



## A comparative analysis of crop pollinator survey methods along a large-scale climatic gradient

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### ABSTRACT

Safeguarding crop pollination services requires the identification of the pollinator species involved and the provision of their ecological requirements at multiple spatial scales. However, the potential for agroecological intensification of pollinator-dependent crops by harnessing pollinator diversity is limited by our capacity to characterise the community of pollinator species for each crop, and to determine how it is influenced by the different survey methods used, as well as by climatic variables at larger geographic scales. Here, we surveyed wild bees using a standardised protocol at an unprecedented scale including 62 commercial apple orchards in Western and Central Europe (i) to validate recent findings on pollinator community divergence as measured by common survey methods (netting and pan trapping) using conventional and alternative biodiversity metrics (phylogenetic and functional diversity), and (ii) to investigate the impact of climatic variation on the patterns observed. Our results confirm the significant divergence in pollinator communities measured using the two common methods at the larger, sub-continental scale, and we provide evidence for a significant influence of climate on the magnitude of pollinator community divergence (beta diversity and its turnover component) between survey methods, particularly when comparing colder to warmer sites and regions. We also found that warmer sites are more dissimilar than colder sites in terms of species composition, functional traits, or phylogenetic affinities. This result probably stems from the comparatively larger species pool in Southern Europe and because apple flowers are accessible to a wide spectrum of pollinator species; hence, two distant survey localities in Southern Europe are more likely to differ significantly in their pollinator community. Collectively, our results demonstrate the spatially-varying patterns of pollinator communities associated with common survey methods along a climate gradient and at the sub-continental scale in Europe.

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## 1. Introduction

Among the major entomophilous crops, apple (*Malus domestica* Borkh., Rosaceae) is the most economically valuable in the European Union with an estimated annual economic value of €5 billion (FAOStat, 2020). In commercial apple orchards, managed honey bees (*Apis mellifera*) are usually introduced by growers to meet the pollination demand (Delaplane and Mayer, 2000; Pérez-Méndez et al., 2020), making this managed bee species the most frequently observed pollinator species during the blooming period (Pardo and Borges, 2020). Concurrently, conventional agricultural management only benefits a limited number of common bee species, including the honey bee and a subset of the local wild bee species pool, resulting in a homogenisation of bee communities across agroecosystems (Kleijn et al., 2015; Scheper et al., 2013). This, in turn, has been shown to provide less reliable pollination services compared to more spatially heterogeneous and diverse pollinator communities (Grab et al., 2019). The biotic homogenisation of bee communities induced by the intensive nature of current cultivation can be countered by the establishment of on-farm habitat restoration, for example in the form of native plant hedgerows (Ponisio et al., 2016).

As wild bee species face increasing anthropogenic threats (Potts et al., 2016; Wagner, 2020), it has become critical to better assess the health of these communities in contemporary cropping systems. To characterise and monitor these communities, two main methods are commonly used by the scientific community that can be divided into two categories: “active” (transect walks and observation plots using nets) and “passive” (e.g. pan traps or trap nests) (Nielsen et al., 2011; Roulston et al., 2007; Westphal et al., 2008). When studying pollinator communities associated with crops, netting has the additional benefit of generating data on insect-plant interactions (when collectors only target specimens they see visiting flowers or collecting pollen). However, netting is labour intensive and strongly depends on the sampler's experience, unlike “passive” methods such as pan traps (Westphal et al., 2008). On the other hand, pan traps may catch smaller species (Cane, 2001; Cane et al., 2000) that do not play an active role in crop pollination, or miss species that have a significant flower constancy for the target crop. Specifically, pan traps seem more efficient at capturing specimens belonging to the family Halictidae and brood parasitic bees, while netting enables to catch a greater proportion of Apidae, Colletidae, and Megachilidae (Hutchinson et al., 2021b; Roulston et al., 2007; Wilson et al., 2008).

Because of these differences in species composition or traits, recent studies comparing survey methods have provided considerable evidence of the divergence between the communities captured by the “active” and the “passive” methods (Hutchinson et al., 2021b; Kuhlman et al., 2021; O'Connor et al., 2019; Thompson et al., 2021). However, these studies are often carried out only at the regional scale and the details of the methods (or their *modus operandi*) still differ among studies, making generalisation at larger spatial scales particularly challenging. The magnitude of this discrepancy between methods has not yet been tested beyond the regional scale, which also means that the interaction between these protocols and metrics driving global bee diversity (such as climate) has been largely overlooked to date. Indeed, climate influences the species richness of bees and conditions are most optimal in xeric and warm climates, such as in the Mediterranean region (Michener, 1979; Orr et al., 2021). One could therefore assume that climate may also have an impact on the communities collected by the two types of methods, but the nature of this relationship remains unknown. The impacts of climate on diversity can only be studied at a broad scale, and its effect could potentially be better analysed using standardised surveys, though to date this has not yet been attempted.

Furthermore, recent studies often focus on differences in abundance or taxonomic diversity (species richness, i.e. species counts) (Hutchinson et al., 2021b; O'Connor et al., 2019) but rarely take into account alternative diversity indices such as phylogenetic diversity (PD) and functional diversity (FD, i.e. the diversity of ecological and behavioural

traits of bee species) (*contra* Thompson et al., 2021). Several studies have reported that these alternative diversity metrics are better suited than species counts in accounting for the provision of ecosystem services, and can also provide information about community assembly processes and ecosystem functioning, such as competition for resources and habitat filtering (Baraloto et al., 2012; Cadotte et al., 2015; Sydenham et al., 2015).

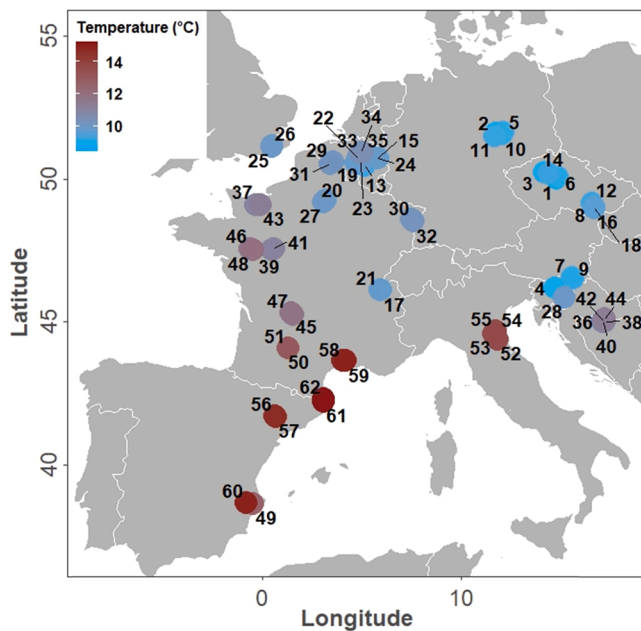
Our study complements and extends the current knowledge on the differences between the survey methods of netting and pan trapping by comparing them at an unprecedented scale in 62 commercial apple orchards in Western and Central Europe. This wide spatial coverage allowed us to characterise the interacting effect of climate on the divergence between methods using standardised protocols. Specifically, we quantified these divergences through measures of beta diversity (hereinafter referred to as “total” dissimilarity) and its partitioning into two essential components, namely turnover (i.e. species replacement) and nestedness (i.e. species loss) (Baselga, 2010). We first compared (i) the species composition, as well as (ii) the taxonomic, functional, and phylogenetic divergences between all netted sites versus all pan trapped sites. We hypothesise that the previously reported divergence in the results between methods (Hutchinson et al., 2021b; O'Connor et al., 2019; Thompson et al., 2021) will also be valid at larger spatial scales. Moreover, we tested how climate affects (i) species richness and patterns of abundance associated with each method, and (ii) the taxonomic, functional, and phylogenetic dissimilarities between both methods at the site level and among sites. We hypothesise that wild bee species richness in apple orchards will increase along the climate gradient, with possible non-linear correlations with functional and phylogenetic diversity (Vereecken et al., 2021). We discuss our findings and the need of large-scale, harmonised, and standardised protocols to understand patterns, drivers, and trends of pollinators, as well as to better inform policymakers, farmers, and the public.

## 2. Materials and method

### 2.1. Study area and sampling method

We conducted this study in 2019 across 62 commercial apple orchards in nine countries (Belgium, Bosnia and Herzegovina, Czech Republic, France, Germany, Italy, Slovenia, Spain, and the United Kingdom) covering a climate gradient across Western and Central Europe (Fig. 1 and Table S1). The commercial apple orchards were separated from each other by at least 2 km to minimise the overlap of their pollinator communities (Zurbuchen et al., 2010). We surveyed the bee communities using netting and pan trapping, following a standardised protocol (see Drooge et al., 2005; Westphal et al., 2008). Each orchard was sampled for three consecutive days during the blooming period, weather permitting. Each day, two distinct survey methods were deployed: (i) traps using three triplets of pan traps (blue, yellow, and white) filled halfway with odourless soapy water, placed on the ground at 9 am and collected at 4 pm, and (ii) netting from apple tree flowers during two sessions of 90 min, first in the morning (between 9.30 am and 12.00 am) and one in the afternoon (between 1.30 pm and 4.00 pm). For the “passive” sampling, the triplets of pan traps were placed at least 30 m from each other at the edges of the orchards near areas with non-apple flowering plants. Across all study sites, we used the same 500 ml plastic bowls (AVA®) which were first painted using a primer (white Motip® primer), and then with white, fluorescent yellow or blue sprays-paints (white and yellow Rocol® paints and fluorescent blue Liquitex® paint). All pan traps were prepared at the Agroecology Lab (ULB, Belgium) and then dispatched to each regional team leader prior to the flowering season. For the “active” sampling, each collector adopted a slow transect walk across the entire orchard, inspecting as many blooming apple trees as possible, and collected only specimens on the apple blossoms.

All specimens collected were identified to species level, except for



**Fig. 1.** Study sites selected in Belgium, Bosnia and Herzegovina, Czech Republic, France, Germany, Italy, Slovenia, Spain, and the United Kingdom and sampled in 2019. Each site is coloured by its average temperature (Tavg) and has a unique code going from 1 (lowest temperature) to 62 (highest temperature). (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article)

*Bombus terrestris* and *B. lucorum* which are virtually indistinguishable and were therefore pooled together as *Bombus terrestris* agg. The specimen records were digitised, and most specimens are curated in the entomological collection of the Agroecology Lab (ULB, Belgium) (other specimens collected are held at co-authors' institutions).

## 2.2. Data analysis

### 2.2.1. Overall differences in sampling methods

To visualise the species composition differences between each method across the entire study area, and more specifically to investigate the shared vs. unique species associated with each survey method, we used a Venn diagram ('VennDiagram' package, version 1.6.20) (Chen, 2018).

**2.2.1.1. Indicator species.** For each method, we extracted the most indicative species using the 'indicspecies' package (version 1.7.9) (De Cáceres and Legendre, 2009). We used the 'multipatt' function with 999 random permutations which computes an indicator value index for each species. This indicator value index is the square root of the product of two components (De Cáceres and Legendre, 2009):

1. The probability (A, "specificity") that the species has been collected by the particular method (0–1)
2. The probability (B, "fidelity") of finding the species in sites belonging to the particular method (0–1)

We displayed the values of the indicator value index, the specificity, and the fidelity components of each indicator species of each method and ordered each list by the values of the indicator value index (most indicative species displayed first).

**2.2.1.2. Non-metric multidimensional scaling (NMDS).** To compute the degree of taxonomic, functional, and phylogenetic global dissimilarity between the two assemblages sampled with pan traps and by netting, we

first applied Hellinger standardisation on the species presence-absence community matrix. We then performed a non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity to compute and visualise the taxonomic dissimilarity between survey methods.

For the functional dissimilarity, we first computed and extracted eight life-history traits relevant for the study of bee ecology and behaviour for all species recorded in this study: the mean inter-tetragal distance (ITD), tongue length, nesting type, sociality, pollen transportation, seasonal activity, pollen specialisation and diet breadth (see data and rationale in Table S2). We measured the ITD of females of each species. This morphological trait is a good proxy for body size (Cane, 1987) and bee foraging range (Greenleaf et al., 2007; Zurbuchen et al., 2010). We also computed the tongue length associated with each species based on their ITD using the "BeeIT" package (version 0.1.0) (Cariveau et al., 2016; see also Kendall et al., 2019). We then converted this mixed qualitative/quantitative matrix to a Gower pairwise distance matrix (Gower, 1971) between sites using the 'gowdis' function of the 'FD' package (version 1.0–12) (Laliberté and Legendre, 2010). This Gower distance matrix was used with the species presence-absence community matrix to compute functional trait MNTD (mean nearest taxon distance) beta diversity using the 'picante' package (version 1.8) (Kembel et al., 2010). We finally performed a NMDS using this functional trait MNTD beta diversity matrix.

To analyse the phylogenetic dissimilarity between methods, we used a phylogenetic tree based on the taxonomic classification (family/tribe/genus/subgenus/species) using the 'ape' package (version 5.3) (Paradis and Schliep, 2018). We built a polytomous, ultra-metric tree where all bee species recorded were grouped together according to their taxonomic classification following Michener (2007) and Nieto et al. (2014). The branch lengths of the tree were calculated by setting the p-parameter to 1 following Hoiss et al. (2012). We then transformed this tree into a distance matrix using the 'cophenetic' function of the 'stats' package (R Core Team, 2019). As for functional traits, we computed, this time, the phylogenetic MNTD beta diversity matrix allowing us to perform a NMDS.

For each NMDS, we ran a permutational multivariate analysis of variance (PERMANOVA) to test if the bee communities, their traits or their phylogenetic affinities associated with each survey method were significantly different from each other. All NMDS and PERMANOVA analyses were run using the 'metaMDS' (taxonomic dissimilarity)/'monoMDS' (functional and phylogenetic dissimilarities) and 'adonis' functions of the 'vegan' package (Oksanen et al., 2019). As a first exploration of the effect of climate on the observed differences between methods, we plotted the sites according to their monthly average temperature (Tavg) (Fick and Hijmans, 2017) on the NMDS (this choice is explained below).

### 2.2.2. Effect of climate on the differences between survey methods

To estimate the variation in taxonomic, phylogenetic and functional diversity between both methods within each site (comparing each time wild bee assemblages associated with pan traps and netting) or between sites (pairwise differences in combined netted and pan trapped assemblages between sites), and the relative effect of climate, we computed beta diversity metrics with the 'betapart' package, version 1.5.1 (Baselga et al., 2018). All calculations were based on the same framework, namely the computation of the Sørensen index of beta diversity ( $\beta_{sor}$ , a measure of total dissimilarity) comparing both presence-absence matrices between two "groups" and its partition into its two components: (i) replacement ( $\beta_{sim}$ , i.e. turnover) and (ii) loss/gain ( $\beta_{nes}$ , i.e. nestedness); following the formula:

$$\beta_{sor} = \beta_{sim} + \beta_{nes}$$

In brief,  $\beta_{sor}$  ranges from 0 (identical species assemblages) to 1 (assemblages with no shared species), and the values of the two components ( $\beta_{sim}$  and  $\beta_{nes}$ ) allow to quantify the relative contribution of

turnover and nestedness (respectively) to the overall differentiation of “groups”. We computed these beta diversities for two types of analyses and “groups”:

1. In each site, comparison between net and pan traps assemblages (one value of beta diversity per site)
2. Pairwise comparison between sites with net and pan traps assemblages grouped together (a beta diversity value for each group of two sites)

The taxonomic beta diversity metrics were computed with the ‘beta.multi’ function from the ‘betapart’ package (version 1.5.1) (Baselga et al., 2018).

The functional beta diversity metrics were computed using the same Gower distance matrix described above for the functional NMDS, then converted into a functional tree using the ‘as.phylo’ function from the ‘ape’ package (version 5.3) (Paradis and Schliep, 2018). Last, we used the ‘phylobeta’ function from the ‘phylregion’ package (Daru et al., 2020) to compute functional beta diversity metrics.

The phylogenetic beta diversity metrics were calculated using a phylogenetic tree based on the taxonomic classification as described above. To compute phylogenetic beta diversity metrics at site level, we used this phylogenetic tree and the community matrix as inputs of the ‘phylobeta’ function.

**2.2.2.1. Effect of climate.** To investigate the observed impact of climate on the patterns of beta diversity i.e. (i) within sites beta diversity to compare methods, and (ii) between sites beta diversity to compare sites, we used 36 climatic variables along with two supplementary variables: elevation and vegetation index. All variables, along with their source, are provided in Table S3 and were selected on the basis of their predictive power for bee species richness (Orr et al., 2021). We then fit multiple generalised linear mixed effects models (GLMM) with a beta regression distribution using the ‘glmmTMB’ package (version 1.0.1) (Brooks et al., 2017). For each model, we first ranked each variable based on their Bayesian Information Criterion (BIC) (Burnham and Anderson, 2004) and then removed, iteratively, all variables collinear ( $>0.7$ ) to the most important variable. Then, BIC stepwise-selection in both directions was performed on the non-collinear set of variables to select the most important explanatory variable(s).

First, for the within-site comparison, we fit nine models, each with a different response variable (three beta diversity metrics that compared methods,  $\beta_{sor}$ ,  $\beta_{sim}$  and  $\beta_{nes}$ , for each of the three diversity indices, taxonomic, functional, and phylogenetic metrics) and the selected explanatory variable(s). To account for spatial dependency and the effect of sampler on the assemblage observed, we included the sampler identity (team leader) as random effect in the model (Table S1). As the team leader always sampled sites within the same region, this choice of grouping considers potential spatial autocorrelation (see Fig. S1). After the variable selection process for the total dissimilarity ( $\beta_{sor}$ ), the selected explanatory variables were: the sum of mean monthly temperature (GDD5) for the taxonomic  $\beta_{sor}$ ; the minimum temperature of coldest month (Bio6) for the phylogenetic  $\beta_{sor}$ ; and the monthly average minimum temperature (Tmin) for the functional  $\beta_{sor}$ . However, for ease of comparison, as they are all temperature related and highly correlated variables (e.g. 0.68–0.95, see Table S4), we chose to show the models with monthly average temperature (Tavg) (Fick and Hijmans, 2017) as explanatory variables (AIC difference with the previous selected variables being lower than four units, see Table S4). The choice of the Tavg variable was also appropriate to describe the variations observed along the climatic gradient. We then used Tavg for each subsequent statistical exploration of the effect of the climatic gradient.

Secondly, we fit a further nine GLMMs to test (i) the effect of the temperature on the difference between wild bee assemblages by site (grouped net and pan trap samples) and (ii) if two close sites are more

similar than two more distant sites. Each model had beta diversities as response variables ( $\beta_{sor}$ ,  $\beta_{sim}$  and  $\beta_{nes}$ , for each of the three diversity indices) and the monthly average temperature (Tavg) (mean of the two values of each site), the spatial distance between sites and the interaction term between them as explanatory variables. Here, we investigated the effect of the climate gradient on the overall differences between sites and no longer between methods within each site. The aim was to see whether two sites located in a warm region were more dissimilar than two sites located in a colder environment in terms of total site diversity.

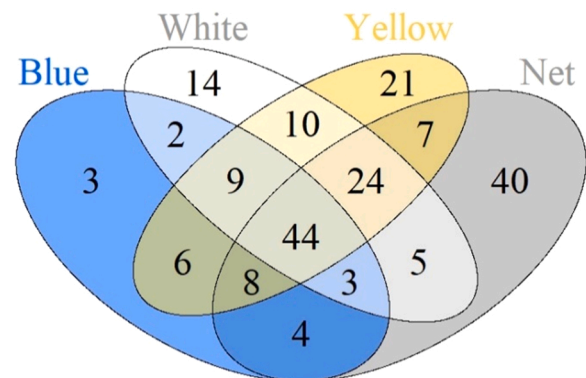
We finally fit four last GLMMs with SR (species richness, i.e. species count) (poisson distribution), PD, FD (gamma distribution), and the relative abundance of common species visiting apple flowers (determined as species in net assemblages having 10% of apple flower visits in at least two sites) (binomial distribution) as response variables. For each model, the interaction between temperature and methods were computed as explanatory variables. Here, we investigated the variation of taxonomic, phylogenetic, and functional diversity and homogenisation of species along the gradient. All statistical analysis were performed using RStudio (RStudio, 2018) for R version 3.6.1 for Windows (R Core Team, 2019).

### 3. Results

A total of 23,799 bee specimens representing 200 species (15 bumblebees, 184 other wild bee species and the honey bee, *A. mellifera*) and five bee families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae) were collected in 2019 in the 62 apple orchards. The Andrenidae was the most diverse family in our dataset, with 73 species (21.7% of the total specimens captured), followed by the Halictidae, with 57 species (11.5%), the Apidae, with 54 species (62.9%), the Megachilidae, with 14 species (3.5%) and the Colletidae, with 2 species (0.4%). The Apidae was, by far, the most abundant family (62.9%) in our field surveys (Fig. S2), with *A. mellifera* representing 48.5% of the total specimens caught (11,534 specimens).

#### 3.1. Overall differences in sampling methods

Netting represented 77.2% of the total specimens collected (18,382 specimens, 135 species) and pan traps 22.8% (5417 specimens, 160 species). Bees of three genera dominated netting sampling: *Apis* (*A. mellifera*) with 61.6% of the netted specimens, *Andrena* (Andrenidae) (15.8%) and *Bombus* (Apidae) (12.5%). Bees belonging to the genera *Andrena* (41.8% of the pan trapped specimens) and *Lasioglossum* (40.1%) were by far the most abundant in pan traps (Table S5). The Venn diagram (Fig. 2) shows that 32.5% of the species (65 species) were only



**Fig. 2.** Pollinator assemblage structure for the different sampling methods (blue, white and yellow pan traps and net catching). The number of unique or shared species between each sampling method is displayed. The total number of species is  $N = 200$ . (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article)



collected in pan traps, followed by 20% (40 species) collected only by netting, and a total of 47.5% (95 species) were shared between the two survey methods. Species specific to pan traps were mainly composed of small species in the families Halictidae and Andrenidae. On the other hand, species collected only by netting were primarily larger species in the families Andrenidae and Apidae (Table S6 and Fig. S3).

Our results also indicated that the two survey methods within each site showed higher species divergence (total dissimilarity,  $\beta_{\text{sor}}$ ) (values of  $0.62 \pm 0.12$ ) than phylogenetic ( $0.33 \pm 0.09$ ) or functional ( $0.26 \pm 0.10$ ) divergence. Moreover, species, phylogenetic, and functional divergence were primarily driven by turnover ( $\beta_{\text{sim}}$ ) ( $0.56 \pm 0.13$ ,  $0.25 \pm 0.08$ , and  $0.17 \pm 0.11$ , respectively) rather than by nestedness ( $\beta_{\text{nes}}$ ) ( $0.07 \pm 0.06$ ,  $0.08 \pm 0.08$ , and  $0.09 \pm 0.08$ , respectively) (Fig. S4).

### 3.1.1. Indicator species

Table 1 lists indicator species, i.e. species statistically associated with each survey method: netting was associated with 16 larger (mean ITD =  $3.82 \pm 1.34$  mm) and more common polylectic species (Table S6), including 12 species known to be definite, likely, or possible apple flower visitors in the UK (with *Apis mellifera* included) (Hutchinson et al., 2021a). By contrast, the 22 indicator species of pan traps consisted of mainly small (mean ITD =  $1.58 \pm 0.50$  mm) Andrenidae, Apidae, Megachilidae, and Halictidae species, including 11 definite, likely or possible apple flower visitors (Hutchinson et al., 2021a). The remaining species consisted of species specialised on non-Rosaceae host plants and of brood parasitic species (Table S6). Moreover, netting indicator species had a higher average index value (0.61 versus 0.46 for pan traps), meaning that netting indicator species were statistically more related to netting than pan traps indicator species are to the pan traps. This is due to the lower fidelity values for the pan traps indicator species as they were "rarer" species and found at fewer sites whereas the netting indicator species had been collected at most sites and were therefore more common. Overall, the presence and abundance of these indicator species in each collection assemblages were probably driving a certain difference between both assemblages.

### 3.1.2. NMDS

To better characterise the assemblages associated with each survey method in terms of species composition but also, functionally, and phylogenetically, we performed NMDS (Fig. 3). The PERMANOVA

results confirmed that the assemblages sampled with pan traps and net were significantly dissimilar compositionally ( $R^2 = 0.144$ ,  $F_{1,122} = 20.522$ ,  $P < 0.001$ ) (Fig. 3. A), functionally ( $R^2 = 0.445$ ,  $F_{1,122} = 97.688$ ,  $P < 0.001$ ) (Fig. 3B) and phylogenetically ( $R^2 = 0.384$ ,  $F_{1,122} = 75.903$ ,  $P < 0.001$ ) (Fig. 3C). Furthermore, our results showed that the bee assemblage sampled by pan traps displayed a wider taxonomic assemblage than that of the netted bees with almost no overlap (Fig. 3A). This result is directly linked to the fact that pan traps yielded more species than netting, but it also shows that between sites dissimilarity seemed to be greater in the pan trapped assemblages.

### 3.2. Effect of climate

In the NMDS, we observed consistent changes in the structure of netted and pan trapped bee assemblages along the climatic gradient, with greater differences for the sites located in warmer regions for each method (Fig. 3A). However, these greater differences in warmer regions were not related to a higher SR, PD nor FD in these zones, as the number of species collected varied greatly among locations. In fact, the overall SR decreased significantly along the climatic gradient, irrespective of the survey method (Fig. 4 and Table S7), while PD and FD showed no significant relationship (Figs. S5 and 6). Moreover, the relative abundance of common species visiting apple flowers (species having 10% of apple flower visits in at least two sites) was not correlated to the temperature gradient (Fig. S7).

#### 3.2.1. Divergences between netted and pan trapped assemblages at site level

Taxonomic  $\beta_{\text{sor}}$  (0.1887, 95% confidence intervals (CI) [0.0239, 0.3535]) (Fig. 5A, Table S8), functional  $\beta_{\text{sor}}$  (0.2157, 95% CI [0.0497, 0.3816]) (Fig. 5B, Table S9) and phylogenetic  $\beta_{\text{sor}}$  (0.1592, 95% CI [0.0254, 0.2929]) (Fig. 5C, Table S10) presented slight increases with increasing average temperatures. The turnover component of beta diversity ( $\beta_{\text{sim}}$ ) showed similar patterns along the temperature gradient. On the other hand, we found no clear evidence for changes in the nestedness component ( $\beta_{\text{nes}}$ ) along the gradient; these values being low (for the models of the components of  $\beta_{\text{sor}}$ ,  $\beta_{\text{nes}}$  and  $\beta_{\text{sim}}$  see Figs. S8–13 and Table S4).

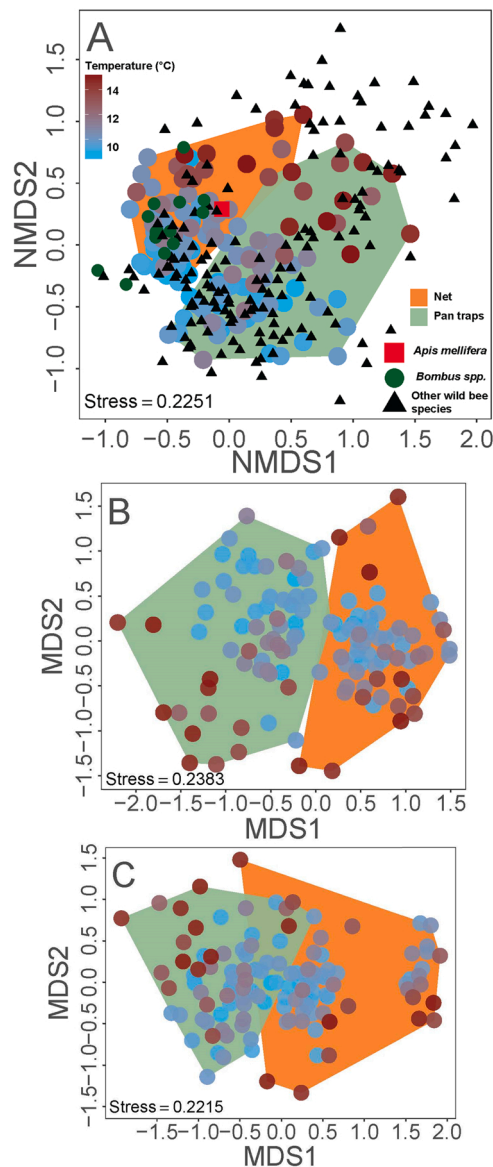
#### 3.2.2. Divergences between sites

In warmer regions (mean Tavg of the two sites), dissimilarity tended to increase between two different sites as the spatial distance between

**Table 1**

Indicator species of netted and pan trapped collections with the associated values of the specificity (A), the fidelity (B) components of the indicator value index (stat). Each list is ordered by the values of the indicator value index. It means that the most indicative species of each method are displayed first.

Net	A	B	stat	Pan traps	A	B	stat
<i>Bombus terrestris</i> agg.	0.87	0.97	0.92	<i>Andrena minutula</i>	0.70	0.73	0.71
<i>Apis mellifera</i>	0.60	1.00	0.77	<i>Lasioglossum malachurum</i>	0.73	0.69	0.71
<i>Bombus pascuorum</i>	0.95	0.58	0.74	<i>Lasioglossum morio</i>	0.97	0.47	0.67
<i>Bombus lapidarius</i>	0.97	0.55	0.73	<i>Lasioglossum paucillum</i>	0.76	0.55	0.64
<i>Andrena scotica</i>	0.92	0.55	0.71	<i>Lasioglossum calceatum</i>	0.69	0.44	0.55
<i>Andrena haemorrhoa</i>	0.63	0.77	0.70	<i>Lasioglossum minutissimum</i>	1.00	0.29	0.54
<i>Bombus pratorum</i>	0.91	0.48	0.66	<i>Andrena humilis</i>	0.86	0.31	0.51
<i>Osmia cornuta</i>	0.88	0.47	0.64	<i>Nomada flavoguttata</i>	0.94	0.26	0.49
<i>Anthophora plumipes</i>	0.92	0.39	0.60	<i>Andrena subopaca</i>	0.81	0.27	0.47
<i>Andrena fulva</i>	0.73	0.39	0.53	<i>Andrena bicolor</i>	0.72	0.29	0.46
<i>Colletes cunicularius</i>	0.83	0.32	0.51	<i>Osmia caerulea</i>	1.00	0.18	0.42
<i>Xylocopa violacea</i>	1.00	0.26	0.51	<i>Nomada fabriciana</i>	0.81	0.21	0.41
<i>Bombus hypnorum</i>	0.94	0.26	0.49	<i>Seladonia tumulora</i>	0.86	0.19	0.41
<i>Andrena helvola</i>	0.77	0.27	0.46	<i>Lasioglossum punctatissimum</i>	1.00	0.16	0.40
<i>Andrena trimmerana</i>	1.00	0.16	0.40	<i>Lasioglossum glabriusculum</i>	0.85	0.18	0.39
<i>Andrena bucephala</i>	1.00	0.10	0.31	<i>Andrena nigroolivacea</i>	0.91	0.16	0.38
				<i>Lasioglossum subhirtum</i>	0.90	0.15	0.36
				<i>Andrena lagopus</i>	0.90	0.15	0.36
				<i>Sphecodes ephippius</i>	0.89	0.13	0.34
				<i>Andrena viridescens</i>	1.00	0.11	0.34
				<i>Nomada bifasciata</i>	1.00	0.11	0.34
				<i>Lasioglossum politum</i>	1.00	0.10	0.31

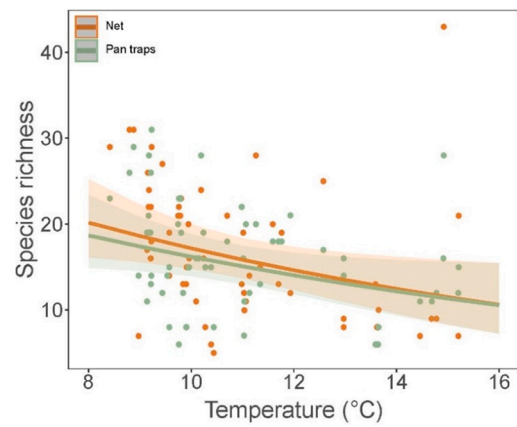


**Fig. 3.** Taxonomic (A), functional (B) and phylogenetic (C) Non-metric multi-dimensional scaling (NMDS) plot of pan traps (green grouping) and net (orange grouping). Larger circles represent sites and their associated assemblage caught either by pan traps or net (each orchard has two circles). Every site is coloured by its average temperature (Tavg). In the taxonomic NMDS (A), bumblebees are shown by dark green circles, *A. mellifera* by a red square and other wild bee species by black triangles. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article)

them also increased (Fig. 6, Table S11). In colder regions the distance between sites had nearly no effect on the dissimilarity. When we analysed net and pan traps separately, we observed similar patterns of pairwise dissimilarity along the gradient with significantly higher dissimilarities observed between pan trapped assemblages than between netted assemblages (for taxonomic  $\beta\text{SOR}$ :  $t_{(1890)} = 29.92$ ,  $P < 0.001$ , phylogenetic  $\beta\text{SOR}$ :  $t_{(1890)} = 3.54$ ,  $P < 0.001$  and functional  $\beta\text{SOR}$ :  $t_{(1890)} = 4.96$ ,  $P < 0.001$ ), confirming the NMDS results (Fig. S14).

#### 4. Discussion

In the present study, we extend the previously observed differences in observed bee communities generated by “active” (netting) and “passive” sampling methods (pan traps) (Hutchinson et al., 2021b; O’Connor et al., 2019; Thompson et al., 2021) at a substantially larger scale and

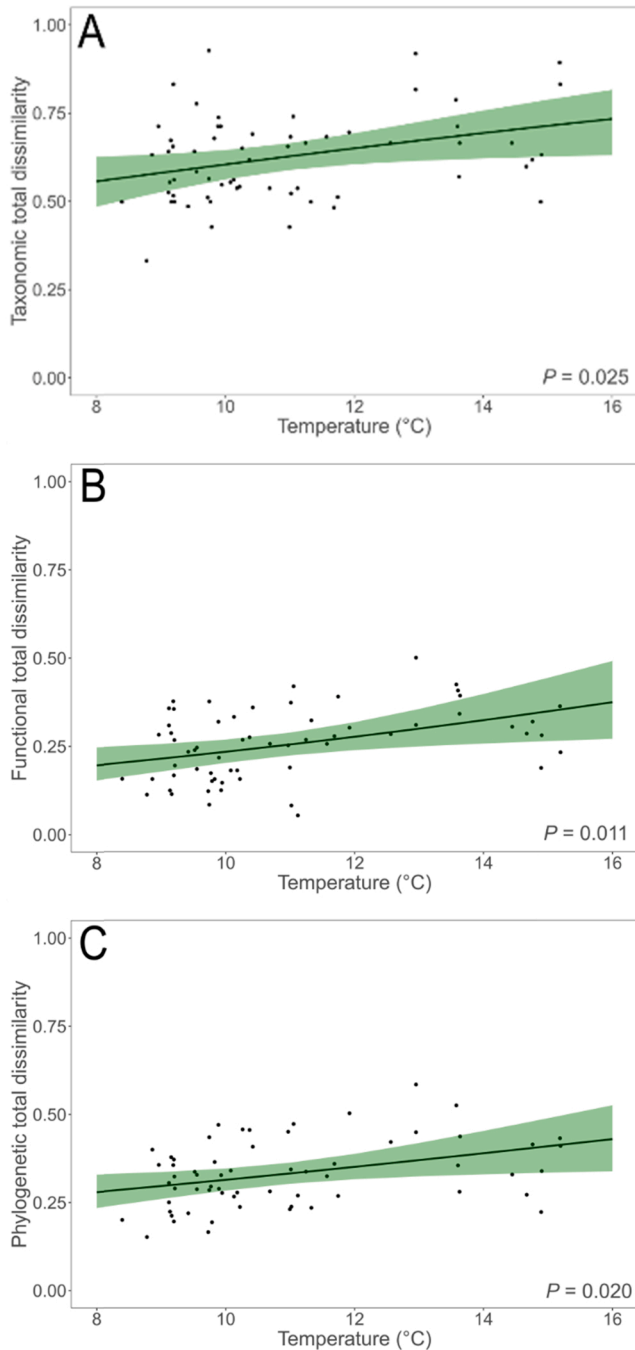


**Fig. 4.** Effect of the monthly average temperature (in °C) on the species richness (i.e. species count) collected within each site for both methods. Circles represent observed SR. Regression line and 95% confidence intervals shown. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article)

integrate alternative diversity measures (PD and FD). More importantly, we show that climate had a significant effect on the differences in community composition observed between the netting and pan trapping sampling approaches.

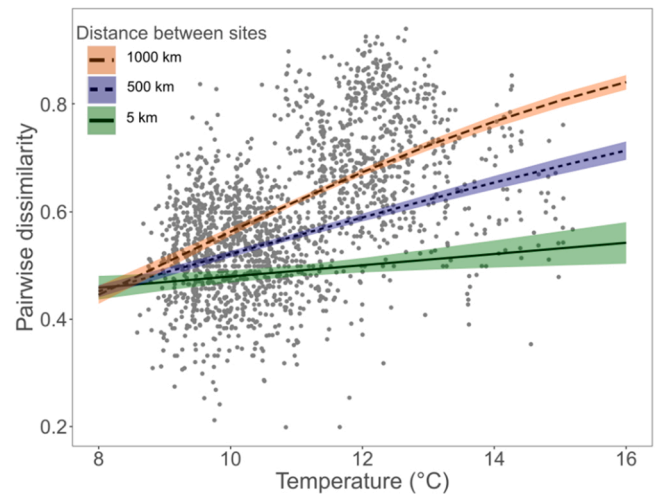
We show that wild bee assemblages associated with apple trees exhibit distinct patterns of species composition, abundance, as well as contrasting functional and phylogenetic assemblage structures depending on whether they were assessed by netting or pan trapping. We hypothesise that these consistent differences are maintained because each sampling method “filters” the spectrum of life-history traits present in bee species at any individual site in contrasting ways, preferentially recording certain groups. Specifically, a larger relative proportion of Halictidae (especially the *Lasioglossum*, *Sphecodes* and *Halictus*) was found in pan traps, which led to this sampling technique recording a higher percentage of species nesting in the ground and of brood parasitic species (*Sphecodes* spp.) compared to the bee assemblage associated with netting surveys (Roulston et al., 2007). Secondly, a higher proportion of monoleptic/oligolectic species was collected in pan traps (these species specialised on non-Rosaceae host plants are unlikely to visit apple blossoms, except for a brief collection of nectar) (Table S6). And finally, a larger relative proportion of Andrenidae (*Andrena*) and Apidae (*Bombus* and *Xylocopa*) was found during netting surveys, which led to a netted bee assemblage characterised by species larger body size values and longer tongue on average (Apidae, see Fig. S3), as well as more primitively eusocial species recorded than in the pan trap assemblage (Wilson et al., 2008).

How the climatic variables influence these divergences between assemblages recorded by both methods had never been addressed to date at a large spatial scale. Here, we find that among all important environmental variables in predicting the presence of bees, temperature explained most of the variation in the divergence between assemblages (i.e. increasing differences between the assemblages associated with each method, from colder to warmer sites) (Fig. 5). This significant effect of temperature on the differences between methods indicates an effect of the climatic gradient in Europe. Particularly, depending the position on this gradient, differences in community composition between the traditional sampling methods will differ. We suggest that this pattern may be explained by several mutually exclusive hypotheses. First, if one assumes that the total species pool of bees active in spring is likely to be greater in warmer regions of Europe such as the Mediterranean basin, as would be consistent with overall patterns of diversity (Michener, 1979; Michez et al., 2019; Nieto et al., 2014), all else being equal we could therefore expect the structurally “open flowers” of apple trees to attract a greater absolute number of bee species at their peak



**Fig. 5.** Effect of the monthly average temperature on the (A) taxonomic, (B) functional and (C) phylogenetic total dissimilarity ( $\beta_{\text{ST}}$ ) within each site between net and pan traps assemblages. Dark circles represent the real values of beta diversity for each site. Regression line and 95% confidence intervals shown.

flowering time. However, our results show that SR in apple orchards significantly decreased along the climatic gradient, with fewer and fewer species observed visiting apple blossoms or collected in pan traps in warmer regions of Europe (PD and FD showed no significant relationship) (Figs. 4, S5–6 and Table S7). The fact that bee diversity in apple orchards, irrespective of the survey method, does not follow the biogeographic pattern of bee diversity in Europe suggests the existence of a relatively strong “filtering” effect of the crop, whereby the floral design, display, and rewards presumably restrict the number of species visiting the apple blossoms (Pisanty and Mandelik, 2015). A variety of



**Fig. 6.** Effect of the monthly average temperature and spatial distance on the pairwise total taxonomic dissimilarity ( $\beta_{\text{ST}}$ ) between sites. Grey circles represent the real values of pairwise beta diversity between each group of two sites. Regression lines and 95% confidence intervals shown for three different distances between sites.

local conditions could also play a role in driving the local bee community structure, including the surrounding landscape, the diversity of co-blooming wildflowers, the availability of micro-habitats used by wild bees, the number of hives installed locally and the dominance of *A. mellifera* (e.g. Marini et al., 2012; Sheffield et al., 2016; Weekers et al., 2022). All these factors individually and collectively account for the rather restricted taxonomic range of genera/species associated with blossoming apple trees (Hutchinson et al., 2021a; Kleijn et al., 2015; Weekers et al., 2022).

We also found that as bee diversity decreased or was not impacted along the climatic gradient (Figs. 4, S5–6 and Table S7), the composition of the bee assemblages, rather than the sheer number of species, impacted the divergence observed between netted and pan trapped bee assemblages. Indeed, we show that the divergence was mainly due to the taxonomic, functional, and phylogenetic turnover between both assemblages (i.e. species/traits/taxa replacement). Two phenomena appear together here: the fact that turnover explains the largest part of the beta diversity and that this beta diversity increases along the climatic gradient explains that the overall diversity does not follow the same trend. That is, a higher turnover between survey methods implies more strongly diverging pollinator communities, irrespective of the diversity observed (Baselga, 2010; Winfree et al., 2018). By contrast, the number of species varies significantly with the total nestedness (but not total turnover) (Baselga, 2010). The increasing turnover is partly due to the comparatively higher proportions of bee specialists species (*sensu* Dötterl and Vereecken, 2010; Rasmussen et al., 2020) in southern (warmer) regions that are not specialised on Rosaceae. For example, southern European bees of the genera *Eucera* (Apidae), *Andrena* (Andrenidae), and *Osmia* (Megachilidae) which include many specialists on non-Rosaceae host plants are less likely to visit apple flowers than many polylectic species such as *A. mellifera*, *Bombus* spp., or predominantly northern vernal species in the genera *Andrena* (Andrenidae), *Osmia* (Megachilidae) or *Lasiglossum* (Halictidae) (Portman et al., 2020) that have broader dietary niches than their southern counterparts.

Furthermore, we showed that pairs of sites in warmer regions were significantly more dissimilar than pairs of sites in colder regions. The distance among sites in colder regions had no effect on the associated bee community divergence, which confirms that in colder regions the pool of active wild bee species is both less diverse and more homogeneous due to landscape homogenisation and biogeographic factors (Carvalho et al., 2013). Last, the increasing divergence between



methods along the climatic gradient was not due to an increase of the homogenisation of the species collected (Fig. S4). Indeed, relative abundance of common species visiting apple flowers was not correlated to the temperature gradient, meaning that dominant visitors made up the same proportion in all sites (Kleijn et al., 2015).

## 5. Conclusion and perspectives

Recent studies have documented the contrasting results obtained on pollinator community structure between the “active” netting and “passive” pan trapping (Hutchinson et al., 2021b; Kuhlman et al., 2021; O'Connor et al., 2019; Prendergast et al., 2020), each method having their own biases and then serving different purposes depending on the question asked. Our findings agree with this assessment, and judicious use of these differing techniques should reduce their inherent biases when used to study bee diversity in agroecosystems. Our data also support findings by Kuhlman et al. (2021), if pan traps are integrated in the monitoring of wild bee communities, only presence-absence analyses are pertinent to describe recorded diversity. We also provide further information to confirm the divergence between the two methods (Hutchinson et al., 2021b; O'Connor et al., 2019; Thompson et al., 2021) at an unprecedented spatial scale for a single crop. Moreover, we highlight how climate and crop-specific factors influence the patterns of life-history traits of the wild bee guilds. As demonstrated, climate amplifies the divergences between assemblages of each method, and it would be interesting to test the validity of our results by studying those relations across time (among cropping seasons) (Kuhlman et al., 2021; Thompson et al., 2021) and among crops (Hutchinson et al., 2021b) at a large, sub-continental scale similar to our study. In addition, the European Pollinator Monitoring Scheme (Potts et al., 2020) and other large-scale study should consider climate for future standardised monitoring in Europe, with expected higher taxonomic, phylogenetic and functional turnovers likely to occur between common sampling methods in warmer regions. Indeed, only the standardisation of protocols via considered choice of survey methods including the changing impact of climate could allow to evaluate and describe status, patterns, and trends of pollinators. Such an approach would help to provide reliable science and data for designing future policies to address the pressing issues that pollinators are facing.

## CRedit authorship contribution statement

N.L., L.M., G.S., P.V., T. Weekers, and N.J.V. conceived and designed the project; A.A., D. Benda, D. Bevk, P.B., D.C., B.D., M.G., M.G., G.G., L. H., N.L., L.M., B.M., D.M., J.-M.M., P.N., J.S., N.J.V., T. Weekers, and, T. J. Wood collected the data; D. Benda, P.B., L.H., J.S., N.J.V. and, T.J. Wood provided specimen identifications. N.L. analysed the data; N.L., L. M., T. Weekers and, N.J.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Declaration of Competing Interest

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

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.107871.

## References

- Baraloto, C., Hardy, O.J., Paine, C.E.T., Dexter, K.G., Craud, C., Dunning, L.T., Gonzalez, M.-A., Molino, J.-F., Sabatier, D., Savolainen, V., Chave, J., 2012. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *J. Ecol.* 100, 690–701. <https://doi.org/10.1111/j.1365-2745.2012.01966.x>.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>.
- Baselga, A., Orme, C.D.L., Villeger, S., De Bortoli, J., Leprieux, F., 2018. betapart: Partit. Beta Divers. into Turnover Nestedness Compon.
- Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400. <https://doi.org/10.32614/RJ-2017-066>.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel Inference. *Sociol. Methods Res.* 33, 261–304. <https://doi.org/10.1177/0049124104268644>.
- Cadotte, M.W., Arnillas, C.A., Livingstone, S.W., Yasui, S.-L.E., 2015. Predicting communities from functional traits. *Trends Ecol. Evol.* 30, 510–511. <https://doi.org/10.1016/j.tree.2015.07.001>.
- Cane, J.H., 1987. Estimation of bee size using intertegular span (Apoidea). *J. Kans. Entomol. Soc.* 60, 145–147.
- Cane, J.H., 2001. Habitat fragmentation and native bees: a premature verdict? *Conserv. Ecol.* 5, 3. <https://doi.org/10.5751/ES-00265-050103>.
- Cane, J.H., Minckley, R.L., Kervin, L.J., 2000. Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. *J. Kans. Entomol. Soc.* 73, 225–231.
- Cariveau, D.P., Nayak, G.K., Bartomeus, I., Zientek, J., Ascher, J.S., Gibbs, J., Winfree, R., 2016. The allometry of bee proboscis length and its uses in ecology. *PLoS One* 11. <https://doi.org/10.1371/journal.pone.0151482>.
- Carvalho, L.G., Kunin, W.E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R., Groom, Q., Hennekens, S., Landuyt, W., Maes, D., Meutter, F., Michez, D., Rasmont, P., Ode, B., Potts, S.G., Reemer, M., Roberts, S.P.M., Schaminée, J., WallisDeVries, M.F., Biesmeijer, J.C., 2013. Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecol. Lett.* 16, 870–878. <https://doi.org/10.1111/ele.12121>.
- Chen, H., VennDiagram: Gener. High-Resolut. Venn Euler Plots 2018.
- R. Core Team, 2019. R: A Language and Environment for Statistical Computing.
- Daru, B.H., Karunaratne, P., Schliep, K., 2020. phylregion: R package for biogeographical regionalization and macroecology. *Methods Ecol. Evol.* 11, 1483–1491. <https://doi.org/10.1111/2041-210X.13478>.
- De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90, 3566–3574. <https://doi.org/10.1890/08-1823.1>.
- Delaplane, K.S., Mayer, D.F., 2000. Crop Pollination by Bees. CABI publishing, Wallingford. <https://doi.org/10.1079/9780851994482.0000>.
- Dötterl, S., Vereecken, N.J., 2010. The chemical ecology and evolution of bee-flower interactions: a review and perspectives. *Can. J. Zool.* 88, 668–697. <https://doi.org/10.1139/Z10-031>.
- Droege, S., Leubhn, G., Williams, N., Minckley, B., Griswold, T., Kremen, C., Messinger, O., Cane, J., Roulston, T.H., Parker, F., Tepedino, V., Buchmann, S., 2005. The bee inventory plot [WWW Document]. URL (<http://online.sfsu.edu/beeplot/>) (Accessed 5 December 20).
- FAOStat, 2020. Crops [WWW Document]. URL (<http://www.fao.org/faostat/en/#data/QC>) (accessed 25 May 20).
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315. <https://doi.org/10.1002/joc.5086>.
- Grab, H., Branstetter, M.G., Amon, N., Urban-Mead, K.R., Park, M.G., Gibbs, J., Blitzer, E. J., Poveda, K., Loeb, G., Danforth, B.N., 2019. Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. *Science* 363, 282–284. <https://doi.org/10.1126/science.aaf6016>.
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596. <https://doi.org/10.1007/s00442-007-0752-9>.



- Hoiss, B., Krauss, J., Potts, S.G., Roberts, S., Steffan-Dewenter, I., 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proc. R. Soc. B Biol. Sci.* 279, 4447–4456. <https://doi.org/10.1098/rspb.2012.1581>.
- Hutchinson, L.A., Oliver, T.H., Breeze, T.D., Bailes, E.J., Brünjes, L., Campbell, A.J., Erhardt, A., de Groot, G.A., Földesi, R., García, D., Goulson, D., Hainaut, H., Hambäck, P.A., Holzschuh, A., Jauker, F., Klatt, B.K., Klein, A.-M., Kleijn, D., Kovács-Hostyánszki, A., Krimmer, E., McKerchar, M., Miñarro, M., Phillips, B.B., Potts, S.G., Pufal, G., Radzevičiūtė, R., Roberts, S.P.M., Samnegård, U., Schulze, J., Shaw, R.F., Tschamtké, T., Vereecken, N.J., Westbury, D.B., Westphal, C., Wietzke, A., Woodcock, B.A., Garratt, M.P.D., 2021a. Using ecological and field survey data to establish a national list of the wild bee pollinators of crops. *Agric. Ecosyst. Environ.* 315, 107447. <https://doi.org/10.1016/j.agee.2021.107447>.
- Hutchinson, L.A., Oliver, T.H., Breeze, T.D., O'Connor, R.S., Potts, S.G., Roberts, S.P.M., Garratt, M.P.D., 2021b. Inventorying and monitoring crop pollinating bees: evaluating the effectiveness of common sampling methods. *Insect Conserv. Divers.* 1–13. <https://doi.org/10.1111/icad.12557>.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>.
- Kendall, L.K., Rader, R., Gagic, V., Cariveau, D.P., Albrecht, M., Baldock, K.C.R., Freitas, B.M., Hall, M., Holzschuh, A., Molina, F.P., Morten, J.M., Pereira, J.S., Portman, Z.M., Roberts, S.P.M., Rodriguez, J., Russo, L., Sutter, L., Vereecken, N.J., Bartomeus, I., 2019. Pollinator size and its consequences: robust estimates of body size in pollinating insects. *Ecol. Evol.* 9, 1702–1714. <https://doi.org/10.1002/ece3.4835>.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelík, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Scilligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tschamtké, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Ward, K.L., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6, 7414. <https://doi.org/10.1038/ncomms8414>.
- Kuhlman, M.P., Burrows, S., Mummey, D.L., Ramsey, P.W., Hahn, P.G., 2021. Relative bee abundance varies by collection method and flowering richness: implications for understanding patterns in bee community data. *Ecol. Solut. Evid.* 2, 1–11. <https://doi.org/10.1002/2688-8319.12071>.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305. <https://doi.org/10.1890/08-2244.1>.
- Marini, L., Quaranta, M., Fontana, P., Biesmeijer, J.C., Bommarco, R., 2012. Landscape context and elevation affect pollinator communities in intensive apple orchards. *Basic Appl. Ecol.* 13, 681–689. <https://doi.org/10.1016/j.baae.2012.09.003>.
- Michener, C.D., 1979. Biogeography of the bees. *Ann. Mo. Bot. Gard.* 66, 277. <https://doi.org/10.2307/2398833>.
- Michener, C.D., 2007. *The Bees of the World*, second ed. The John Hopkins University Press, Baltimore.
- Michez, D., Rasmont, P., Terzo, M., Vereecken, N.J., 2019. *Bees of Europe*. N.A.P. Edit.
- Nielsen, A., Steffan-Dewenter, I., Westphal, C., Messinger, O., Potts, S.G., Roberts, S.P.M., Settele, J., Szentgyörgyi, H., Vaissière, B.E., Vaitis, M., Woyciechowski, M., Bazos, I., Biesmeijer, J.C., Bommarco, R., Kunin, W.E., Tschaulin, T., Lamborn, E., Petanidou, T., 2011. Assessing bee species richness in two Mediterranean communities: Importance of habitat type and sampling techniques. *Ecol. Res.* 26, 969–983. <https://doi.org/10.1007/s11284-011-0852-1>.
- Nieto, A., Roberts, S.P.M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P., De Meulemeester, T., Dehon, M., Dewulf, A., Ortiz-Sánchez, F.J., Lhomme, P., Pauly, A., Potts, S.G., Praz, C., Q., Window, J., Michez, D., 2014. European Red List of Bees, Luxembourg: Publication Office of the European Union.
- O'Connor, R.S., Kunin, W.E., Garratt, M.P.D., Potts, S.G., Roy, H.E., Andrews, C., Jones, C.M., Peyton, J.M., Savage, J., Harvey, M.C., Morris, R.K.A., Roberts, S.P.M., Wright, I., Vanbergen, A.J., Carvell, C., 2019. Monitoring insect pollinators and flower visitation: the effectiveness and feasibility of different survey methods. *Methods Ecol. Evol.* 10, 2129–2140. <https://doi.org/10.1111/2041-210X.13292>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. *vegan: Community Ecology Package*.
- Orr, M.C., Hughes, A.C., Chesters, D., Pickering, J., Zhu, C.-D., Ascher, J.S., 2021. Global patterns and drivers of bee distribution. *Curr. Biol.* 31, 451–458. <https://doi.org/10.1016/j.cub.2020.10.053>.
- Paradis, E., Schliep, K., 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526–528. <https://doi.org/10.1093/bioinformatics/bty633>.
- Pardo, A., Borges, P.A.V., 2020. Worldwide importance of insect pollination in apple orchards: a review. *Agric. Ecosyst. Environ.* 293, 106839. <https://doi.org/10.1016/j.agee.2020.106839>.
- Pérez-Méndez, N., Andersson, G.K.S., Requier, F., Hipólito, J., Aizen, M.A., Morales, C.L., García, N., Gennari, G.P., Garibaldi, L.A., 2020. The economic cost of losing native pollinator species for orchard production. *J. Appl. Ecol.* 57, 599–608. <https://doi.org/10.1111/1365-2664.13561>.
- Pisanty, G., Mandelík, Y., 2015. Profiling crop pollinators: life history traits predict habitat use and crop visitation by Mediterranean wild bees. *Ecol. Appl.* 25, 742–752. <https://doi.org/10.1890/14-0910.1>.
- Ponisio, L.C., M'Gonigle, L.K., Kremen, C., 2016. On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. *Glob. Chang. Biol.* 22, 704–715. <https://doi.org/10.1111/gcb.13117>.
- Portman, Z.M., Bruninga-Soclar, B., Cariveau, D.P., 2020. The state of bee monitoring in the United States: a call to refocus away from bowl traps and towards more effective methods. *Ann. Entomol. Soc. Am.* 1–6. <https://doi.org/10.1093/aesa/saaa010>.
- Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220–229. <https://doi.org/10.1038/nature20588>.
- Potts, S.G., Dauber, J., Hochkirch, A., Oteman, B., Roy, D.B., Ahnre, K., Biesmeijer, K., Breeze, T., Carvell, C., Ferreira, C., Fitzpatrick, Ú., Isaac, N.J.B., Kuussaari, M., Ljuboimirov, T., Maes, J., Ngo, H., Pardo, A., Polce, C., Quaranta, M., Settele, J., Sorg, M., Stefanescu, C., Vujic, A., 2020. Proposal for an EU Pollinator Monitoring Scheme. Publications Office of the European Union, Luxembourg. <https://doi.org/10.2760/881843>.
- Prendergast, K.S., Menz, M.H.M., Dixon, K.W., Bateman, P.W., 2020. The relative performance of sampling methods for native bees: an empirical test and review of the literature. *Ecosphere* 11. <https://doi.org/10.1002/ecs2.3076>.
- Rasmussen, C., Engel, M.S., Vereecken, N.J., 2020. A primer of host-plant specialization in bees. *Emerg. Top. Life Sci.* 4, 7–17. <https://doi.org/10.1042/ETLS20190118>.
- Roulston, T.H., Smith, S.A., Brewster, A.L., 2007. A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) Fauna. *J. Kans. Entomol. Soc.* 80, 179–181. [https://doi.org/10.2317/0022-8567\(2007\)80\[179:ACOPTA\]2.0.CO;2](https://doi.org/10.2317/0022-8567(2007)80[179:ACOPTA]2.0.CO;2).
- RStudio Team, 2018. RStudio: Integrated Development for R. RStudio.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecol. Lett.* 16, 912–920. <https://doi.org/10.1111/ele.12128>.
- Sheffield, C.S., Ngo, H.T., Azzu, N., 2016. A Manual on Apple Pollination. Food and Agriculture Organization of the United Nations (FAO), Rome.
- Sydenham, M.A.K., Moe, S.R., Totland, Ø., Eldegard, K., 2015. Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? *Ecography* 38, 140–153. <https://doi.org/10.1111/ecog.00938>.
- Thompson, A., Frenzel, M., Schweiger, O., Musche, M., Groth, T., Roberts, S.P.M., Kuhlmann, M., Knight, T.M., 2021. Pollinator sampling methods influence community patterns assessments by capturing species with different traits and at different abundances. *Ecol. Indic.* 132, 108284. <https://doi.org/10.1016/j.ecolind.2021.108284>.
- Vereecken, N.J., Weekers, T., Leclercq, N., De Greef, S., Hainaut, H., Molenberg, J.-M., Martin, Y., Janssens, X., Noël, G., Pauly, A., Roberts, S.P.M., Marshall, L., 2021. Insect biomass is not a consistent proxy for biodiversity metrics in wild bees. *Ecol. Indic.* 121. <https://doi.org/10.1016/j.ecolind.2020.107132>.
- Wagner, D.L., 2020. Insect declines in the anthropocene. *Annu. Rev. Entomol.* 65, 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>.
- Weekers, T., Marshall, L., Leclercq, N., Wood, T.J., Cejas, D., Drepper, B., Hutchinson, L., Michez, D., Molenberg, J.-M., Smagghe, G., Vandamme, P., Vereecken, N.J., 2022. Dominance of honey bees is negatively associated with wild bee diversity in commercial apple orchards regardless of management practices. *Agric. Ecosyst. Environ.* 323, 107697. <https://doi.org/10.1016/j.agee.2021.107697>.
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyörgyi, H., Tschaulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring bee diversity in different European habitats and biogeographical regions. *Ecol. Monogr.* 78, 653–671. <https://doi.org/10.1890/07-1292.1>.
- Wilson, J.S., Griswold, T., Messinger, O.J., 2008. Sampling bee communities (Hymenoptera: Apiformes) in a desert landscape: are pan traps sufficient? *J. Kans. Entomol. Soc.* 81, 288–300. <https://doi.org/10.2317/JKES-802.06.1>.
- Winfree, R., Reilly, J.R., Bartomeus, I., Cariveau, D.P., Williams, N.M., Gibbs, J., 2018. Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science* 359, 791–793. <https://doi.org/10.1126/science.aao2117>.
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biol. Conserv.* 143, 669–676. <https://doi.org/10.1016/j.biocon.2009.12.003>.