within each biogeographical zone: (i) all temperate forests, temperate grasslands, and tundra biomes into the "Temperate" biome; (ii) all tropical & subtropical forests and tropical & subtropical grasslands biomes into the "Tropical & Subtropical" biome; (iii) "Mediterranean forests, woodlands & scrub" and "deserts & xeric shrublands" biomes into the "Mediterranean & Xeric" biome. The "Mountain" biome was retained. Within the Palearctic realm, China and Pakistan sites were very distant from the rest of the locations (Europe, North Africa, and the Middle East), and therefore, are very likely to contain different bee assemblages (Michener, 2007). Therefore, we decided to divide the Palearctic realm into three parts: West Palearctic (Europe, North Africa, and the Middle East), Central Palearctic (Pakistan), and East Palearctic (China).

2.3. Beta diversity between biogeographical zones

To quantify the patterns of apple-visiting bee assemblages in terms of taxonomic, phylogenetic, and functional dissimilarity between biogeographical zones, we computed the Sørensen index of beta diversity (βsør, a measure of total dissimilarity) and its repartition into its two components: (i) turnover (βsim, i.e. replacement) and (ii) nestedness (βnes, i.e.

loss/gain). Here, we considered two types of dissimilarity: incidence-based and abundance-based dissimilarity. Incidence-based dissimilarity (i.e. presence-absence) treats each species equally and was used to compare biogeographical zones with respect to their underlying species pool (i.e. shared species/traits). Abundance-based dissimilarity was chosen to account for patterns of abundance in fields that are more likely to be related with the provision of ecosystem services, as numerically dominant species provide most of the ecosystem services (Kleijn et al., 2015; Senapathi et al., 2015; Vázquez et al., 2005; Willcox et al., 2019).

We computed pairwise values to compare sites with the *beta* function of the 'betapart' package (version 1.5.6) (Baselga et al., 2018) for each of the three diversity metrics. We then took the mean of the pairwise values for each pair of biogeographical zones, as well as the mean of pairwise values within each biogeographical zone (i.e. intra-zone dissimilarity).

Measures of phylogenetic diversity (PD) and functional diversity (FD) may capture distinctive aspects of assemblage composition and diversity (Cadotte et al., 2011; De Palma et al., 2017) that emphasise the ecosystem services provided by bees (Dorchin et al., 2018). PD reflects the evolutionary history within an assemblage (Webb et al., 2002), while FD represents the life-history traits of that assemblage (Petchey and Gaston, 2006). Phylogenetic beta diversity measures included a phylogenetic tree based on the hierarchical Linnean taxonomic classification (superfamily/position/family/subfamily/tribe/genus/subgenus/species) (Danforth et al., 2006) (Table A.2) using the 'ape' package (version 5.3) (Paradis and Schliep, 2018). For morphospecies without subgenus information, we considered their subgeneric affiliation as "unknown". We carefully checked for synonyms and spelling and extracted taxonomic classifications using Michener (2007), the Discover Life checklist (Ascher and Pickering, 2022) and most up-to-date classifications (Bossert et al., 2022; Bossert et al., 2019; Pisanty et al., 2022b) (Table A.2).

To calculate functional beta diversity values, we computed the Gower distance matrix (Gower, 1971) on the qualitative traits matrix. We then converted the Gower distance matrix into a functional tree using the *hclust* function of the 'stats' package (version 4.1.3) (R Core

Team, 2022). We considered five different qualitative traits: size (small: inter-tegular distance (ITD) < 2 mm; medium: 2 mm ≤ ITD ≤ 3 mm; and large: ITD > 3 mm), tongue length (short, long), pollen transportation (abdomen, accidental, corbiculae, crop, legs, both legs and body), nesting type (above-ground, below-ground, both below and above-ground), and sociality (cleptoparasite, communal, eusocial, primitively eusocial, primitively social, social parasite, solitary, solitary and communal, solitary and primitively social) (Table A.2). As there is no consensus on size classification, we choose our three categories as we expect that they represent differences in foraging distances (Greenleaf et al., 2007). The traits and their level of precision represent the best approximation of what is currently available to account for all the species and morphospecies considered in this study.

2.4. Diversity metrics and models

To test the influence of habitat characteristics, management, and land cover on wild bee diversity, we fit multiple Generalised Linear Mixed Models (GLMM) with taxonomic diversity (TD), phylogenetic diversity (PD), and functional diversity (FD) as the response variables. As proxies for TD, PD, and FD, we computed taxonomic, phylogenetic, and functional Hill Shannon diversity (see Roswell et al., 2021) using the *obs3D* function of the 'iNEXT.3D' package (version 1.0.1) (Chao et al., 2021). For PD, we used the same phylogenetic tree as for beta-diversity, and for FD, we used the same Gower distance matrix. Hill Shannon diversity emphasises neither rare nor common species and represents a suitable choice when species abundance distributions are uneven at the site level, such as in our data (Roswell et al., 2021).

We included management type (organic, non-organic) and land use and land cover (LULC) proportions as explanatory variables for all sites. LULC proportions in a radius of 2000 m around sites were extracted using 2019 ESA Sentinel-2 imagery at 10 m resolution (Karra et al., 2021). LULC with too-low proportions for each site were excluded from the analyses (i.e water, flooded vegetation, bare ground, and snow/ice areas). GLMMs were fitted with a gamma regression distribution using the 'glmmTMB' package (version 1.1.3) (Brooks et al., 2017). Information for the size of the orchard (ha – log10-transformed; 155 sites), yield in 2018 (Ton/ha – log10-transformed; 123 sites) and number of hives within the orchard (log10-transformed; 162 sites) were not available for all sites. Therefore, additional models were made on the subset of sites with available data with the explanatory variable alone. We also tested the effect of the log10-transformed number of hives on log10-transformed *A. mellifera* abundances (gaussian distribution). We included the sampler identity (team leader) as a random effect in all models to address spatial dependency, the influence of sampler on the assemblage collected, and it is related to biogeographical affiliation (Table A.1). Considering that the team leader consistently sampled sites within the same region, this grouping approach was chosen to account for possible spatial autocorrelation.

All statistical analyses were performed using R statistics (version 4.1.3) for Windows (R Core Team, 2022).

3. Results

We collected 54,166 bee specimens from 177 commercial apple orchards in 33 different countries covering six continents (Figs. 1 & A.1 and Table A.1). They consisted of 644 species/morphospecies (eight managed or manageable species and 636 exclusively wild bee species) from five different families: Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae (Table A.2).

The top four most abundant genera varied greatly among biogeographical zones, except for *Apis* that was, in general, the most abundant genus, followed in most cases by the genera *Andrena* (Andrenidae), *Bombus* (Apidae), and *Lasioglossum* (Halictidae) (Fig. A.2). Managed or manageable species represented 69 % of the specimens collected across all sites, *Apis mellifera* alone accounting for 60 % (Fig. 1). *Apis mellifera*

was collected in all sites (except one site in Bhutan), in all biogeographical zones, and was typically the most abundant bee species in apple orchards. The next most globally abundant species was *Bombus terrestris* with 6 %. Other species accounted for <2 % each. *Bombus terrestris* was also the only species other than *A. mellifera* to be collected outside its native range (collected in Chile, Tasmania, and New Zealand). At the zonal level, the dominance of managed or manageable species ranged from 13 % in the Central Palearctic Mountain zone (Pakistan) to 92 % in the East Palearctic Temperate zone (China) (Figs. 1 and A.3). *Apis cerana* was collected only in the Temperate Indomalayan zone, (i.e. not in the Mountain Central Palearctic zone) where it dominated Bhutanese and Indian sites in a similar manner (33 % for *A. cerana* and 30 % for *A. mellifera*). Therefore, the dominance of non-*Apis* managed or manageable species was low, but could be considered even lower when taking into account the possibility that most of the specimens themselves were wild.

3.1. Beta diversity between biogeographical zones

To compare biogeographical zones globally, we used two different approaches: incidence-based dissimilarity (i.e. presence-absence) and abundance-based dissimilarity. Overall, pairs of biogeographical zones were highly dissimilar at the taxonomical level (mean βsør = 0.85 (presence-absence) and 0.71 (abundance-based)), but less dissimilar at phylogenetic (mean βsør = 0.45 (presence-absence) and 0.54 (abundance-based)) and functional levels (mean βsør = 0.37 (presence-absence) and 0.55 (abundance-based)) (Fig. 2 and Table A.3). The incidence-based phylogenetic clustering was mainly driven by the widespread distribution of *Lasioglossum* spp. and *Andrena* spp. across all biogeographical zones and their comparatively high species richness in our dataset (Fig. A.4). The incidence-based functional clustering was mainly driven by the comparatively high richness of species presenting the following traits: solitary, small, short-tongued, nesting below-ground, and/or carrying pollen on both their legs and their body (Fig. A.5). The reduction in taxonomic dissimilarity between biogeographical zones when using the abundance-based metrics was caused by overlapping abundant species, principally *Apis mellifera* (Figs. 2 and A.2). In both phylogenetic and functional comparisons, the abundance-based metric increased dissimilarity between biogeographical zones relative to the incidence-based metric, because some sites have housed closely related and/or functionally similar sets of species but not at the same frequencies. Therefore, the abundance-based taxonomic, phylogenetic, and functional clustering was almost exclusively driven by the uniformly high abundance of *Apis mellifera* and its specific traits (i.e. eusocial, long-tongued, large species nesting above-ground and carrying pollen on corbiculae) (Fig. A.6 and Table A.2). Dissimilarity between different biogeographical zones was always greater than dissimilarity within biogeographical zones. Furthermore, pairs of biogeographical zones in the same realm were overall less dissimilar compared to pairs of biogeographical zones sharing the same biomes in different realms, or to any other pairs that did not share any biomes/realms (Fig. 2 and Table A.3).

The incidence-based taxonomic dissimilarity (βsør - mean ± standard deviation (SD) = 0.85 ± 0.13) was primarily driven by turnover (βsim – 0.51 ± 0.24) rather than by nestedness (βnes - 0.35 ± 0.23), while turnover (0.22 ± 0.12 (PD); 0.20 ± 0.13 (FD)) and nestedness (0.23 ± 0.16 (PD); 0.17 ± 0.13 (FD)) components showed similar values for phylogenetic and functional dissimilarities. Abundance-based taxonomic (0.71 ± 0.20), phylogenetic (0.54 ± 0.20), and functional (0.55 ± 0.20) dissimilarity were all driven by nestedness (0.41 ± 0.25 (TD); 0.41 ± 0.25 (PD); 0.41 ± 0.25 (FD)) rather than by turnover (0.31 ± 0.22 (TD); 0.13 ± 0.14 (PD); 0.14 ± 0.14 (FD)) (Fig. A.7). This is associated with global high abundance of *A. mellifera* (Fig. A.3).

Finally, our analysis using a random selection of morphospecies names revealed no significant impact of the decision to keep morphospecies designations at the country scale. There was no potential inflated
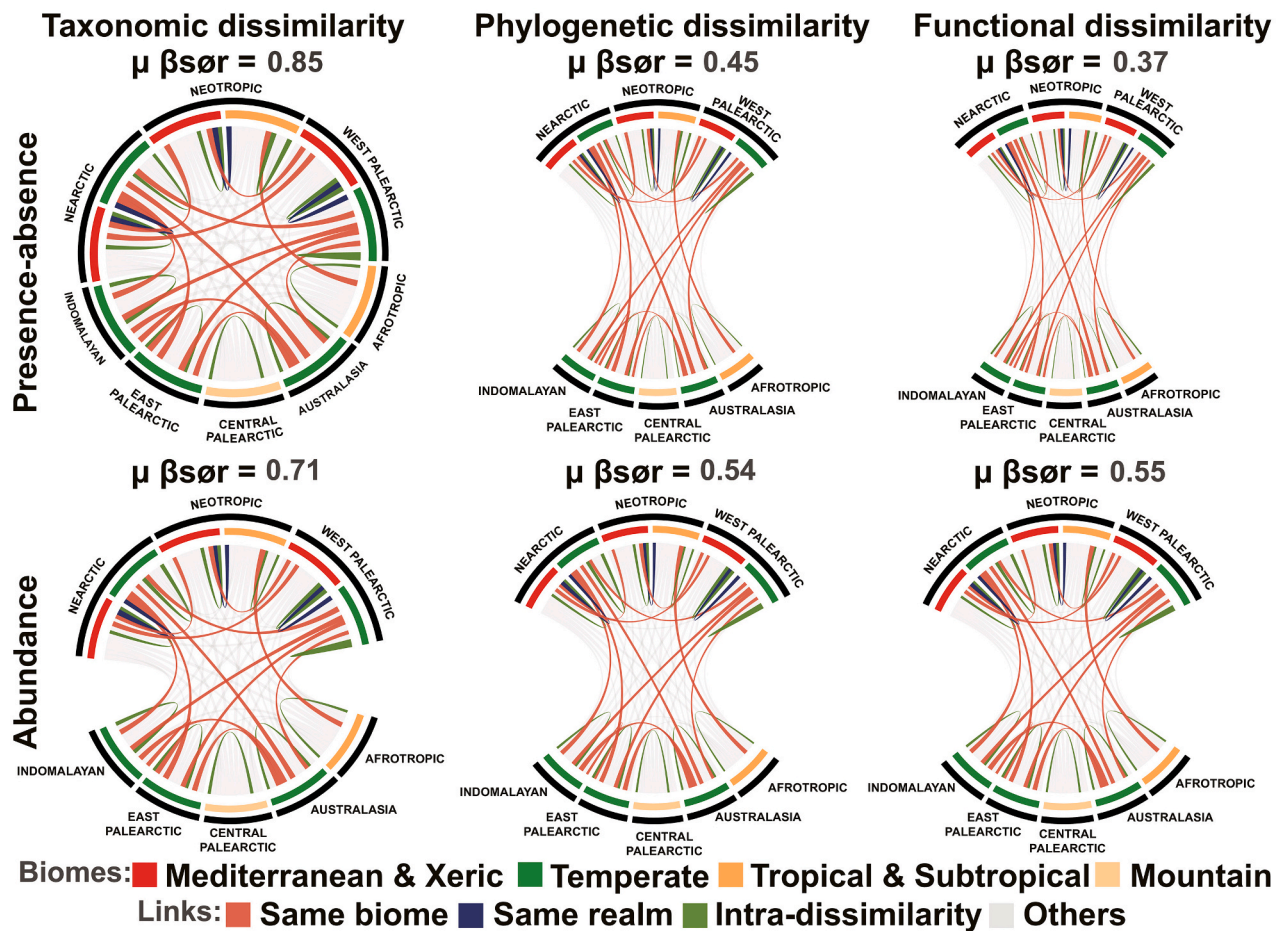
Fig. 2. Incidence-based and abundance-based taxonomic, phylogenetic, and functional dissimilarity (Sørensen's total beta diversity, βsør) among biogeographical zones. For visual clarity, we highlighted the links of interest: (i) links that compare the same biome in different realms (dark orange), (ii) links that compare different biomes within the same realm (dark blue) or (iii) links that compare sites within the same biogeographical zone (green). Other links are shown in light grey, i.e. pairs of biogeographical zones that did not share any biomes/realms. For all links, the thickness of the link represents the value of the total dissimilarity. The scale is equivalent for each figure, with the total dissimilarity values ranging from 0.10 (thinnest link) to 0.99 (thickest link). Averaged-pairwise total dissimilarities between biogeographical zones are given in Table A.3, along with turnover and nestedness values.

for taxonomic dissimilarity between sites (Fig. A.8). Moreover, this concern could only realistically have been problematic for Pakistan, India, and Bhutan (Table A.2).

3.2. Local drivers of diversity

All Hill Shannon diversity metrics were significantly, but weakly, associated with the type of management (i.e organic vs non-organic - excepted phylogenetic diversity) and the percentage of rangeland open areas around sites (Fig. 3 and Table A.4). Rangeland open areas ("rangeland") are characterised by homogeneous grass coverage, with little to no taller vegetation, with no obvious cropping fields (Karra et al., 2021). Indeed, we found a weak positive association between rangeland cover and all diversity metrics (taxonomic diversity (TD): 0.26, [0.04, 0.48], p = 0.023; phylogenetic diversity (PD): 0.14, [0.02, 0.26], p = 0.019; functional diversity (FD): 0.20, [0.04, 0.35], p = 0.011). Organic management, in comparison with non-organic management, was associated with slightly higher TD (0.17, [0.02, 0.33], p = 0.030) and FD (0.12, [0.02, 0.23], p = 0.024), while PD showed a non-significant relation (0.08, [0.00, 0.16], p = 0.061) (Fig. 3 and Table A.4). The other explanatory variables showed less to no effect on bee diversity (Table A.4). However, the log10-transformed number of hives (model using only this explanatory variable on a subset of 162 sites) exhibited a slight, marginally significant negative association (including null effect)

with TD (estimate = −0.12, CI = [−0.25, 0.00], p = 0.063), while no association was observed with FD (−0.08, [−0.17, 0.01], p = 0.101), and PD (−0.02, [−0.09, 0.05], p = 0.501) (Fig. A.9 and Table A.4). Finally, log10-transformed number of hives was strongly and positively associated with log10-transformed *Apis mellifera* abundances (0.15, [0.04, 0.27], p = 0.006) (Fig. A.10 and Table A.4).

Raw relationships between the number of hives, the type of management, and rangeland with all diversity metrics per team leader (sampler identity, i.e. the random effect of the models) are shown in Fig. A.11. The number of hives showed no clear patterns with all diversity metrics, only samples in Germany and Slovenia followed a negative trend (Fig. A.11.A-C). By most measures, organic sites performed on par with or better than non-organic sites (especially in Europe) (Fig. A.11.D-F). Higher proportions of rangeland around sites were associated with higher diversity, especially in Australia, Estonia, France, Portugal, continental Spain, and the United States of America (Fig. A.11.G-I).

4. Discussion

Our study provides the first characterisation of bee diversity and its drivers in commercial apple orchards at a global scale using a standardised framework. More specifically, we show that the diverse assemblages of wild bees exhibit a significant taxonomic dissimilarity between
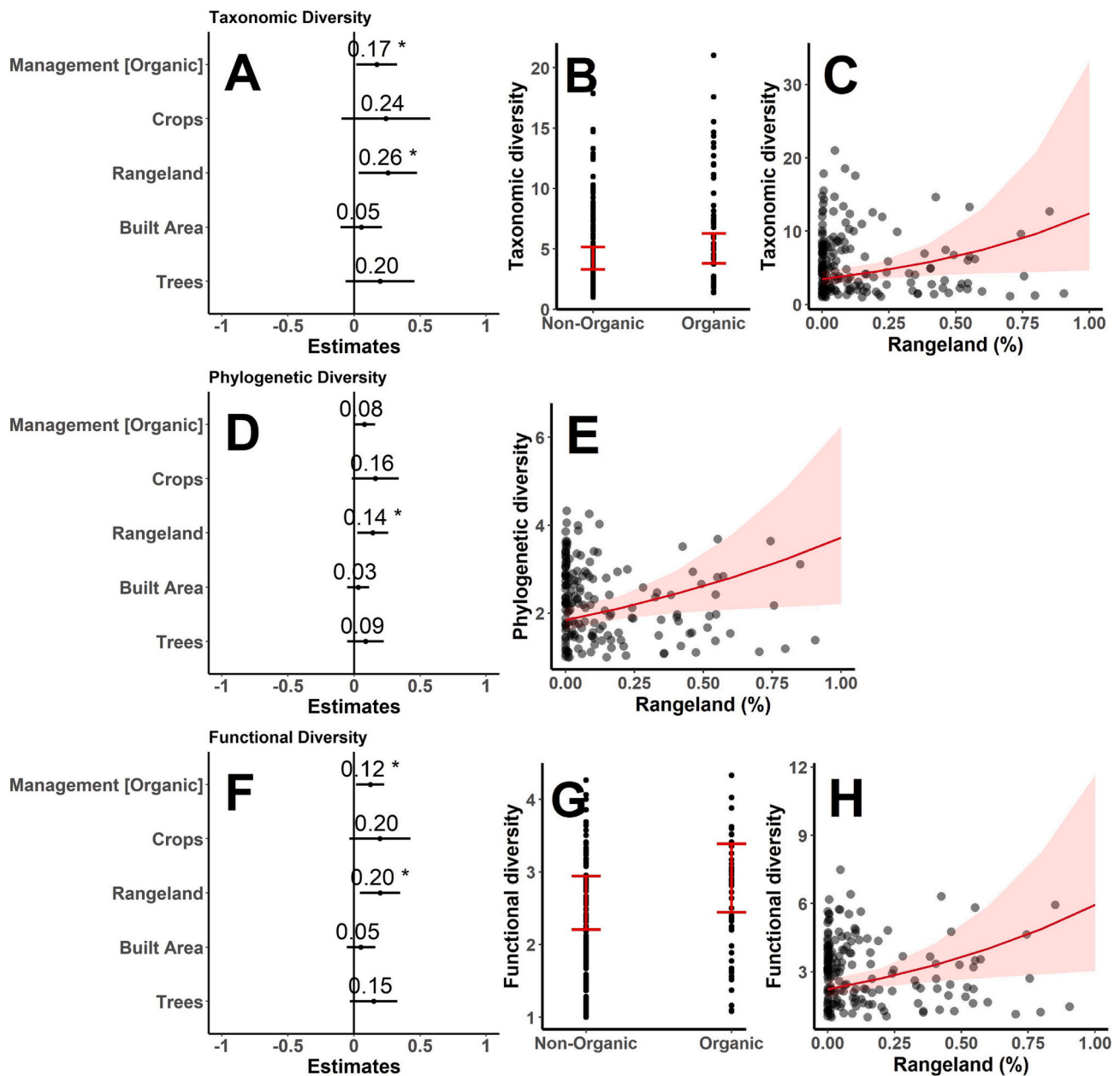
Fig. 3. Generalised Linear Mixed Models (GLMM) results for the Hill Shannon taxonomic, phylogenetic, and functional diversity. Plots A, D, and F show the coefficient values and their 95 % confidence intervals of explanatory variables for each model. Plots B, C, E, G, and H show the raw observations (dark points) and the predicted values (in red) of explanatory variables (with the 95 % confidence intervals for continuous variables) that are significant to explain the variation of each diversity metric. Random effect is the sampler identity.

biogeographical zones and that, in contrast, apple visitors tend to be both functionally and phylogenetically clustered as they belong to similar higher-level phylogenetic groups (genera, tribes), and that they are characterised by similar distributions of functional traits. We also show that, globally, managed bee species, especially the western honey bee (*A. mellifera*), outnumber other species in apple orchards and drive abundance-based dissimilarity metrics between biogeographical zones.

Our current knowledge of global bee taxonomic and phylogenetic biogeography is largely based on the pioneering study by Michener (1979) and also the more recent modelling of global bee distributions by Orr et al. (2021). Here, we described the diversity patterns of apple-visiting bee assemblages in terms of dissimilarity across biomes and realms (i.e. biogeographical zones). Our results confirm theoretical expectations concerning the variation in bee species diversity between global biogeographical zones (Michener, 1979; Orr et al., 2021; Smith

et al., 2020; Smith et al., 2018), namely that each biogeographical zone, by and large, hosted specific assemblages of bee species (incidence-based approach), but were numerically dominated by *A. mellifera* (abundance-based approach). As expected from the continent-scale phylogeographic patterns described above, our results indicate that even if biogeographical zones are a significant factor in explaining community composition, biogeographical zones that are spatially closer to one another, such as the Temperate and the Mediterranean West Palearctic zones, tend to have more overlapping bee communities (67 shared species) than spatially separated biogeographical zones (Fig. 2 and Table A.3). In such cases, the bee species responsible for this increased community overlap are more commonly widespread taxa with an overall broader ecological niche (at the genus level), e.g. mainly *Andrena* spp. (Andrenidae), *Bombus* spp. (Apidae), *Lasioglossum* spp. (Halictidae), and *Osmia* spp. (Megachilidae) in the Temperate and the

Mediterranean West Palearctic zones (see Leclercq et al., 2022).

The significant functional and phylogenetic clustering found in wild bee communities, despite high levels of taxonomic dissimilarity (Fig. 2), illustrates that different suites of potential pollinator species in the local species pool of bees bearing similar ecological traits and belonging to similar higher-level taxonomic groups are co-opted as apple bee visitors in different regions of the world. We assume that it is the widespread distribution of *Lasioglossum* spp. (Halictidae) and *Andrena* spp. (Andrenidae) that drove the overlap of taxa (i.e. incidence-based phylogenetic similarity) between orchards globally due to their comparatively larger richness in our dataset (Fig. A.4). Indeed, the Halictidae most likely originated in Africa or South America (Danforth et al., 2004; Hedtke et al., 2013) and later dispersed into the Northern Hemisphere with subsequent dispersal and diversification. In particular, the tribe Halictini underwent a massive diversification after the Cretaceous/Tertiary event (Danforth et al., 2004). The *Andrena-Cubiandrena* group is thought to have dispersed from the Nearctic to the Palearctic and subsequently underwent dispersal events to the Nearctic or back to the Palearctic (Pisanty et al., 2022a). The incidence-based functional clustering was driven by small, solitary, ground-nesting, short-tongued species carrying pollen on both their legs and their body (i.e. *Andrena* and *Lasioglossum* species) (Fig. A.5) (see Leclercq et al., 2022; Weekers et al., 2022b). This phenomenon is reinforced by the redundancy of functional and phylogenetic diversity, which stems from their hierarchical nature; behavioural and ecological traits are highly conserved among species in the same genus and family.

Our results show that at the global scale, visits to apple orchards are ensured by bee species that diverge among regions, whereas within regions, a narrower taxonomic spectrum of common species actually delivers pollination (Kleijn et al., 2015; Winfree et al., 2015). We hypothesise that the functional and phylogenetic clustering of wild bee communities, as shown in this study, is the result of a habitat filtering effect driven by perennial crops, management practices and landscape structure, with agricultural intensification being previously reported to homogenise vegetation structure and diversity, ultimately eroding (pollinator) beta-diversity across large spatial scales (Clough et al., 2007; Gabriel et al., 2006; Karp et al., 2012). Indeed, we observed that rangeland open areas and organic management in some cases showed a positive relationship with wild bee diversity, suggesting that less intensive systems will harbor more species with greater trait diversity. Also, limiting the addition of *A. mellifera* hives will reduce *A. mellifera's* dominance and will increase diversity because there will be more evenness in all species' abundances, while simultaneously having no negative effect on yield (Weekers et al., 2022a). Moreover, in contrast to morphologically complex flowers, the radially-symmetrical apple flowers exhibit an open structure that is readily accessible for most generalist bee species that forage during springtime, and less so for bee species that are specialised on other plant species or that emerge later in the season (Krishna and Keasar, 2018; Sheffield et al., 2016). We argue that future research should further investigate the impact of land use intensification by comparing nearby natural areas to low- and high-intensity agricultural habitats and observing (i) the extent to which changes in dissimilarity across regions is dependent on more specific management practices not taken into account in this study (i.e. pesticides use, floral diversity) and (ii) to what extent intensively farmed crops act as a filter of local bee assemblage, and whether that filtering effect varies regionally. Furthermore, we argue that the restricted functional space occupied by global visitors of apple blossoms could be increased with (i) lower intensity management (Roquer-Beni et al., 2021), (ii) an increase in the functional diversity of the local plant communities to decrease the floral resource overlap with managed species (Cappellari et al., 2022; Garibaldi et al., 2014), (iii) a focus on native flowers that are important for specialised species (Prendergast et al., 2021; Seitz et al., 2020), (iv) a lower density of managed species (Weekers et al., 2022b), and (v) higher crop diversification (Aguilera et al., 2020; Tamburini et al., 2020). It would be also interesting to

include all pollinators of apple, not only bees, but also hoverflies, beetles, butterflies, moths, and others (Pardo and Borges, 2020; Rader et al., 2020).

Kleijn et al. (2015) found that 13 % of bee species in regional species pools can be observed at crop flowers, and that 80 % of crop flower visitation is provided by only 2 % of bee species in the regional species pool. Additionally, they showed that these most important ecosystem-service-providing species are resilient to intensification effects and their presence and participation can be enhanced by management actions (Kleijn et al., 2015). However, the dominance effect of these species is much smaller than the spatial turnover of species with increasing spatial extent (Winfree et al., 2018). Here, we used standardised data to confirm that a few bee species, especially managed species, dominate in apple orchards worldwide, outnumbering wild and native species. The recurrent use of managed species in intensive cropping systems increases the managed pollinator population size and consequently may result in an overlap in floral resource use with other pollinators (Geslin et al., 2017; Russo et al., 2021; Vanbergen et al., 2018). However, a continuum of ecological impacts of the management of pollinator species from harmful to neutral to positive may be observed (Russo, 2016; Russo et al., 2021). The impacts depend strongly on the bee species in question, whether it was introduced or native, the local floral resource diversity and, more importantly, the local density of managed bee species (Russo, 2016; Russo et al., 2021). For example, introducing species outside their native range risks introducing non-native pests and diseases to other regions of the world (Dafni et al., 2010; Goulson et al., 2015; Russo et al., 2021; Vanbergen et al., 2018), and this risk is amplified if the bees concerned are (eu)social and managed at high local densities (Geslin et al., 2017). Sociality amplifies any positive or negative impacts of managed species because they tend to have longer periods of activity than solitary bees (Geslin et al., 2017), which may be exacerbated in habitats largely relying on managed bee species, such as intensive monocultures.

In this study, we included two manged eusocial species that have been introduced outside their native range, namely *A. mellifera* and *B. terrestris*. Both species may impact native wild bee communities, such as other *Bombus* spp., through competitive exclusion (Herbertsson et al., 2016; Morales et al., 2013), or the spillover or spillback of pathogens (Alger et al., 2019; Dafni et al., 2010; Fürst et al., 2014; McMahon et al., 2015; Sachman-Ruiz et al., 2015; Vanbergen et al., 2018). Recent reports estimate that the impact of native managed bee species is potentially less detrimental for wild bees than non-native managed bee species (Russo et al. (2021), but see Geslin et al. (2017)), although both native and non-native managed bee species can disseminate pests and pathogens to native wild bee populations (Colla et al., 2006). The four *Osmia* spp. in this study are also native to their own regions (Europe for *O. cornuta* and *O. bicornis*, North America for *O. lignaria*, and Asia for *O. excavata*), but represent the only solitary managed or manageable species that we have collected. *Osmia* spp. are cavity-nesters and are therefore more likely to establish populations in new areas than ground-nesting bees, suggesting that many of these species were potentially non-managed during our field surveys. Indeed, farmers less often manage *Bombus* spp., *Osmia* spp., and other bee species than honey bees (Osterman et al., 2021). Furthermore, the solitary life cycle of *Osmia* spp. and their comparatively lower numbers (whether managed or not) compared to managed (eu)social bee species suggest that they might have a lower impact on local wild bee populations (Bosch and Kemp, 2001; Russo, 2016; Sedivy and Dorn, 2014). Our results are indicative of a global trend, namely the strong reliance by growers on *A. mellifera* for pollinating large monocultures of pollination-dependent crops (see Osterman et al. (2021)) and should inform conservation initiatives to take into account the conservation of wild bee species and functional diversity (see also Dorji et al., 2022; Prendergast et al., 2021). Moreover, while sites with high levels of pollination might rely on a limited set of few pollinator species, sites with the lowest levels of pollination might rely on all bee species, including the rarest ones, to maintain sufficient

pollination services ([Winfree et al., 2018](#)). It is therefore essential to identify all pollinator species across cropping systems to redesign production areas by improving their suitability for these valuable pollination providers.

5. Conclusion

In conclusion, our study provides valuable insights into the diversity of bee species within economically significant apple orchards on a globally. We observed a high heterogeneity of bee assemblages across different orchard sites. However, our findings also reveal a trend of homogenisation in both phylogenetic and functional diversity. Honey bees were found to dominate bee communities consistently across biogeographical zones.

These results underscore the vulnerability of pollination services and emphasise the impact of globalised agricultural practices on food production. Understanding the factors influencing wild bee diversity, such as habitat characteristics, management practices, and land cover, becomes critical in ensuring resilient pollination services. Here, the presence of non-cropping grassland and organic management are highlighted as possible drivers of improved assemblage diversity. By prioritising the conservation of diverse bee taxonomic, phylogenetic, and functional assemblages, we can promote ecosystem stability and enhance food security in pollination-dependent crops like apples.

This study serves as an important initial step in characterising bee diversity within intensive cropping systems at the global scale, emphasising the need for further research to inform effective management and conservation strategies. By expanding our knowledge in this field, we can develop targeted approaches that safeguard pollinator populations and foster sustainable agricultural practices.

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Author contributions statement

The study was conceptualised by NL, LM, TWeekers, and NJV; all other authors are listed alphabetically. All authors either found suitable apple orchards, collected the data and/or identified specimens. NL analysed the data. NL, LM, and NJV led the writing of the manuscript. All authors have read and agreed with this version of the manuscript.

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.

Data availability

The data that supports the findings of this study are available on dryad, https://doi.org/10.5061/dryad.cfxpnvxb8

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