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ORIGINAL RESEARCH

# Biotic homogenization and functional restructuring of bee communities in northern France: implications for conservation priorities

**Alessandro Fisogni**[1] · **Yves Piquot**[1] · **Denis Michez**[2] · **Ahlam Sentil**[2] · **Magalie Franchomme**[3] · **Thomas J. Wood**[2,4] · **Simone Flaminio**[2] · **Bastien De Tandt**[2] · **Shawn Lemaire**[2] · **Nina Hautekèete**[1]

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## Abstract

Anthropic-related pollinator decline is a major challenge. To ensure that we characterize the underlying ecological processes and implement appropriate conservation measures, it is important to consider multiple dimensions of diversity. Here, we use a rare dataset of bee communities spanning over 100 years (1910–2019) in northern France, an area subject to severe land use alteration. By analyzing species-level data together with functional traits, we demonstrate a significant decline and homogenization of taxonomic diversity associated with a functional restructuring of bee communities. By combining extinction probabilities based on Red List categories with functional characteristics, we identified species critical for maintaining functional diversity and in need of urgent conservation actions. Present-day communities exhibited functional shifts favoring larger, eusocial generalist species with a long phenology, likely reflecting greater adaptability to reduced resource availability in space and time. Species with higher thermal resistance and warmer climatic niches were favored over time, indicating functional filtering of species adapted to climatic warming. In addition, recent bee communities were characterized by species with larger habitat breadth and stronger affinity for artificial habitats. These changes resulted in decreased functional evenness and increased dominance of species with extreme trait combinations, reducing functional redundancy and potentially destabilizing ecosystem processes. Suitable habitats and host plants are identified and recommended for supporting the most functionally threatened bee species. Our findings underscore the importance of considering functional traits in conservation prioritization efforts, and advocate a more integrated approach that incorporates both taxonomic and functional perspectives to effectively mitigate bee biodiversity loss.

**Keywords** Extinction risk · Functional traits · FUSE index · Historical biodiversity changes · IUCN Red List · Species decline

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Extended author information available on the last page of the article

## Introduction

The accelerating decline and loss of species reported over the last decades constitute a pressing challenge (Díaz et al. 2019; Jaureguiberry et al. 2022). Within this context, the reduction in pollinator populations has received particular attention due to its pervasive occurrence across diverse regions (Potts et al. 2010; Nieto et al. 2014; Millard et al. 2021). Although a few species are favored by global environmental changes, the majority is showing declining population trends (Ghisbain et al. 2021). The repercussions of such declines may extend beyond the species themselves, potentially affecting intricate interspecific interactions, with wide-ranging impacts on ecosystems and human societies (Ramos-Jiliberto et al. 2020; Dicks et al. 2021). These changes are driven primarily by a convergence of anthropogenic factors, including land use alterations, climate change, urbanization, pollution (e.g., nitrogen and heavy metals), invasive species, and extensive pesticide use (Potts et al. 2010; Harrison and Winfree 2015; LeBuhn and Luna 2021; Jaureguiberry et al. 2022; Ghisbain et al. 2024).

Bees are among the most important pollinators of crops and wild flowering plants (Klein et al. 2007; Willmer et al. 2017). Environmental changes exert profound influences on the ecological dynamics of bee communities, and can act as selective biological filters that favor species with functional traits that are better adapted to the new conditions. Thermophilic species may be advantaged in urban landscapes by urban heat-island effects (Hamblin et al. 2017). Larger bee species with high dispersal capabilities can potentially better navigate fragmented habitats in search of foraging resources (Stang et al. 2006; Greenleaf et al. 2007; Gérard et al. 2020), although increased urbanization can constrain their mobility (Buchholz and Egerer 2020; O'Connell et al. 2021), while smaller species can better cope with smaller green spaces (Zaninotto et al. 2023). The diversity of parasitic bee species is closely related to the diversity of their hosts, and their decline tends to be accentuated by decreasing landscape diversity (Sheffield et al. 2013; Prendergast et al. 2022). The availability of suitable nesting sites and food resources also plays a key role in sustaining local populations, and the increase in impervious surfaces at the expense of bare land can reduce suitable areas for ground-nesting species (Quistberg et al. 2016; Buchholz and Egerer 2020). Flower richness and abundance is often positively correlated with pollinator richness and flower visitation in human-managed areas (Baldock et al. 2019; Theodorou et al. 2020), while the loss of preferred host plants can drive declines of pollen specialist bees (Scheper et al. 2014). In addition, higher temporal dynamics in food resource availability in heavily anthropized areas can influence the phenology of pollinator communities, favoring species with phenologies that match those of the visited plants (Banaszak-Cibicka et al. 2018) or species with prolonged activity that can potentially increase their pollination efficiency (Zaninotto et al. 2020). The complexity of these traits and how they interact in response to past and present challenges can be associated to substantial alterations in the affected communities.

Many studies have thus focused on the environmental filtering of traits and assemblages of pollinator species, particularly bees, in urban and agricultural environments. While studies along urbanization gradients are now relatively numerous, mostly with mixed results on species diversity (Wenzel et al. 2020) and some congruent results on trait filtering (Wenzel et al. 2020; Fauviau et al. 2022; Ferrari and Polidori 2022; Liang et al. 2023), diachronic studies are still sparse due to the scarcity of historical data and the difficulties inherent in comparing datasets with different amounts of data and sampling methods. Among these, studies in neighboring countries have shown congruent results on bee decline over time related to landscape modification and resource availability in Belgium (Duchenne et al. 2020), the Netherlands (Biesmeijer et al. 2006) and the UK (Powney et al. 2019). However, no such studies have yet been conducted in France. Here, we used a rare dataset spanning more than 100 years including wild bee species in northern France. This region has undergone intense anthropogenic transformations that have profoundly affected its biodiversity, leading to a strong biotic homogenization of plant assemblages (Hautekèete et al. 2015). Biodiversity assessments have shown the loss of many native plant species from rare and predominantly oligotrophic habitats, followed by the arrival of cosmopolitan species found predominantly in typical anthropogenic habitats (Hautekèete et al. 2015). Moreover, bird communities have experienced substantial functional homogenization in response to increased urbanization and landscape disturbance (Devictor et al. 2007, 2008a; Luczak 2017). However, detailed information on the long-term modifications to local pollinator faunas is still lacking.

IUCN Red Lists are among the most important tools for species conservation worldwide (Rodrigues et al. 2006). Along with assessing extinction risks at the global and continental level, Red Lists have been developed to assess species extinction risk at the national and regional levels, where conservation policies are often implemented (www.iucn.org). Although included among the criteria in species assessments (IUCN 2012), population trends remain difficult to apply at the larger continental scale (Nieto et al. 2014), while they can be used more efficiently at lower geographic scale, where knowledge of local population trends can be higher (Drossart et al. 2019). However, gathering precise information on pollinator trends remains challenging for most species (Maes et al. 2012, 2015).

Despite the high variation in ecological traits found among species, functional diversity is not incorporated into IUCN Red List risk assessments. High functional diversity is needed to maintain ecosystem functioning (Isbell et al. 2011), and losses of some species could have greater implications for ecosystem functioning than others (Isbell et al. 2017), potentially influencing the functional diversity of assemblages in different ways (Cadotte et al. 2011). Moreover, although functional redundancy (i.e., different species sharing similar functional traits) can increase the resistance of functional richness to species loss, projected extinctions are expected to significantly alter the functional spectra of most groups, increasing their vulnerability to future extinctions (Carmona et al. 2021). Including the functional component into conservation prioritization is therefore an important step towards species conservation, especially because mismatches can occur between the loss of taxonomic and functional diversity (Devictor et al. 2010; Jarzyna and Letz 2018).

Here, we evaluated changes in bee taxonomic and functional diversity over the past century (1910–2019) in northern France. First, we used detailed species-level data to assess changes that occurred in bee communities from the perspective of taxonomic diversity. We used Hill diversities (Jost 2006) to estimate changes in species richness, diversity and dissimilarity over time. In a second step, we considered a suite of 12 functional traits that are pertinent to understanding the adaptive responses of bee communities to environmental transformations, and built multivariate functional spaces to estimate changes in functional diversity between historic and present communities. Finally, we integrated species functional traits into conservation priorities by using a recently developed index (FUSE: functionally unique, specialized and endangered; Pimiento et al. 2020) that captures the variation and ecological roles of species in combination with IUCN Red List threat status.

While originally developed to study marine megafauna, FUSE can potentially be applied across different taxa and scales according to conservation challenges (Pimiento et al. 2020). Here, we propose to apply the FUSE index to insects, and specifically bees, to identify species whose likely extinction may cause a disproportionate loss of trait diversity at the community level, enabling the targeting of species in need of conservation priorities. Overall, the integrated approach proposed in this study allows for a nuanced exploration of the multiple factors influencing bee diversity change and conservation issues over time, contributing to a broader understanding of the impacts of land use and climate change on these crucial pollinators.

## Materials and methods

### Study area

We studied changes in bee community composition in the Nord Department, which comprises the northernmost territories of France. This area has a population of more than 2.5 million inhabitants, with a density of 454 inhabitants per km$^2$ (www.insee.fr). The Nord Department includes a metropolitan area (Métropole Européenne de Lille) of about 1.2 million inhabitants (www.insee.fr), has among the highest levels of agricultural intensification in France (Deguines et al. 2014) and the lowest surface of natural areas among all French Departments (Schmitt 2009). The intense anthropogenic transformations this area has undergone over the past century have profoundly affected its biodiversity, causing major restructuring of plant (Hautekèete et al. 2015) and bird (Devictor et al. 2007, 2008a) communities linked to habitat changes and increased landscape disturbance. Moreover, urbanization has negatively affected pollinator communities, altering functional traits such as species phenology (Fisogni et al. 2020) and restructuring plant-pollinator interactions (Fisogni et al. 2022).

To study temporal changes in bee communities, we drew a grid of 10×10 km over the study area projected on the Universal Transverse Mercator (UTM) coordinate system. This is a common spatial resolution used to study changes in species communities at the local scale (e.g., Carvalheiro et al. 2019; Rollin et al. 2020). Moreover, this resolution allowed us to reduce differences in the distribution of sampling points between the historical and recent periods, resulting in a more comparable amount of data in the grid cells in the two periods.

### Database

Data were obtained from the SAPOLL project (https://sapoll.eu/). This database contains over 24,800 unique records for wild bees collected in northern France between 1853 and 2019 (see details of database origin in Folschweiller et al. 2020). Historical data for the Nord Department (i.e., before 1950) were mainly retrieved from museum collections. The largest collection belonged to Ernest Cavro (1880–1972), with 1,066 records spanning from 1890 to 1957. More recent data were collected from different sources as part of the Interregional European Project Sapoll (http://sapoll.eu), including records from local nature conservation centers and associations, amateur entomologists, passionate citizens, and Universities. Historical collections were re-assessed and determined between 2009 and 2014 by expert taxonomists (regional fauna expertise: Morgane Folschweiller, Maxime Drossart; taxonomic expertise: for Apidae (including bumblebees), Pierre Rasmont; Melittidae, Denis Michez; Halictidae, Alain Pauly; Xylocopinae, Michael Terzo; Andrenidae, Sebastien Patiny), directly accessing the museum collections. Recent specimens were determined by expert taxonomists between 2016 and 2020 (including those mentioned above, and Jens D'Haeseleer for the regional fauna, and Thomas J Wood for Andrenidae; full list in Folschweiller et al. 2020). Species taxonomic names were updated to the most recent checklist of European bees (Ghisbain et al. 2023).

To compare historical and recent periods, we considered two 30-year time intervals: 1910–1939 (hereafter P1) and 1990–2019 (hereafter P2). We considered equal interval durations to reduce biases related to fluctuations in bee populations (Guzman et al. 2021). Data recorded before 1910 and between 1940 and 1989 were too sparse and scattered to allow comparisons with P1 or P2 at any grid cell, and were therefore excluded from the analysis (Figure S1); 9.2% and 80.1% of records occurred in P1 and P2, respectively. The two periods chosen encompass the major changes that have occurred in the intensification of agriculture and use of fertilizers (Mazoyer and Roudart 2006; Batáry et al. 2015), urbanization (Fuchs et al. 2013), and climate (EEA 2023) over the past century in the study area and throughout Europe.

## Species functional traits

To analyze temporal changes in the functional diversity of bee communities, we selected a set of quantitative and categorical traits that could be affected by the major climatic and habitat changes occurred in the study area (Table 1). Traits were retrieved from a database maintained in the Zoology Lab at the University of Mons in the framework of the Safeguard project (Miličić and Vujić 2023), which collects bibliographic information and direct measurements made on specimens collected throughout Europe. First, we included species sociality, lecty, voltinism and nest location, as these are widely utilized life-history traits in similar studies (reviewed in Liang et al. 2023). For parasitic species, we used the host species categories to define lecty and nest location, because they play a key role in influencing larvae development. We included inter-tegular distance as a proxy for bee size, which is related to the potential maximum foraging distance (Cane 1987; Greenleaf et al. 2007). We considered time before heat stupor as a direct measure of resistance to heat stress (Martinet et al. 2015), and hairiness as a proxy for thermoregulation (Roquer-Beni et al. 2020). We also included the species temperature index and the species continentality index as indicators for climatic conditions and their variability within species distribution ranges (Devictor et al. 2008b; Rasmont et al. 2015; Duchenne et al. 2020). We included two phenological traits, species seasonality (e.g., March – May = spring) and phenology duration (e.g., March – May = three months), to account for changes in the annual activity periods of species. Finally, we included habitat breadth (number of suitable habitats listed in the IUCN Red List of Threatened Species) to characterize changes in the spatial niche of bee species. Full description of traits and related bibliographical references are given in Table 1.

We retrieved habitat types from the IUCN Red List of Threatened Species (Nieto et al. 2014) to characterize habitat suitability of all bee species analyzed. Habitat types are compiled by experts during Red List assessments to identify species habitat preferences and primary ecological requirements, in order to establish habitats in need of conservation to prevent extinctions and ensure favorable conservation status for bees. Overall, we

**Table 1** Functional traits included in the functional diversity analysis between the historic (P1: 1910–1939) and recent (P2: 1990–2019) periods

| Trait | Type | Categories | Description | References |
|---|---|---|---|---|
| Sociality | Categorical | Solitary, eusocial, kleptoparasite, social parasite | Species social behavior | Michez et al. 2019 |
| Lecty | Categorical | Narrowly oligolectic, oligolectic, polylectic | Diet breadth based on pollen collection by females/workers. Narrowly oligolectic: pollen collected from a single plant species or a variety of plant species within a genus; oligolectic: pollen collected from members of a single botanical family; polylectic: pollen collected from more than one botanical family | Müller and Kuhlmann 2008 |
| Voltinism | Categorical | Univoltine, bivoltine, multivoltine | Number of generations a species displays within a year. Univoltine: single generation; bivoltine: two generations; multivoltine: more than two generations per year | Michez et al. 2019 |
| Nest location | Categorical | Above ground, generalist (i.e., both above and below ground), under ground | Location of the nest | Michez et al. 2019 |
| Inter-tegular distance (ITD) | Continuous | NA | Mean inter-tegular distance of females/workers | Cane 1987; Greenleaf et al. 2007 |
| Time before heat stupor (THS) | Continuous | NA | Resistance of females/workers to heat stress (40°C), expressed in number of minutes | Martinet et al. 2015 |
| Hairiness index | Continuous | NA | Quantitative measure of hair density × hair length in the mesoscutum of females | Roquer-Beni et al. 2020 |
| Species Temperature Index (STI) | Continuous | NA | Mean temperature of a species' distribution area, derived from the occurrence data of a given species and the corresponding climatic data in Europe | Devictor et al. 2008b; Duchenne et al. 2020 |
| Species Continentality Index (SCI) | Continuous | NA | Temperature index, measured by the variability of the climatic conditions experienced by a species through its geographic range in Europe | Rasmont et al. 2015; Duchenne et al. 2020 |
| Seasonality | Categorical | Spring, summer, autumn, spring to summer, spring to autumn | Season of the year in which a species is most active | Scheuchl and Willner 2016; Miličić and Vujić 2023 |
| Phenology length | Continuous | NA | Number of months during which a species is active | Miličić and Vujić 2023 |
| Habitat breadth | Continuous | NA | Number of suitable habitats | Nieto et al. 2014 |

identified nine main habitats associated to bee species: forest, shrubland, grassland, wetlands, rocky areas, marine coastal supratidal, marine intertidal, artificial terrestrial, artificial aquatic. Within the artificial terrestrial habitat, we also included five sub-habitats that are present in the study area to better characterize these complex areas: arable land, pastureland, plantations, rural gardens, urban areas (see Table S1 for detailed information on habitat and sub-habitat types).

### Estimation of taxonomic diversity changes

All analyses were performed using R v4.3.1 (R Core Team 2023), and plots were drawn using the R package 'ggplot2' (Wickham 2016).

Comparing datasets issued from different temporal periods can be challenging. Datasets can present biases linked to different monitoring programs and methodologies, different sampling efforts in space and time, or personal bias such as preferences for particular habitats, rare species or species appearance (Dennis et al. 1999, 2006; Isaac and Pocock 2015; Maes et al. 2015). Before proceeding with the diversity analysis, we filtered data using the method proposed by Carvalheiro et al. (2013) to exclude low-quality cells. First, we excluded grid cells with a sampling effort (i.e., number of records) lower than 20% of the maximum value among all grid cells. Then, we excluded cells with a greater than 10-fold difference in records between periods. Finally, we excluded cells with a ratio between the number of records and the number of species lower than 1.5 in either period. After data filtering, 12 grid cells (13% of total grid cells) were retained for comparisons between P1 and P2. Prior to estimating species diversities, we standardized samples in each cell using coverage to allow for adequate comparisons in bee communities between the two periods. Coverage is based on the relative abundance of species in a sample, and takes into account both the sampling effort and the true diversity of communities. Coverage measures how completely a community has been sampled, and estimates the proportion of individuals belonging to undetected species based on the frequency of species already present in the sample (Chao and Jost 2012).

To analyze differences in bee taxonomic diversity between P1 and P2, we estimated coverage-standardized Hill diversities for each of the 12 grid cells retained from data filtering. Hill diversities are estimated on the relative abundance of species in a sample, and are equivalent to the diversity of a community that has the same diversity and is composed of equally common species (Jost 2006). Hill diversities are calculated using the same function, only differing for the order of a variable 'q'. When $q=0$, Hill diversity is equivalent to species richness and emphasizes rare species; when $q=1$, diversity is equivalent to the exponential of Shannon entropy (hereafter: Hill-Shannon) and weights rare and common species equally; when $q=2$, diversity is equivalent to the inverse of the traditional Simpson index (hereafter: Hill-Simpson) and emphasizes common species (Jost 2006; Roswell 2021). To test for temporal changes in overall diversity, we fitted three separate linear mixed-effects models (LMMs) including each (log-transformed) Hill diversity measure as response variable and period (P1 vs. P2) as predictor. Grid cell ID was included as random effect in all models (R packages 'lme4', Bates et al. 2015; 'lmerTest', Kuznetsova et al. 2017). Distribution of the residuals was checked using the R package 'DHARMa' (Hartig 2022). We then visualized differences between P1 and P2 for each grid cell by using continuous diversity profiles and 95% bootstrapped confidence intervals ('inext' R package, Hsieh et al. 2022), highlighting values in correspondence of orders q = 0, 1, and 2 (Roswell 2021). Values can be considered to differ significantly between periods when confidence intervals do not overlap (Chao and Jost 2012). We checked for spatial autocorrelation of bee species abundance in the 12 grid cells ('ape' R package, Paradis and Schliep 2019), and no significant patterns were highlighted in either P1 (Moran's $I = -0.03$, $P = 0.31$) or P2 (Moran's $I = -0.15$, $P = 0.37$).

To evaluate changes in bee assemblages between historical and recent periods, we estimated species dissimilarity in the 12 grid cells between P1 and P2. Coherently with the Hill numbers framework, we computed pairwise Horn dissimilarities, which are built from Hill numbers of order q = 1 and weight species by their relative abundance (Barwell et al. 2015; Ohlmann et al. 2019). We then performed a PERMANOVA ($n = 999$ permutations) to test for differences in the location of points between the two periods (P1 vs. P2) through partitioning of the multivariate variation in the space of the computed dissimilarity matrix, by comparing intra-group pairwise distances with the inter-group pairwise distances (Anderson 2017). Because we compared the same sites in two periods, we used a pairwise design constraining permutations within grid cell ID ('pairwiseAdonis' R package, Martinez Arbizu 2020). We visualized temporal dissimilarities in bee communities using a Principal Coordinate Analysis (PCoA) with Lingoes correction for negative eigenvalues (Lingoes 1971; 'vegan' R package, Oksanen et al. 2022; 'ape' R package, Paradis and Schliep 2019). To evaluate if bee assemblages in the two periods were homogeneously dispersed (Anderson et al. 2006), we performed a permutation test ($n = 999$ permutations) on the multivariate homogeneity of group dispersions to estimate differences between P1 and P2 in the average distance of points from the group centroid in the multivariate space. To analyze changes in compositional $\beta$-diversity between periods, we estimated the additive partitioning of Jaccard dissimilarity into turnover (hereafter $\beta_{\mathrm{TURN}}$) and nestedness (hereafter $\beta_{\mathrm{NES}}$) components (Baselga 2012; 'betapart' R package, Baselga et al. 2023). $\beta_{\mathrm{TURN}}$ estimates the fraction of $\beta$-diversity related to species replacement, while $\beta_{\mathrm{NES}}$ implicates that the smaller of the two communities is a subset of the richer community (Baselga 2010).

## Estimation of functional diversity changes

To evaluate changes in the functional diversity of bee communities between P1 and P2, we built a multidimensional functional space (Mouillot et al. 2013) based on species abundance and functional traits in the 12 grid cells in the two periods ('mFD' R package, Magneville et al. 2022). We included all 12 functional traits in the analysis (Table 1), even though THS and Hairiness index contained NA values (61% and 52% of species, respectively; Johnson et al. 2020), because results did not change by excluding them and they are informative of important bee physiological responses to climate change (100% completeness for the other traits). We first computed trait-based distances using a Gower matrix, which handles continuous and non-continuous traits (Gower 1971; de Bello et al. 2021). We then estimated the quality of the multidimensional spaces by computing a principal coordinates analysis (PCoA), and selected the 5-dimensional trait-based functional space as it minimized the mean absolute deviation (MAD = 0.036, Figure S2) between trait-based distances and distances in the functional space (Maire et al. 2015). We estimated significant correlations between individual traits and PCoA axes based on p-values issued from linear models and the associated $r^2$

values for continuous traits, and from Kruskall-Wallis tests and the associated eta2 statistics for categorical traits.

We then performed the same analysis on the 14 habitat types. Because using only categorical traits implies a finite number of combinations, we first gathered species into functional entities (FE) based on unique combinations of trait values (i.e., habitat suitability; Mouillot et al. 2014). We estimated Gower distance matrices based on the trait values of each FE, and selected the 4-dimensional trait-based functional space as it minimized the mean absolute deviation (MAD = 0.049, Figure S3) between trait-based distances and distances in the functional space. Finally, we calculated the correlation of each habitat to the PCoA axes using Kruskal-Wallis tests and the associated p-values.

We estimated the variation in functional alpha diversity using four indices that highlight different aspects of the multidimensional functional spaces (Mouillot et al. 2013). Functional richness (FRic) measures the proportion of the functional space filled by species communities, and is calculated as the total volume inside the convex-hull shaping the communities. Functional evenness (FEve) represents the regularity of species abundance distributions in the functional space, and is calculated as the shortest minimum spanning tree linking all the species. Functional specialization (FSpe) quantifies how generalist (i.e., close to the center of the functional space) or specialist (i.e., having extreme trait combinations) species change in abundance, and is estimated as the weighted mean distance of species abundance to the mean position of species from the global pool. Functional originality (FOri) measures the level of isolation of each species inside the functional space, and is estimated as the weighted mean distance to the nearest species from the global species pool. Differences in functional alpha diversity indices between P1 and P2 were tested by fitting LMMs with each of the four (log-transformed) indices as response variables and time period as predictor (R packages ‘lme4’, Bates et al. 2015; ‘lmerTest’, Kuznetsova et al. 2017). Grid cell ID was included as random effect in all models, and distribution of model residuals was checked using the R package ‘DHARMa’ (Hartig 2022).

### Red List categories and functionally threatened species

To assess the threat level of the species considered for the diversity analysis, we assigned IUCN Red List categories to every species recorded in P1 and P2 in the 12 grid cells. Red List categories are designed to determine a taxon’s risk of extinction based on quantitative criteria linked to population trends, population size and structure, and geographic range (IUCN 2012). Because the study area was geographically limited and only 2.5% of studied species were included in threatened categories, likely not reflecting local pressures to bee populations, and because 5.5% of studied species were assessed as Data Deficient in the European Red List of Bees (i.e., high loss of information; Nieto et al. 2014), we focused on National Red Lists. A National Red List of bees is not available for France yet. However, because northern France shares many characteristics with neighboring Belgium (e.g., high population density, agricultural intensification and urbanization in the last century), we assessed species based on the National Belgian Red List of Bees (Drossart et al. 2019). 21.5% and 1.7% of studied species were included in threatened categories and were assessed as Data Deficient when considering the Belgian Red List of Bees, respectively. To evaluate differences in the frequency of species distributions in the Red List categories (excluding Data Deficient species) between species recorded in P1 but not in P2 (i.e., potential local extinctions) and species assessed in the Belgian Red List of Bees, we used a Pearson's Chi-squared test. To assess relationships between threat status and local extinction, we used a Pearson's Chi-squared test between the frequency distributions of threatened (Vulnerable, Endangered, Critically Endangered, Regionally Extinct) and non-threatened (Least Concern, Near Threatened) species that were either recorded in P2 or not. We included the Regionally Extinct category for bees recorded in our dataset, because although some species are extinct in Belgium but not in France, it can potentially highlight species at high risk of extinction.

To integrate species functional traits into conservation priorities, we used the FUSE (functionally unique, specialized and endangered) index (Pimiento et al. 2020). FUSE combines species FSpe and FOri (FOri is termed "functional uniqueness" in Pimiento et al. 2020), which are based on the functional space determined by the species' traits combination and their abundance, with IUCN extinction threat status, thus incorporating the uniqueness of species based on their trait assemblages with their vulnerability. First, we calculated FSpe, FOri and FUSE scores considering the overall pool of species from P1 and P2, to assess the potential vulnerabilities of species in both periods. Then, we calculated the same indices only considering species in P2, to assess how species functional roles and conservation risks changed over time in the newly established communities. We associated projected extinction probabilities to each IUCN category following 50-year and 100-year extinction risk scenarios (Table S2; Mooers et al. 2008). Species with high fuse scores are threatened with extinction and present more unique and extreme combination of traits than other species in the community. At the same time, because the index integrates both species vulnerability and their unique contribution to functional diversity, the top FUSE species are not necessarily at the highest level of risk although potentially threatened with extinction.

## Results

### Taxonomic diversity changes

A total of 2,817 individual bee records belonging to 237 species in 12 grid cells (1,378 individuals and 194 species in P1, 1,439 individuals and 136 species in P2) were retained after filtering and were used for all analyses. Overall taxonomic diversity was significantly lower in P2 than in P1 for all Hill diversity measures (Fig. 1a, Table S3), indicating a generalized decline regardless of species rarity.

When considered separately, half of the 12 retained grid cells showed a significant decrease in Hill species richness (Fig. 1b) and Hill-Simpson diversity in P2 (Figure S4), indicating a decrease in both rare and common species over time, respectively.

Five grid cells showed significantly lower Hill-Shannon diversity in P2, indicating a decrease in overall species diversity, and one showed increased Hill-Simpson diversity in P2. Five grid cells did not show any significant change in diversity between time periods (Figure S4).

Distributions of bee assemblages in the multivariate space were significantly dissimilar between P1 and P2 ($F=5.52$, $P=0.003$) without significant interaction between period and grid cell ID ($F=0.49$, $P=0.99$), and showed significant differences in within-group dispersion ($F=48.94$, $P=0.001$), indicating homogenization of bee community composition in P2

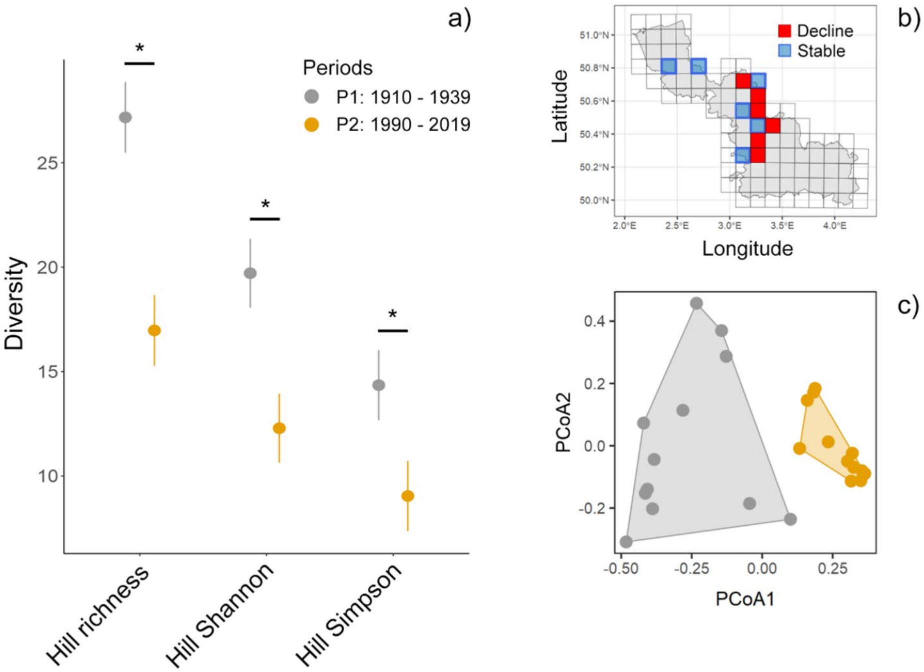

**Fig. 1** **a**) Mean (±SE) taxonomic diversity values for Hill richness (gives more weight to rare species), Hill-Shannon (equal weight to rare and common species), and Hill-Simpson (more weight to common species) indices in the historical (P1: 1910–1939, gray) and recent (P2: 1990–2019, yellow) time periods. **b**) Map of Hill species richness change between the two time periods in the 12 grid cells (10×10 km) retained for diversity analyses in the Nord Department (France). **c**) Plot of Principal Coordinates Analysis (PCoA) for community dissimilarity among the 12 grid cells in historic (P1, gray) and recent (P2, yellow) periods. Convex hulls include all points within each period to highlight group separation and dispersion. Total inertia retained from the two dimensions was 42.6% (PCoA1 = 30.6%, PCoA2 = 12.0%). *: $P < 0.05$

(Fig. 1c). Total compositional $\beta$-diversity between periods was high ($\beta_{TOT} = 0.84 \pm 0.01$), and was mostly due to species turnover ($\beta_{TURN} = 0.73 \pm 0.01$) with a low portion attributable to the nestedness component ($\beta_{NES} = 0.11 \pm 0.01$).

## Functional diversity changes

The 5-D functional space built on traits retained 76.7% of the total PCoA inertia, most of which was retained by the first two axes (45.1%). The first dimension mainly separated species based on their phenology length, seasonality, lecty, sociality, nesting habit, hairiness and habitat breadth (Table S4). The functional space associated with bee communities in P2 was mainly correlated to eusocial polylectic habitat-generalist species and their parasites, with generalist nesting habits and a long phenology (Fig. 2a, S5). The second dimension separated species based on their dimension (ITD) and resistance to heat (Table S5), with larger and more heat-resistant species occupying the functional space associated with communities in P2 (Fig. 2a, S5). The third and fourth dimensions further separated species based on voltinism and to a lesser extent on STI and SCI (Table S4). Bivoltine species with higher STI and lower SCI occupied the functional space associated with communities in

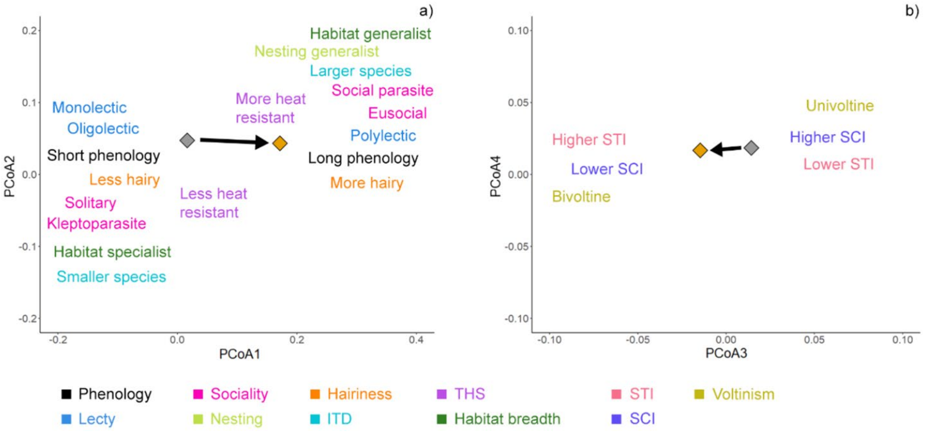

**Fig. 2** Multidimensional functional trait space showing changes in abundance-weighted community centroid position between the historic (P1: 1910–1939, gray diamonds) and recent (P2: 1990–2019, yellow diamonds) periods, related to **a**) PCoA axes 1 and 2 (27.5% and 17.6% inertia retained, respectively), and **b**) PCoA axes 3 and 4 (13.4% and 9.9% inertia retained, respectively). ITD: inter-tegular distance; THS: time before heat stupor; STI: species temperature index; SCI: species continentality index

P2 (Fig. 2b). The fifth dimension mainly separated species based on lecty and seasonality (Table S4), with polylectic and summer species occupying the functional space associated with communities in P2 (Figure S6).

The 4-D functional space built on habitat suitability retained 66.1% of the total PCoA inertia (44.2% retained by the first two axes). The first two axes separated species related to artificial habitats from species related to natural habitats (Table S5). The functional space associated with bee communities in P2 was mainly correlated to artificial terrestrial habitats, including urban habitats, rural gardens, and more agricultural habitats such as plantations, arable lands and pastures (Fig. 3a, S7). Bee communities in P2 were also correlated to natural grasslands, while those in P1 were strongly correlated with wetlands (Fig. 3a, S7). Functional axes 3 and 4 separated natural habitats (Table S5), with communities in P2 being more related to forests and communities in P1 more related to shrubland and less strongly to marine coastal habitats (Fig. 3b, S7).

Functional richness (FRic) did not change significantly between periods (Fig. 4a), while FEve was significantly lower in P2 than in P1 (Fig. 4b, Table S6). Both FSpe and FOri were significantly higher in P2 than in P1 (Fig. 4c, d, Table S6), indicating an increase in species with more unique and extreme functional trait combinations.

## Red List categories and functionally threatened species

One hundred and one (42.6%) of the total 237 bee species were not recorded in P2. Of these, more than half were included in Threatened Categories in the Belgian Red List of Bees (Vulnerable: 13, Endangered: 9, Critically Endangered: 16, Regionally Extinct: 13). Four species were assessed as Data Deficient, 31 as Least Concern and 11 as Near Threatened, while four species did not occur in Belgium or were not assessed in the Belgian Red List of Bees. Species frequency distribution within Red List categories was comparable between species not recorded in P2 and the Belgian Red List of Bees ($\chi^2=6.44$, df=5, $P=0.27$). The

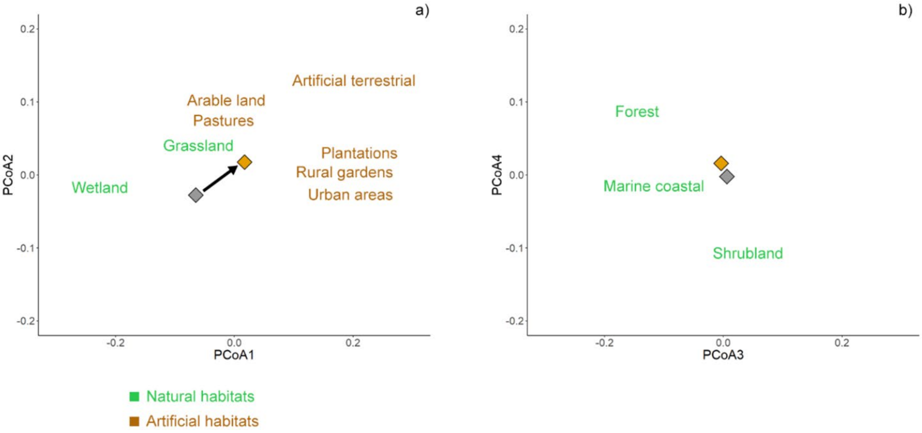

**Fig. 3** Multidimensional space showing correlations between changes in abundance-weighted community centroid positions (P1: 1910–1939, gray diamonds; P2: 1990–2019, yellow diamonds) and habitats on **a**) PCoA axes 1 and 2 (24.8% and 19.4% inertia retained, respectively), and **b**) PCoA axes 3 and 4 (12.1% and 9.8% inertia retained, respectively)

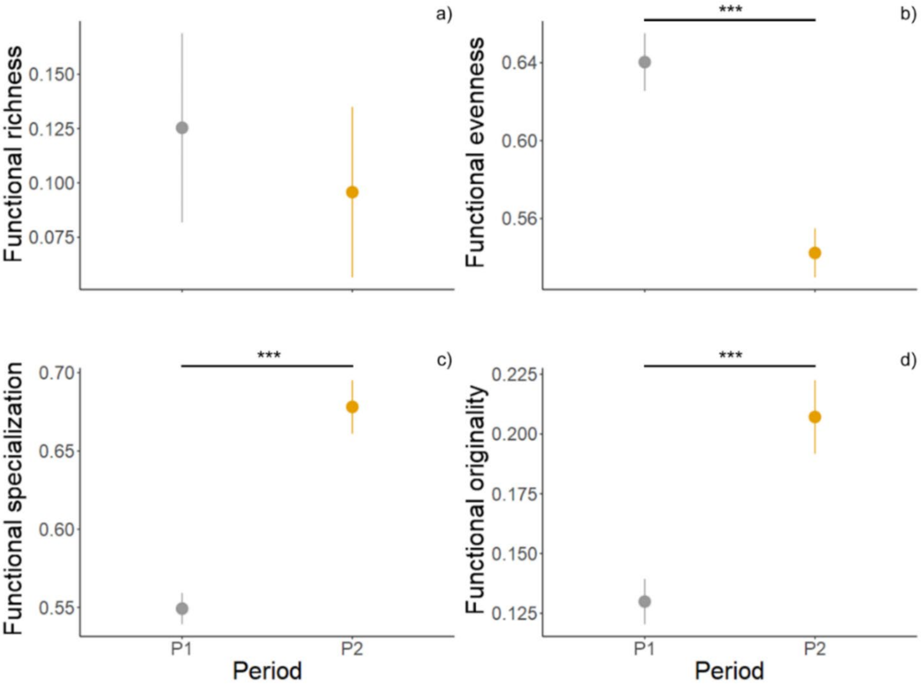

**Fig. 4** Mean (±SE) functional diversity values for **a**) functional richness (FRic), **b**) functional evenness (FEve), **c**) functional specialization (FSpe), and **d**) functional originality (FOri) indices in the historical (P1: 1910–1939, gray) and recent (P2: 1990–2019, yellow) time periods. ***: $P < 0.001$

frequency distribution of species either recorded in P2 or not was significantly associated with threat status ($\chi^2 = 33.27$, df = 1, $P = 8.035\ e^{-09}$), with positive associations between species not recorded in P2 and threatened categories (Pearson residuals = 3.69), and between species recorded in P2 and non-threatened categories (Pearson residuals = 2.19).

When considering species-level contributions to the overall functional diversity and their current conservation status, 48% and 60% of species with high (> 0.5) FSpe and FOri values were not recorded in P2, respectively, independently of their extinction risk (Fig. 5a, b, Table S7). Among the top 20 FSpe and FOri species that were recorded in P2, only *Nomada distinguenda* and *Bombus rupestris* had a high extinction risk (Fig. 5a, b, Table S7). When integrating FSpe and FOri with IUCN extinction risk in the 50-year scenario, all species with high (> 0.5) FUSE scores had high extinction risk and 75% of them were not recorded in P2 (Fig. 5c, Table S7). Three bumblebee species (*B. ruderatus*, *B. barbutellus*, *B. sylvarum*) had the highest FUSE scores among the species observed in P2, and are Critically Endangered in Belgium (Fig. 5a, c). FUSE scores considering the 100-year extinction scenario highlighted increased risk for *N. distinguenda* and *B rupestris*, while the top species remained comparable to the 50-year scenario (Figure S8, Table S7). Species FSpe, FOri and FUSE index ranking did not change considerably when considering only bee communities observed in P2, although *B. sylvarum* showed increased FOri and FUSE scores (Figure S9).

## Discussion

We demonstrated a significant decrease and homogenization of bee taxonomic diversity associated with a functional restructuring of bee communities over the last century in northern France. We highlighted the importance of combining regional extinction probabilities with functional characteristics to highlight species in need of conservation priorities, which is a key issue at both societal and local policy levels.

### Bee taxonomic decline and community homogenization

Bee diversity has declined sharply in the Nord Department over the past 100 years. Hill diversities showed comparable reductions among both rare and common species, highlighting a generalized trend of species decline. Moreover, we showed significant shifts in bee community composition related to changes and homogenization of species identity. Northern France has experienced increasing urbanization and agricultural intensification as well as dramatic biotic homogenization of plant communities in the second half of the twentieth century (Fuchs et al. 2013; Deguines et al. 2014; Hautekèete et al. 2015), similarly to global trends (Matson et al. 1997; Li et al. 2021). Such land-use changes are among the leading causes of species loss worldwide (Carmona et al. 2020; Li et al. 2022). In particular, pollinator communities have declined significantly in neighboring European countries such as Belgium (Vray et al. 2019), the Netherlands (Carvalheiro et al. 2013) and Germany (Ganuza et al. 2022) in relation to increased anthropogenic pressures comparable to those experienced by the communities in our study, suggesting that similar trends have occurred in northern France.

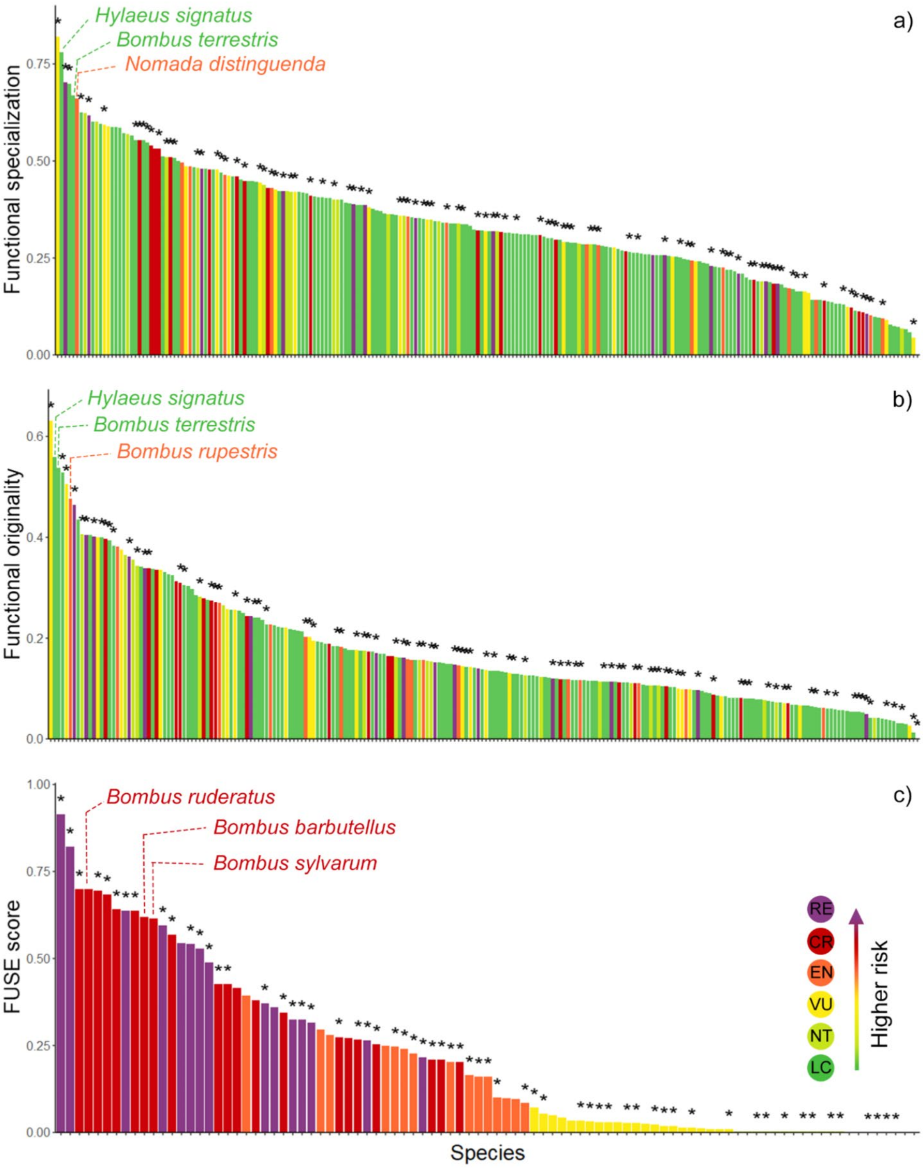

**Fig. 5** Species-level **a**) functional specialization, **b**) functional originality, and **c**) FUSE scores in the 50-year extinction scenario considering bee communities observed in both historical (P1) and recent (P2) periods. Species with FUSE = 0 (*n* = 129) were excluded for clarity (full list in Table S7). Bar and species name colors refer to current IUCN status in the Belgian Red List of Bees. Asterisks above bars indicate species recorded in P1 but not in P2. The top three species that were recorded in P2 are highlighted for each index

## Functional filtering of bee communities

We showed a significant restructuring of wild bee communities from a functional perspective, in addition to taxonomic homogenization, over the last century in the study area. While land-use change and the loss of suitable habitats are considered among the main threats to wild bees (Ollerton et al. 2014; Senapathi et al. 2015), their effects on natural communities are often mediated through the sensitivity of species functional traits to such modifications. Species with traits better adapted to the changing conditions can be favored over others, leading to ecological filtering and rearranging of bee community compositions (De Palma et al. 2015).

Present-day bee communities were characterized by larger eusocial generalist species with a long phenology. Polylectic species tend to be less sensitive to agriculture and urban intensification, as they can exploit the various floral resources associated with these habitats (De Palma et al. 2015; Fauviau et al. 2022). Moreover, larger eusocial species (e.g., bumblebees) were likely advantaged over smaller solitary species by their ability to fly longer distances from the nest to forage in increasingly fragmented habitats (Greenleaf et al. 2007; Wright et al. 2015; Gérard et al. 2020; LeBuhn and Luna 2021). Species with long phenology and multiple generations per year were favored over species with shorter phenology, likely reflecting higher synchrony with key floral resources. Social parasites were likely indirectly advantaged by increased prevalence of their social hosts (Lhomme and Hines 2018). Conversely, kleptoparasites have suffered from the sharp decline of solitary species and anthropogenic intensification of land-use (Sheffield et al. 2013; Prendergast et al. 2022). As the structure of parasitic bee communities follows that of their host species and can play a stabilizing role in bee communities, the diversity of kleptoparasites can be indicative of the status of entire bee communities (Sheffield et al. 2013). The loss of several parasitic bees (e.g., half of the species in the genera *Nomada*, *Stelis* and *Melecta*) over the last century is a further indication that the environmental disturbances occurred in the study area have caused severe direct and indirect negative impacts on the local bee communities.

Species in P2 tended to be hairier than those in historical communities. Increased hairiness has been associated with colder environments (Peat et al. 2005; Peters et al. 2016), as it helps to maintain the heat generated by flight muscles in the thorax (Heinrich 1993). However, as global warming and increasing urbanization led to warmer temperatures, we would have expected an opposite trend. Indeed, we found greater heat stress resistance in bee species in P2. The hairiness index we used is a composite index including both hair length and density (Roquer-Beni et al. 2020). It has been shown that there is a positive relationship between bee body size and hair length, mainly due to allometric and mechanical constraints, whereas there is no significant relationship between body size and hair density (Roquer-Beni et al. 2020; Perez and Aron 2020). We hypothesize that the increased hairiness was primarily determined by selection for large body size in P2. Because heat stress resistance is not only correlated with bee size (Martinet et al. 2015; Oyen at al. 2016; Martinet et al. 2021) but also with taxonomy and phylogeny (Herrera 2024), the benefits of larger body size (e.g., greater flight distance) and greater thermal resistance likely played a stronger role than hairiness in filtering traits over time.

The prevalence of species in P2 with higher TSI and lower SCI suggests that communities have changed in response to a generalized increase in temperature, whether due to global warming or the urban heat-island effect, favoring species with narrower climatic niches that are better adapted to the new climatic conditions. Shifts in species range can vary considerably depending on climatic specialization and dispersal capabilities. Warm-adapted bee species can expand their range in response to global warming (Kerr et al. 2015; Vertommen et al. 2024), while species constrained to specific climatic niches may suffer from substantial deviations from their optima (Casey et al. 2015; Silva et al. 2015; Dew et al. 2019; Ghisbain et al. 2024). Moreover, climate change can interact with both human-related disturbance (e.g., habitat destruction and fragmentation) and species functional traits (e.g., dietary specialization), complicating and exacerbating the observed patterns (Rasmont et al. 2015; Silva et al. 2015; Aguirre-Gutiérrez et al. 2016). On a more local scale, species with spring phenology were disadvantaged over summer species. Spring bees may suffer from reduced phenological synchrony with their host plants, because early-flowering plants tend to respond more readily to temperature changes than their mutualistic partners, and the availability of co-flowering species is lower at the beginning of the flowering season (Kehrberger and Holzschuh 2019a; Kudo and Cooper 2019; Stemkowski et al. 2020; Fisogni et al. 2022; but see Bartomeus et al. 2011, 2013; Hofmann et al. 2019). Asymmetric shifts can have negative cascading effects on plant reproductive fitness, and are expected to aggravate as temperatures continue to rise (Kehrberger and Holzschuh 2019b; de Manincor et al. 2023).

Bee communities in P2 were characterized by a larger habitat breadth with higher affinity for artificial habitats. Increased agricultural and urban areas likely favored fewer species better adapted to fragmented environments with highly modified resource availability in space and time (St. Clair et al. 2022; Weber et al. 2023), consistent with changes observed in functional traits. Moreover, communities in P2 were also characterized by affinities to grassland and forest habitats. Grassland and forest remnants within patchy landscapes can serve as refuges for pollinators adapted to such environments, maintaining their diversity through high floral and nesting resources (Hall et al. 2019; Proesmans et al. 2019; Rollin et al. 2020). Species associated with wetland habitats were the least represented in present-day communities. Most of these habitats have been destroyed throughout Europe (Verhoeven 2014), and major species losses have been reported in oligotrophic freshwater habitats in northern France (Hautekèete 2015), highlighting their key role in biodiversity conservation.

## Functionally threatened species and conservation priorities

We did not find a significant decrease in overall functional richness between time periods. However, we observed a sharp decrease in functional evenness, which can be related to the filtering of species susceptible to high anthropogenic disturbance (Hillebrand et al. 2008; Pakeman 2011). Moreover, communities in P2 were characterized by species with more extreme trait combinations (i.e., higher functional specialization) that occupy less similar functional niches (i.e., higher functional originality), thus reducing functional redundancy (Mouillot et al. 2013). Increased dominance of a few unique functional traits can alter interspecific interactions, destabilizing associated ecosystem processes (Micheli and Halpern 2005; Hillebrand et al. 2008) and potentially hindering ecosystem multifunctionality on a larger scale (Le Bagousse-Pinguet et al. 2021). In turn, the presence of only one or a few species with unique combinations of functional traits can expose ecosystems to additional risks, as the loss of just one of them would alter the newly established functional communities.

Several species with high levels of FSpe and FOri declined over time, while fewer were still observed in P2, suggesting that some rare and extreme combinations of traits may play an essential role in current and near-future ecosystems. *Hylaeus signatus* and *Bombus terrestris* were the two most functionally specialized and original species that were present in both P1 and P2. The uniqueness of *H. signatus* derives from the rarity of bivoltine oligoleges with generalized nesting behavior in the studied bee communities. Its persistence is likely related to the fact that despite being a narrow oligolege, its host plants (genus *Reseda*; Müller 2023) are typically found in degraded green spaces or wastelands and can thrive in urban and peri-urban areas (Fisogni et al. 2022; Sirohi et al. 2022; Weissmann et al. 2023). Increasing urbanization can thus lead to an expansion of such plants and consequently of this host-plant opportunist (Ghisbain et al. 2021). Moreover, *H. signatus* has high thermal tolerance and is found in a wide range of habitats, which facilitates adaptation to increasingly artificial environments. On the other hand, *Bombus terrestris* is a large, broad polylectic eusocial species, with long bivoltine phenology, broader thermal tolerance compared to some other *Bombus* and non-*Bombus* species (Hamblin et al. 2017; Maebe et al. 2021; Martinet et al. 2021; Sepúlveda and Goulson 2023; Boustani et al. 2024), and a wide habitat affinity. Such unique combination of traits has made *B. terrestris* a super-generalized species that can adapt to several habitats and environmental conditions, allowing it to expand its range over the last few decades (Rollin et al. 2020; Herbertsson et al. 2021; Ghisbain et al. 2024). Since neither of these species is at risk of extinction, they do not require conservation actions. In contrast, highly functionally specialized and original species at high risk of extinction require precise and timely conservation actions to ensure the persistence of their local populations. *Nomada distinguenda* and *Bombus rupestris* are both listed as endangered in the Belgian Red List of bees. *N. distinguenda* is a kleptoparasite with small populations and a reduced distribution range (Drossart et al. 2019), although its main host (*Lasioglossum villosulum*) is widespread throughout Europe (Pauly and Michez 2015). Its main threat is likely related to its narrow habitat breadth, and the most appropriate conservation action would be to preserve the (semi-)natural grasslands to which the species is associated (Smit 2013). *Bombus rupestris* is a social parasite with decreasing distribution range, although its host species (*B. lapidarius*) is still abundant and widespread (Rollin et al. 2020). The main potential threats are related to its relatively narrow climatic niche (Rasmont et al. 2015) and limited availability of thistles, the main floral resource of *B. rupestris* males (Vray et al. 2017). Unfortunately, France and other European countries enforce strict legal regulations against thistles, as they are deemed harmful weeds in agricultural landscapes (Vray et al. 2017). Re-evaluation of these outdated regulations (Andreasen and Andresen 2012; Balfour and Ratnieks 2022) and modification of weed management standards (Nicholls and Altieri 2013) are therefore necessary to maintain and possibly expand the presence of thistles in suitable habitats. The implementation of the proposed conservation actions would have larger ecosystem benefits (Folschweiller et al. 2019), as these habitats and floral resources are exploited by a wide range of species. The use of classic umbrella species strategies can promote the implementation of habitat conservation solutions (Roberge and Angelstam 2004; Caro 2010). However, the protection of single species might not be sufficient to represent broader patterns of biodiversity. Diversifying the choice of species to protect (Wang et al. 2021; Chen et al. 2023; Ardiantiono et al. 2024), including less-regarded species such as insects and bees in particular, could thus be the key to achieving robust approaches in conservation efforts.

Most of the top FUSE species in P1 were not recorded in P2. Because they are considered extinct or critically endangered in neighboring Belgium, we hypothesize that the absence of recording accurately reflects local extinctions or high levels of vulnerability in northern France. By combining functional specialization and originality with species extinction risk through the FUSE index, we were able to identify vulnerable species that are particularly important for functional diversity and thus ecosystem functioning (Pimiento et al. 2020, 2023). Species with high FUSE scores that have been recorded in present-day communities should therefore be regarded as high-priority conservation species. *Bombus ruderatus* and *B. sylvarum* are critically endangered species that have declined over the past century in Belgium and most of Europe (Rasmont et al. 2015; Rollin et al. 2020). Likely threats to both species are related to climatic warming and anthropogenic factors (Rasmont et al. 2015). Conservation of suitable habitats and implementation of climatic and ecological corridors are thus the most feasible actions to preserve their populations and their associated communities. *Bombus barbutellus* is a critically endangered social parasite with declining distribution. Its host species (*B. hortorum*) is still abundant and widespread (Rasmont et al. 2015; Rollin et al. 2020), although some populations have regressed in Belgium over the last century (Folschweiller et al. 2020). Similar to *B. rupestris*, major threats to *B. barbutellus* relate to the narrow climatic niche and limited availability of thistles (Rasmont et al. 2015; Vray et al. 2017), hence the conservation actions suggested above for *B. rupestris* would also be appropriate here. When considering the 100-year extinction scenario, results on FUSE scores were exacerbated for almost all species, indicating that if appropriate conservation actions are not implemented, the decline of these pollinators may be irreversible in the longer term.

Here, we considered bee communities over a 100-year time span, taking into account the current threat status in neighboring Belgium due to the lack of suitable extinction-risk assessments for the study area. Despite the limitations associated with this approach, we obtained comparable results in species-level functional diversity indices when considering the overall community (P1 and P2) and only the recent one (P2), indicating that the stringent filtering and data analysis methods utilized were effective in reducing potential sampling bias. In addition, although we considered a smaller territory that lost many natural and fragile habitats (e.g., wetlands) that are still present in Belgium, our results suggest that there were comparable declines between the two areas. We think that the FUSE index can be a support and guide towards prioritizing species conservation, as it combines information from both functional uniqueness and conservation status, complementing existing IUCN assessments based on temporal and spatial trends (IUCN 2012). Moreover, such an approach would allow both the identification of conservation actions targeting functionally unique and vulnerable species, and the identification of conservation areas or habitats based on trait uniqueness and species threat (similar to the EDGE approach; Pipins et al. 2024). Certainly, a thorough understanding of trait and habitat associations with species will be critical to obtaining the most informed and accurate results possible. Although not an easy task, this would boost our ability to understand critical issues and predict future trends, enabling more targeted conservation actions.

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**Author contributions** This study was conceived and designed by AF, YP, DM, and NH. Prior data collection was performed within the SAPOLL project, and information on functional traits was collected by AS, TJW, SF, BDT, and SL. Analyses were performed by AF. Funds were acquired and administered by NH and DM. The first draft of the manuscript was written by AF, with contributions from NH, YP, DM, and TJW. All authors read and approved the final manuscript.

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**Data availability** The datasets analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Competing interests** The authors declare no competing interests.

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## Authors and Affiliations

**Alessandro Fisogni[1] · Yves Piquot[1] · Denis Michez[2] · Ahlam Sentil[2] · Magalie Franchomme[3] · Thomas J. Wood[2,4] · Simone Flaminio[2] · Bastien De Tandt[2] · Shawn Lemaire[2] · Nina Hautekèete[1]**

✉ Alessandro Fisogni
a.fisogni@gmail.com

[1] Univ. Lille, CNRS, UMR 8198 — Evo-Eco-Paleo, Lille F-59000, France

[2] Laboratoire de Zoologie, Research Institute of Biosciences, University of Mons, Mons, Belgium

[3] Univ. Lille, Univ. Littoral Côte d'Opale, ULR 4477 – TVES – Territoires Villes Environnement & Société, Lille F-59000, France

[4] Naturalis Biodiversity Center, Darwinweg 2, Leiden 2333 CR, The Netherlands