Variation in the pollen diet of managed bee species across European agroecosystems

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A B S T R A C T

Bee-mediated pollination plays a crucial role in sustaining global food production. However, while the demand for these pollination services is increasing, many bee species are in decline. To address this discrepancy, farmers use managed bee species to improve crop pollination. One key factor affecting pollination efficiency is the affinity for the crop of interest (*i.e.*, the extent to which a bee integrates floral resources of a crop into its diet). In this study, we characterised and compared the pollen foraging preferences of three managed bee species: *Apis mellifera*, *Bombus terrestris*, and *Osmia bicornis*, across European agricultural landscapes and across biogeographic regions. Managed populations of each bee species were experimentally established at 128 agricultural sites growing either apple or rapeseed, in landscapes representing gradients in terms of the proportion of cropland, in eight European countries. We conducted pollen store sampling and employed palynological analyses to describe the foraging preferences of these species and to extrapolate their suitability as pollinators for both crops. Our findings reveal that *A. mellifera* and *B. terrestris* exhibited a more generalised pollen diet compared to *O. bicornis*, which showed stronger preference to certain pollen forage plants, but these were mainly non-crop rather than crop plants. These results question the relevance of using *O. bicornis* in apple orchards and rapeseed crops given their poor affinity with these crops. Overall, *A. mellifera* collected the highest proportion of rapeseed pollen in its diet, and *A. mellifera* and *B. terrestris* collected higher proportions of apple pollen than *O. bicornis*. Our findings also highlight substantial variation in the percentage of focal crop pollen in the diet across biogeographic regions, while landscape composition had virtually no impact. These results provide valuable insights for selecting the most suitable managed bee species to enhance the pollination of two key crops in Europe.

1. Introduction

Animal pollination enhances the yields of 76 % of the world main cultivated plant species (Klein et al., 2007). Pollinators therefore contribute to a major ecosystem service, valued globally at 267–657 billion US dollars annually (Lautenbach et al., 2012; Porto et al., 2020). Among these pollinators, bees (Hymenoptera: Anthophila, > 20,100 species) are undoubtedly major contributors, with life cycles that are entirely dependent on floral resources, and morpho-ethological adaptations that optimise pollen collection and transport (Michener, 2000). All bee species rely on two floral resources to ensure their nutrition: nectar, as the main source of carbohydrates (Nicolson and Thornburg, 2007) and pollen, as the main source of lipids, proteins and micronutrients (Campos et al., 2008). By visiting flowers for food, wild bees contribute to crop pollination and increase crop yield (Garibaldi et al., 2013). However, while there is an increase in the human population and pollinator dependence on food production (Aizen et al., 2008; Roser and Ritchie, 2023), bees are experiencing declines in several regions of the

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world due to synergistic threats (Dicks et al., 2021), including habitat loss and degradation (Baude et al., 2016) and concomitant loss of floral food resources and nesting sites (Naug, 2009), pesticide exposure (Sánchez-Bayo and Goka, 2014) and climate change (Ghisbain et al., 2024). To boost crop production and mitigate the low density of wild pollinators, farmers increasingly use managed bee species as pollinators of their crops (Bohart, 1972; Sabara and Winston, 2003; Gruber et al., 2011; Chandler et al., 2019). Two honey bee, nine bumble bee and eight solitary bee species are used as managed pollinators worldwide, with a further 35 potentially suitable species (reviewed in Osterman et al., 2021). The diversity of managed bee species and their commercial use have both increased over the last seven decades (Russo, 2016; Osterman et al., 2021) to pollinate a diverse set of fruit trees (*e.g.*, almond, peach, cherry), greenhouse cultivated plants (*e.g.*, tomatoes, strawberry) and crop species (*e.g.*, rapeseed, alfalfa) (Delaplane and Mayer, 2000).

In Europe, apple and rapeseed are two key crops of major economic importance that are largely dependent on (apple) or benefit from (rapeseed) insect pollination (Garratt et al., 2014; Perrot et al., 2018). Apple covers about half a million hectares in EU member states and production is 12 million tons of apples each year (www.statista.com; accessed on 1 March 2021), while rapeseed covers about 11 million hectares and 30 million tons production (agridata.ec.europa.eu; accessed on 1 March 2021). Both perennial apple orchards and annual winter-sown rapeseed crops are mass flowering in spring and produce large quantities of pollen and nectar (Mallinger and Gratton, 2015; Blitzer et al., 2016). Apple orchards and rapeseed crops attract and benefit (to varying extents according to variety) from managed bees to increase seed and fruit production (Williams et al., 1986; Stanley et al., 2013). Three managed species are usually used for crop pollination in Europe. First, the western honey bee, *Apis mellifera* (Apidae), has been by far the most widely used managed bee species in Europe (Kevan et al., 1990; Crane, 1999). This species is social and highly polylectic (Delaplane and Mayer, 2000). Second, the buff-tailed bumble bee, *Bombus terrestris* (Apidae), has been the second most managed bee species (Potts et al., 2016). *B. terrestris* is also social and highly polylectic, even in agricultural landscapes (Goulson, 2010; Foulis and Goulson, 2014). Third, the solitary red mason bee, *Osmia bicornis* (Megachilidae), has been used more recently, mainly for orchard pollination as it is supposed to have a high affinity (*i.e.*, tendency to collect pollen from a specific plant group or species) for Rosaceae pollen (Haider et al., 2014). However, studies in agroecosystems have demonstrated its use of a wide range of woody and herbaceous species (Coudrain et al., 2016; Persson et al., 2018; Eckerter et al., 2022; Yourstone et al., 2023), pollen preferences can vary among populations, and its foraging behaviour across

cropping systems and landscapes remains poorly understood. These three bee species are used as managed pollinators but diverge in their nutritional requirements (Leonhardt and Blüthgen, 2012; Vaudo et al., 2016; Barraud et al., 2022). As plant species vary in their pollen nutritional profiles (Vaudo et al., 2020, 2024), polylectic bees display foraging plasticity to adapt their foraging behaviour in relation to available resources (Michez et al., 2008; Cane, 2021; Vaudo et al., 2024). Even if agricultural landscapes are dominated by cultivated species, they also contain semi-natural patches that are rich in other flower species (Russo and Danforth, 2017; Nicholson et al., 2019). Therefore, these three managed bee species may interact with other plant species in their landscape to greater and lesser extents to meet their nutritional needs, and may therefore vary in their efficacy as pollinators of cultivated species (Jaumejoan et al., 2023).

Although other parameters must be considered, such as the abundance and degree of geitonogamy in the deposited pollen, or pollination following nectar foraging (Thomson and Goodell, 2001; Roquer-Beni et al., 2022), one key factor in defining bee efficacy in crop pollination, particularly for oligolectic species, is their affinity for the pollen from these crops. In addition, a high proportion of the pollen of a specific species in the pollen loads, reduces the deposition of heterospecific pollen, which can enhance fruit set and seed set (Morales and Traveset, 2008; Brosi and Briggs, 2013). Therefore, a proxy to assess bee species suitability for apple orchard and rapeseed crop pollination is the ratio of pollen from focal crop species over pollen from other flower species in the pollen they collect. The few studies that assessed the pollen profile (*i. e.*, diversity of plant species found in bee-sampled pollen) of managed pollinators in apple orchards highlighted the high prevalence of apple pollen, especially in honey bees and mason bees (Russo and Danforth, 2017; Jaumejoan et al., 2023; but see Knapp et al., 2023; Knauer et al., 2024). Research focusing on rapeseed crops also demonstrated an increase in crop production with the inclusion of the three managed bee species for pollination (Jauker et al., 2012; Stanley et al., 2013; Lindström et al., 2016). However, standardised comparison of the pollen diet of these three managed bee species (*i.e.* sampling at the same time in the same field) is still lacking for apple orchards and rapeseed fields, although such observations are needed to compare their suitability as crop pollinators.

In apple orchards and rapeseed fields, managed bee species also benefit from pollen collection from surrounding wild plant species (Stanley et al., 2013; Joshi et al., 2016). Assessing the alternative plant families used by these species within agricultural landscape, may provide insights into their foraging behaviour based on the surrounding flora composition. Moreover, their affinity for focal crops is therefore also likely to be influenced by the availability of co-flowering species in the surrounding environment, whose diversity varies with both continental and landscape-level factors. At the continental level, biogeographic regions (Boreal, Atlantic, Continental, Mediterranean) exert significant influence on wild plant communities and species richness (Thuiller et al., 2005; Ronk et al., 2015). For instance, while it has never been investigated, *B. terrestris* might primarily forage on apple or rapeseed pollen in Boreal Europe but bypass focal crops in more plant species-rich Mediterranean countries. At the landscape level, natural and semi-natural habitats (*e.g.*, woodlands, grasslands) or even urban areas, can host diverse plant species communities that sustain high wild bee richness and may also attract managed bee species away from crops with low floral diversity (Rivers-Moore et al., 2020; Theodorou et al., 2020; Maurer et al., 2022). Landscape composition (*e.g.*, the proportion of arable, grassland, orchard, urban or woodland habitats) could therefore affect the plant species visited by managed bee species (Knapp et al., 2023; Yourstone et al., 2023). Biogeographic regions (*i.e.*, continental level) and landscape composition (*i.e.*, landscape level) are therefore likely key factors that may influence crop pollen affinity and affect the suitability of managed bee species for pollination management. Despite the importance of these factors, they have not been thoroughly investigated due to a previous lack of standardized

landscape and pollen foraging data across Europe for managed bee species.

In this current context of drastically increasing needs for agricultural productivity, a better understanding of the pollen collection behaviour of managed bee species in agroecosystems seems essential. Therefore, through a European-wide study, we specifically addressed the following questions: (i) Do pollen collected by diverse sympatric populations of the three different managed bee species differ in pollen species richness and predominance? (ii) How abundant is the pollen of apple and rapeseed (*i. e.*, focal crops) in the pollen diet of these managed bee species? (iii) Which other plant families are represented in the pollen diets? (iv) Is the proportion of focal crop pollen in the diet affected by (a) biogeographic regions at the continental level and (b) landscape composition at the landscape level? We hypothesise that *A. mellifera* and *B. terrestris* carry a higher pollen richness than *O. bicornis*, which should be more specialised (Haider et al., 2014). We expect that pollen foraging will vary along biogeographic regions with a switch to not focal crop species in regions with higher plant species richness (*i.e.*, Southern Europe). Finally, we postulate an effect of landscape composition, with high proportions of woodlands, grasslands and urban areas containing non-crop plants that attract bees away from crops, while high proportions of orchards and arable land could enhance bee fidelity for the focal crops.

2. Material and methods

2.1. Study design and site selection

In agroecosystems, we described the pollen diet of three managed bee species, namely the European honey bee *Apis mellifera* L., the buff-tailed bumble bee *Bombus terrestris* L. and the red mason bee *Osmia bicornis* L. The profile of their pollen diet was studied in eight countries selected across Europe to represent four major European biogeographic regions: Boreal (Sweden and Estonia), Atlantic (Ireland and the United Kingdom), Continental (Germany and Switzerland) and Mediterranean (Spain and Italy). For each of these countries, 16 sites were studied (total sites = 128), namely eight apple orchard (*Malus domestica*) sites and eight winter-sown rapeseed crop (*Brassica napus*) sites (Fig. 1), selected across a gradient of land-use intensity (Hodge et al., 2022). Each site was separated by at least 6 km from any other site, to reduce foraging overlap according to current knowledge of the flight distances of the managed bee species (Hagen et al., 2011; Hagler et al., 2011; Hofmann et al., 2020). The two focal crop species differ greatly in their ecologies and management methods. The apple tree is a long-growing (5–10 years) perennial Rosaceae cultivated in orchards for its fruit and with white hermaphroditic and self-incompatible flowers (Hegedűs, 2006). Conversely, rapeseed is an annual Brassicaceae grown as a source of vegetable oil, planted irregularly as a break crop in arable rotations and with yellow, hermaphroditic, self-compatible flowers (Raboanatahiry et al., 2021). All sites were sampled in late spring / early summer 2019 using a standardised protocol (Hodge et al., 2022) established as part of the European Union PoshBee project (http://poshbee.eu).

2.2. Installation of managed bees on sites

Three colonies or aggregations of the three bee species were placed at each of the 128 sites. The country-specific native subspecies of *A. mellifera* were used and commercially produced *Bombus terrestris terrestris* was used in all countries except in Ireland and in the United Kingdom where it was replaced by *Bombus terrestris audax* (Table S1). To prevent exotic species introduction, *Osmia bicornis* was not studied in the latter countries since it is not native. On each site, we installed three *A. mellifera* hives (adult population that cover seven to ten hive frames each, for details, see Hodge et al., 2022), three *B. terrestris* colonies (80 individuals each, from local suppliers) and three *O. bicornis* nest tube boxes (100 individuals each, sex ratio 1:1, from The Red Beehive Company Ltd). All populations used were confirmed parasite-free at the
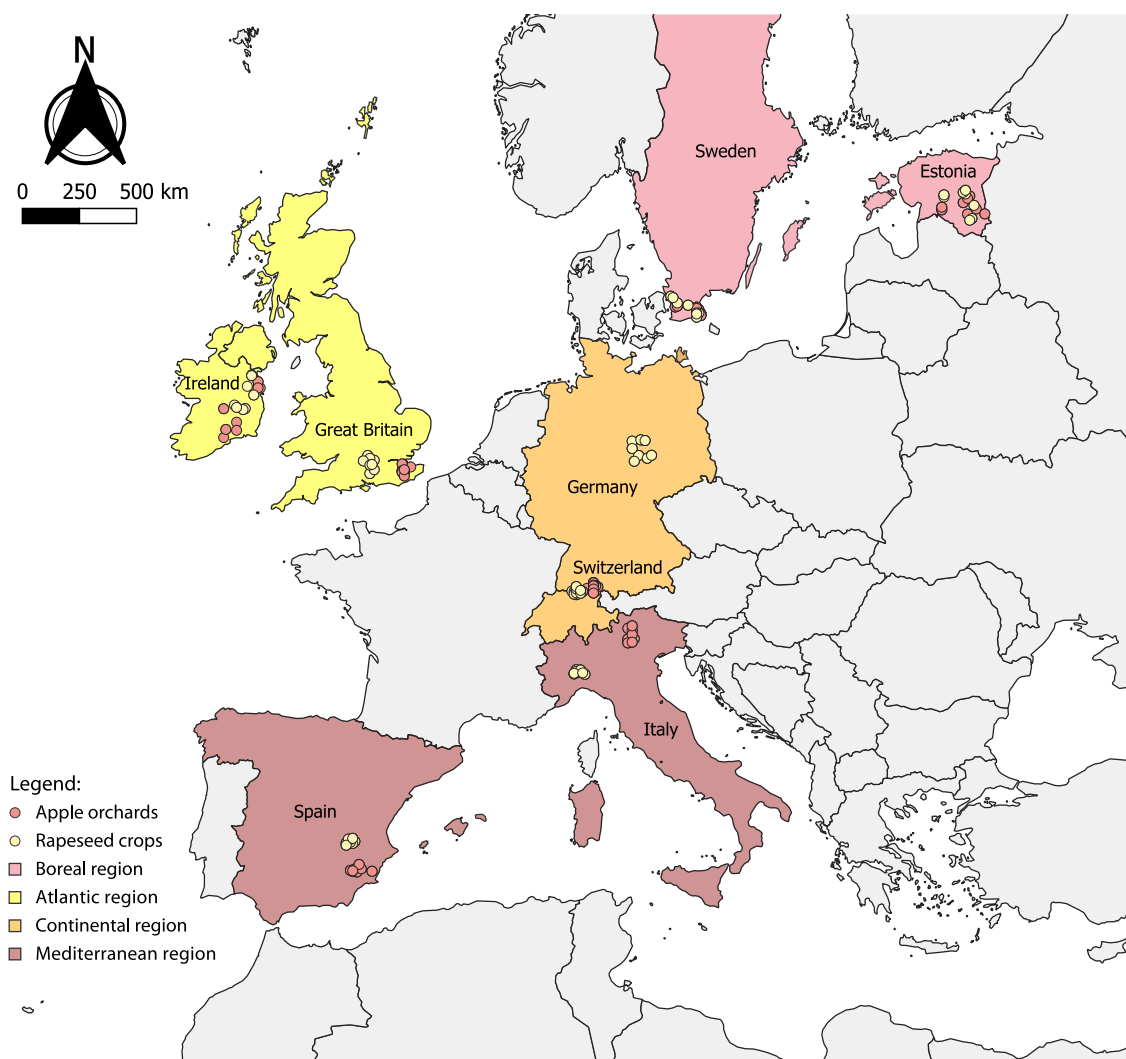
Fig. 1. Investigated agroecosystem sites across Europe. Hives/colonies/nests of *Apis mellifera*, *Bombus terrestris* and *Osmia bicornis* were installed in each site to study their pollen-foraging preferences. Eight countries are coloured according to major biogeographical regions. In each country, bees were placed in eight rapeseed fields and eight apple orchards (total = 128 sites).

beginning of the experiment (Hodge et al., 2022). More information on the maintenance and structure supporting these colonies is available in Hodge et al. (2022). The hives/colonies/nest boxes were placed facing south, on the north edge of rapeseed crops and apple orchards. They were spaced at least 2 m apart for the same species and at least 5 m apart between species to avoid species disturbance. They were placed about a week before the local flowering period of the crop until the end of it.

2.3. Pollen store sampling and identification

In each site and for each of the three species, a total of 5 g of pollen was collected. Due to the number of sites, pollen samples were collected only once, from *A. mellifera* hives and *B. terrestris* colonies at the end of the flowering period, whereas pollen from *O. bicornis* nest tubes was sampled at the flowering peak to prevent larvae from feeding on it. Accounting for colony deaths or losses due to various problems, pollen loads could be sampled from 124 sites for *A. mellifera*, 108 sites for *B. terrestris*, and 88 sites for *O. bicornis*. Pollen loads were then pooled by species and sites before being homogenised and stored at −20 °C. All pollen grains were identified to the species level when possible or grouped by morphotypes (*i.e.*, several species or genera with identical pollen, *e.g.*, typically for the Asteraceae or Lamiaceae) by the Agriculture and Environment Research Centre (CREA; Italy). Palynological analyses

were performed according to the standard method described in Von Der Ohe et al. (2004). From each pollen sample, 1 g of the homogenised pollen was collected using a stainless-steel spatula and dissolved in 20 ml of distilled water. A drop was then spread on a slide to cover an area of about 18 × 18 mm. The slides were then dried, and the pollen fixed using glycerine jelly. Pollen grains were then identified under a microscope (magnification 400–1000X) and the abundance of each morphotype was quantified by counting the pollen grains along equi-distant parallel lines until 500 pollen grains per slide were identified. Based on the palynological data, we calculated for each pollen store two parameters describing the pollen diet for each species and for each site: (i) pollen richness, calculated as the total number of different pollen morphotypes identified and (ii) pollen predominance, measured as the proportion occupied by the most represented pollen morphotype in the diet. This predominant pollen may vary among samples and is not specific to the crop species. Finally, the percentages of apple and rapeseed pollen were also assessed for pollen stores collected from apple orchards and rapeseed fields respectively.

2.4. Data analysis

All data analyses were conducted with R studio using R v.4.1.0 (R Core Team, 2021). Figures were plotted using the ggplot2 package

v.3.4.0 (Wickham, 2016). Statistical analyses were performed using generalised linear models (GLMs) and generalised linear mixed-effects models (GLMMs) using *glmmTMB* from the R-package glmmTMB v.1.1.4 (Brooks et al., 2017). First, to perform interspecific comparisons of pollen richness and pollen predominance among the three bee species, we used GLMMs with Poisson and Beta distribution (link = logit), respectively. Pollen richness and pollen predominance were used as response variables, the type of crop, bee species and their interaction were used as explanatory variable, and country as random factor. Second, to study the interspecific variation of the proportion of focal crop pollen in the diet of the three studied bee species, we built one GLMM for each crop type using a Beta distribution (link = logit), with the proportion of apple pollen and rapeseed pollen in the diet as response variables, each bee species as explanatory variable and country as a random factor. To assess potential bias from the absence of *O. bicornis* in Ireland and the United Kingdom leading to a lower number of sites for the latter species, GLMMs of these two first biological questions were also analysed by excluding these countries for the three bee species. Since the results remained unchanged, models including all sites were selected. Third, to test the effect of biogeographic regions on the proportion of focal crop pollen in the diet, we used European biogeographic areas (*i.e.*, Boreal, Atlantic, Continental and Mediterranean regions). Climatic variables (*i.e.*, mean and delta of temperature and precipitation) were not used since local data specific to the time frame sampled were not available and since preliminary results highlighted a predominant impact of biogeographic regions on pollen foraging. We built one GLM for each bee species and for each focal crop using a Beta distribution (link = logit), with the proportion of apple pollen and rapeseed pollen in the diet as response variables and biogeographic region (factor with different regions as levels) as explanatory variable. Finally, landscape-level impacts were assessed by calculating the proportion of land cover categories that may influence crop pollen affinity (*i.e.*, proportion of arable, grassland, orchard, urban and woodland areas). Land cover categories were derived from manually digitised habitat maps within a 1 km radius around the sampling sites, using remote sensing data provided by World Imagery (ESRI) and GIS tools (ArcGIS Pro 2.4.1, ESRI) (further details in Bottero et al., 2023). To investigate the impact of landscape composition on the percentage of focal crop pollen in the diet, we built for each bee species, one GLM by focal crops, including only apple / rapeseed crop sites respectively and using a Beta distribution (link = logit). The percentage of apple pollen and rapeseed pollen in the diet was used as response variables, and proportion of land cover categories as explanatory variables. To account for correlations stemming from the compositional nature of land cover variables, an isometric log-ratio transformation was applied (Filzmoser et al., 2018). This method reduced correlations among the predictors, thereby addressing issues related to collinearity (Egozcue et al., 2003; Hron et al., 2012). This issue was not addressed by removing variables to avoid multi-collinearity, as this approach does not resolve the inherent challenges of compositional data and could result in misleading conclusions (Pawlowsky-Glahn et al., 2015). Null values were treated according to Martín-Fernández et al. (2003), (2011). All model assumptions were checked using the DHARMa R-package v.0.4.6 (Hartig, 2022). Statistical metrics were obtained using the *Anova* function from the R-package car v.3.1–2 on our models (Fox and Weisberg, 2019). Post-hoc tests were realised for all analyses using the *emmeans* function (Tukey method) from the R-package emmeans v.1.8.2 (Lenth, 2022).

3. Results

3.1. Interspecific variation in pollen richness and predominance in pollen diet

Profiles of the pollen stores showed that both the pollen richness (GLMM, $\chi^2 = 235.1$, df = 2, p < 0.0001, Fig. 2A) and the percentage of predominant pollen (GLMM, $\chi^2 = 37.17$, df = 2, p < 0.0001, Fig. 2B)

varied significantly between the two social species and *O. bicornis*. *A. mellifera* and *B. terrestris* collected on average over 80 % more different pollen species than *O. bicornis* (mean pollen richness: *A. mellifera*: 13.8, *B. terrestris*: 13.5, *O. bicornis*: 7.4; pairwise comparisons: *Apis vs Bombus*: z = 0.830, p = 0.6843; *Apis vs Osmia*: z = 14.59, p < 0.0001; *Bombus vs Osmia*: z = 13.75, p < 0.0001). Conversely, regarding the percentage of predominant pollen, *O. bicornis* showed significantly higher values than the two other bee species (mean percentage of predominant pollen: *A. mellifera*: 55.8, *B. terrestris*: 51.4, *O. bicornis*: 66.3; pairwise comparisons: *Apis vs Bombus*: z = 1.831, p = 0.1596; *Apis vs Osmia*: z = -4.52, p < 0.0001; *Bombus vs Osmia*: z = -6.04, p < 0.0001). The type of crop and its interaction with bee species were not significant for both pollen richness and predominance in the pollen diet (p > 0.05).

3.2. Interspecific variation of the proportion of the focal crop in the pollen diet

The bee species showed significant differences in the proportion of collected apple (GLMM, $\chi^2 = 11.35$, df = 2, p = 0.0034, Fig. 3A) and rapeseed pollen (GLMM, $\chi^2 = 44,57$, df = 2, p < 0.0001, Fig. 3B). Pairwise comparisons showed that *A. mellifera* and *B. terrestris* collected a higher proportion of apple pollen than *O. bicornis* (*Apis vs Bombus*: z = 0.365, p = 0.9291; *Apis vs Osmia*: z = 3.173, p = 0.0043; *Bombus vs Osmia*: z = 2.855, p = 0.0120). The mean proportion of apple pollen in the pollen diet was 19 % for *A. mellifera*, 22 % for *B. terrestris* and 9 % for
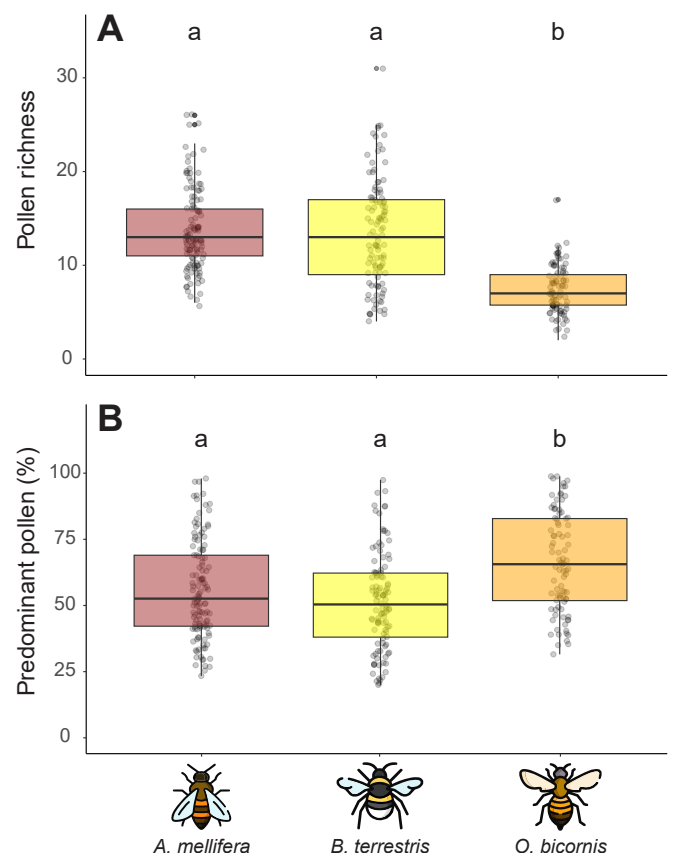
Fig. 2. Analysis of the pollen collected by *Apis mellifera* (n = 124), *Bombus terrestris* (n = 108) and *Osmia bicornis* (n = 88). **(A)** Pollen richness (*i.e.*, number of different pollen morphotypes found in each pollen store). **(B)** Predominant pollen percentage (*i.e.*, percentage of the most abundant pollen morphotype in the pollen stores). The middle line and the box in the boxplot represent the median and the interquartile range, respectively. Different letters above the boxplots indicate significant differences between bee species according to post hoc tests.

O. bicornis. Regarding rapeseed crops, *A. mellifera* was found to collect a significantly higher proportion of rapeseed pollen than the two other species (*Apis vs Bombus*: z = 4.757, p < 0.0001; *Apis vs Osmia*: z = 6.362, p < 0.0001; *Bombus vs Osmia*: z = 2.064, p = 0.0975). The mean percentage of rapeseed pollen in the pollen diet was 50 % for *A. mellifera*, 28 % for *B. terrestris* and 18 % for *O. bicornis*.

3.3. Diversity of the plant families in the pollen diet

Analysis of the pollen collected by the three bee species across all the European study sites, showed that they collected pollen on a wide variety of flowering plants alongside the two focal crop species (Fig. 4). In apple orchards, *A. mellifera* collected the highest diversity of pollen, with a total of 118 different pollen morphotypes (from 55 plant families) found in the 62 pollen stores, compared with 105 morphotypes (42 families) for *B. terrestris* in 52 pollen stores and 51 morphotypes (30 families) for *O. bicornis* in 42 pollen stores. In rapeseed crops, once again *A. mellifera* collected the highest diversity of pollen, with a total of 115 different pollen morphotypes (from 49 plant families) found in 62 pollen stores, compared with 104 morphotypes (43 families) for *B. terrestris* in 56 pollen stores and 53 morphotypes (31 families) for *O. bicornis* in 46 pollen stores. Both in apple orchards or rapeseed crops, the most represented families in the pollen collected by *A. mellifera* and *B. terrestris* were the Rosaceae and Brassicaceae, respectively (*i.e.*, the families of the two focal crop species). By contrast, the most represented plant families in the pollen collected by *O. bicornis* were the Fagaceae followed by the Ranunculaceae in apple crops and the Papaveraceae in rapeseed crops.
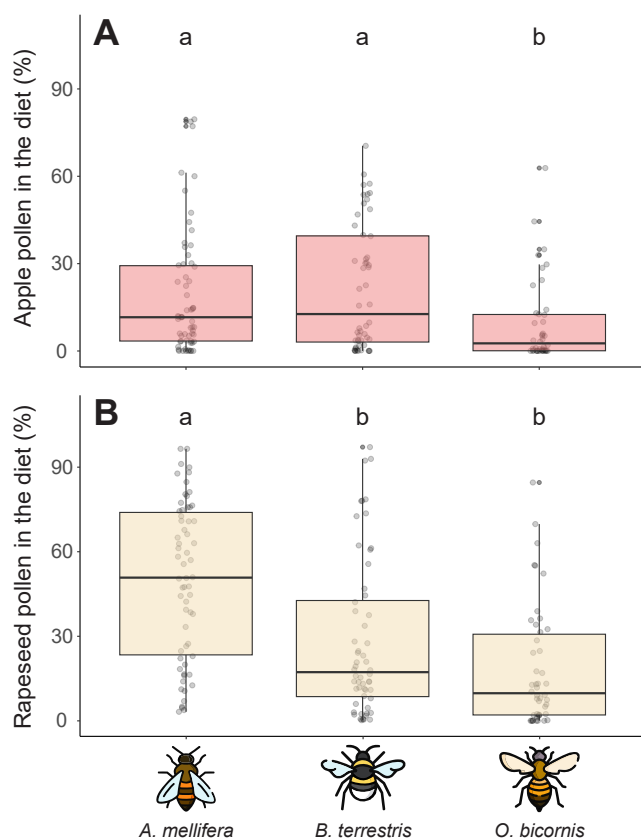
Fig. 3. Percentage of pollen of the focal crop in the pollen stores of *Apis mellifera* (n = 124), *Bombus terrestris* (n = 108) and *Osmia bicornis* (n = 88). **(A)** Percentage of apple pollen in apple orchards and **(B)** percentage of rapeseed pollen in rapeseed fields. The middle line and the box in the boxplot represent the median and the interquartile range, respectively. Different letters above the boxplots indicate significant differences between bee species according to post hoc tests.

The Rosaceae and Brassicaceae families came third in the pollen stores of *O. bicornis* in apple orchards and rapeseed fields, respectively. The main plant families collected in the two studied crop types by the three bee species across the biogeographic regions are presented in the supplemental materials (Fig. S1).

3.4. Intraspecific variation of pollen in relation to biogeographic regions and land covers

The percentage of focal crop pollen in the pollen stores showed some variations among the biogeographic regions (Fig. 5). While the latter did not significantly affect the apple pollen percentage collected by *A. mellifera* (GLM, χ^2 = 6.739, df = 3, p = 0.081, Fig. 5A) and *B. terrestris* (GLM, χ^2 = 7.744, df = 3, p = 0.052, Fig. 5C), the percentage varied significantly for *O. bicornis* (GLM, χ^2 = 14.63, df = 2, p = 0.0007, Fig. 5E) which collected more apple pollen in the continental region (Boreal *vs* Continental: z = -3.663, p = 0.0007; Continental *vs* Mediterranean: z = 2.910, p = 0.0101). By contrast, biogeographic regions significantly impacted rapeseed pollen collection of *A. mellifera* (GLM, χ^2 = 17.811, df = 3, p = 0.0005, Fig. 5B), *B. terrestris* (GLM, χ^2 = 19.274, df = 3, p = 0.0002, Fig. 5D) and *O. bicornis* (GLM, χ^2 = 38.458, df = 2, p < 0.0001, Fig. 5F). *A. mellifera* collected a higher percentage of rapeseed pollen in Continental region than in all other biogeographic regions (Atlantic *vs* Continental: z = -3.899, p = 0.0006; Boreal *vs* Continental: z = -3.368, p = 0.0042; Mediterranean *vs* Continental: z = -2.576, p = 0.0491). *B. terrestris* collected a higher percentage of rapeseed pollen in the Atlantic region than all other biogeographic regions (Atlantic *vs* Boreal: z = 3.142, p = 0.0091; Atlantic *vs* Continental: z = 2.595, p = 0.0467; Atlantic *vs* Mediterranean: z = 4.254, p = 0.0001). *Osmia bicornis* collected a higher percentage of rapeseed pollen in Boreal and Continental regions (Boreal *vs* Mediterranean: z = 4.522, p < 0.0001; Continental *vs* Mediterranean: z = 6,.112, p < 0.0001). Contrastingly, land covers had no significant effect on the percentage of focal crop pollen in the diet of the three bee species (Table S2), except that rapeseed pollen decreased in the diet of *O. bicornis* at rapeseed fields with increasing orchard covers in the landscape (GLM, Estimate = −0.101, Std. Error = 0.032, p = 0.0018).

4. Discussion

4.1. Pollen diet of managed bees in agroecosystems

Based on palynological analysis of a total of 320 pollen stores (*A. mellifera*: 124; *B. terrestris*: 108; *O. bicornis*: 88), collected by the three managed bee species across 128 sites, we described and compared (i) their pollen diet range as well as (ii) the relative abundance of the main pollen resource. *Apis mellifera* and *B. terrestris* showed the highest generalist behaviour with a pollen richness reaching up to 26 and 31 pollen morphotypes per site, respectively. Furthermore, the generalism exhibited by *A. mellifera* and *B. terrestris* is likely underestimated, since the studied time frame does not encompass the full foraging period of these social species, in contrast to *O. bicornis*. While we are not aware of any research that described pollen profiles across the three studied bee species at the European level, our results align with other studies that highlighted the very generalist pollen diet of *A. mellifera* (Requier et al., 2015; Simanonok et al., 2021), *B. terrestris* (Yourstone et al., 2023) and, to a lower extent, *O. bicornis* (Haider et al., 2014) at national and regional scales (Jaumejoan et al., 2023). Accordingly, we found that these managed species rarely harboured only one pollen morphotype in their provisions. In a landscape dominated by one crop species, we could expect these bees to mainly forage on the most abundant resources (Leonhardt and Blüthgen, 2012). However, our results contrast with this assumption, since bees did not only focus on the abundant pollen resources provided by the crop but also tended to collect pollen from diverse origins by visiting other plants in the landscape (Requier et al., 2015). Monotonous diets have been found to limit larval development,
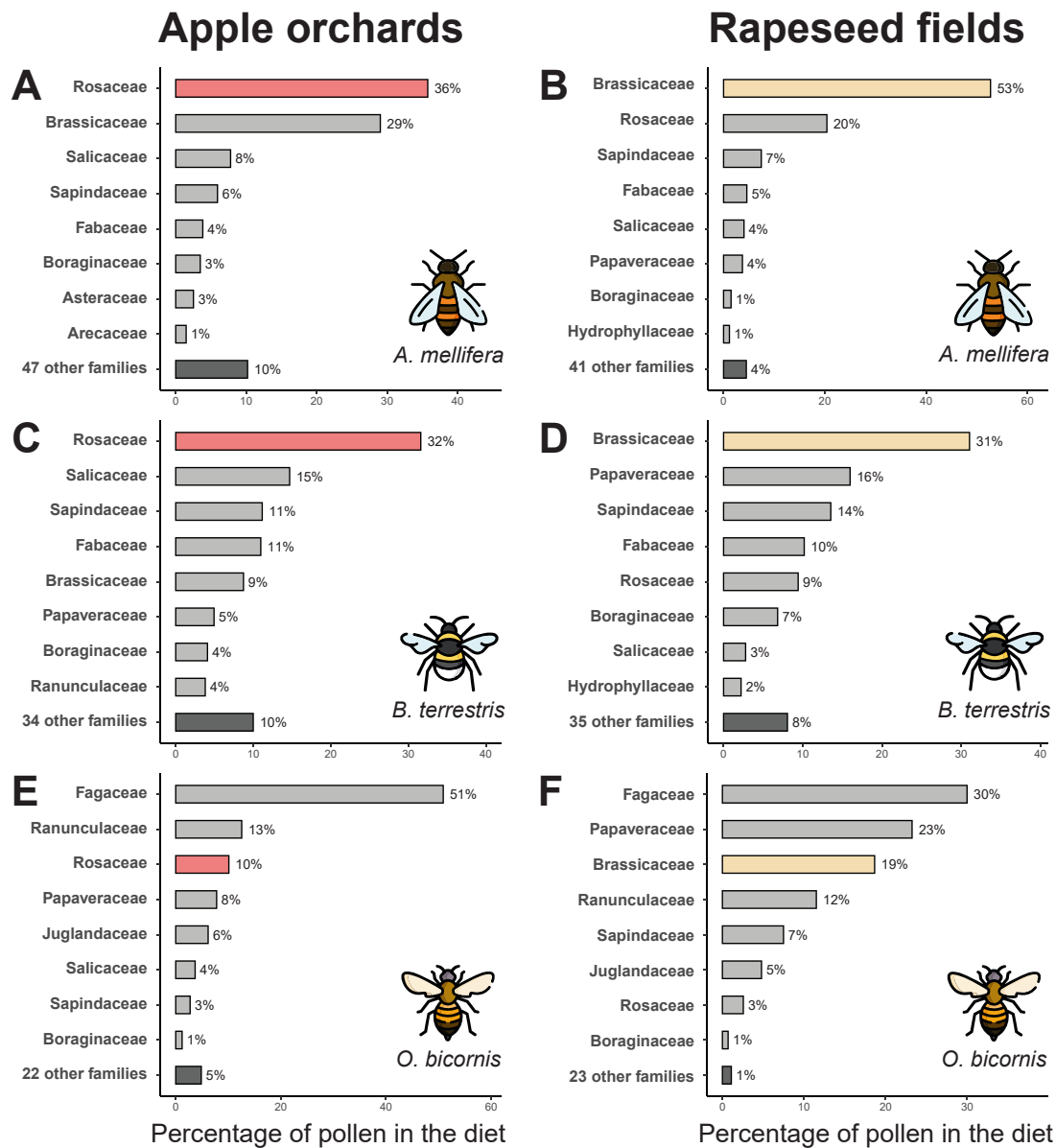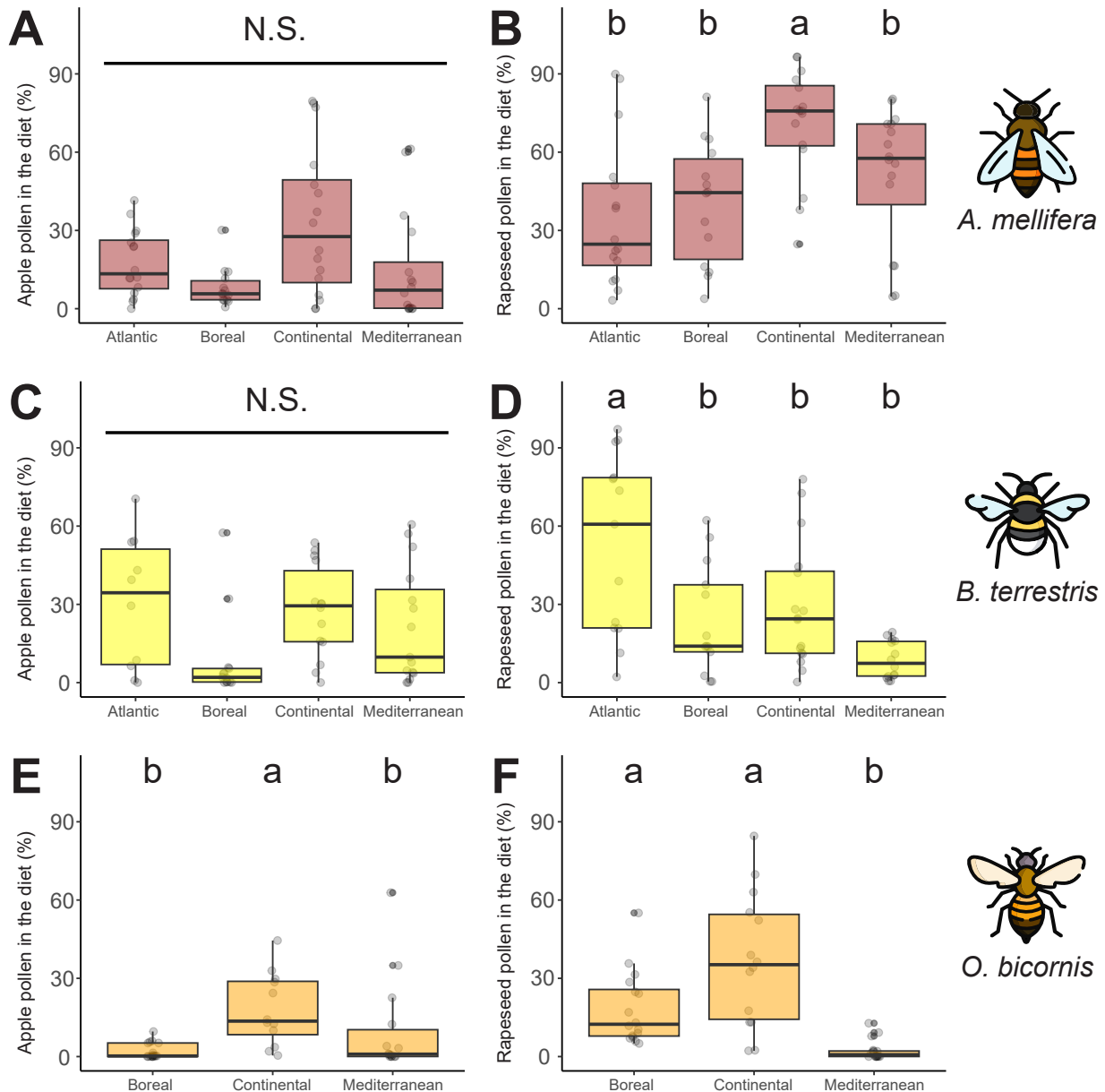
Fig. 4. Comparison of the plant families found in the pollen stores of **(A, B)** *Apis mellifera*, **(C, D)** *Bombus terrestris* and **(E, F)** *Osmia bicornis* in (**A, C, E**) apple orchards and **(B, D, F)** rapeseed fields. Only eight plant families are represented in the plot (covering > 90 % of pollen). Other plant families are aggregated at the bottom of each plot. Bars in colour highlight the families of the focal crop species: Rosaceae in red with mainly *Malus domestica* pollen and Brassicaceae in yellow with mainly *Brassica napus* pollen.

decrease adult health, and increase susceptibility to pesticides and other threats (Alaux et al., 2010; Goulson et al., 2015; Dance et al., 2017; Schwarz et al., 2024). Therefore, our results support the hypothesis that managed bee species forage on wild plant species in the landscape surrounding crops to balance their diet (Sutter et al., 2017). In light of the need for managed bee species to include diverse sources of pollen in their diet, agri-environmental policies and measures that aim to support bees should promote plant richness in the surrounding landscape of crops (Sutter et al., 2017).

4.2. Managed bee affinity for focal crops

Our results describe, to our knowledge for the first time, the affinity of three managed bee species to apple and rapeseed pollen at the European scale. Honey bees and bumble bees showed the highest affinity for apple pollen, while only honey bees showed a strong affinity for rapeseed pollen. The predominance of focal crop pollen in the diet of

A. mellifera is not surprising given their affinity with highly abundant floral resources (Hung et al., 2019). Indeed, because of their sociality and associated high number of individuals, *A. mellifera* tends to forage on the plant species providing the most abundant floral resource regardless of its nutritional profile (Leonhardt and Blüthgen, 2012; Rodney and Purdy, 2020). Therefore, *A. mellifera* flower fidelity per foraging bout leads to pollen loads that can consist almost exclusively of apple or rapeseed pollen, and consequently improve crop pollination quality and yield (Jauker et al., 2012; Stanley et al., 2013; Lindström et al., 2016; Russo and Danforth, 2017). This strong preference for abundant crop species is of interest for wild bee conservation, as it may reduce (though not eliminate), *A. mellifera* reliance on wildflower patches and its competition with native bee species. (Iwasaki and Hogendoorn, 2022). However, *B. terrestris* foraging patterns are more strongly driven by pollen quality compared to those of *A. mellifera*, with bumble bees tending to forage preferably on pollen with a high protein/lipid ratio (Leonhardt and Blüthgen, 2012; Vaudo et al., 2020).

Fig. 5. Variation in the percentage of focal crop pollen in the pollen stores according to four biogeographic regions. **(A, C, E)** apple pollen collected in apple orchards and **(B, D, F)** rapeseed pollen collected in rapeseed fields by **(A, B)** *Apis mellifera*, **(C, D)** *Bombus terrestris* and **(E, F)** *Osmia bicornis*. Countries are assigned to biogeographic regions as follows: Boreal (Sweden and Estonia), Atlantic (Ireland and the United Kingdom), Continental (Germany and Switzerland) and Mediterranean (Spain and Italy). *O. bicornis* was not studied in the Atlantic region because it is not native to Ireland and the United Kingdom. The middle line and the box in the boxplot represent the median and the interquartile range, respectively. Different letters above the boxplots indicate significant differences between bee species according to post hoc tests. "N.S." = Not significant.

Therefore, *B. terrestris* pollen choices seem more influenced by landscape composition and availability of plant species providing protein-rich pollen (Jaumejoan et al., 2023). These requirements may explain why *B. terrestris* collected less rapeseed pollen than *A. mellifera* in rapeseed crops since it was partly replaced by Papaveraceae and Fabaceae pollen which are richer in protein content (Vaudo et al., 2020, 2024). Similarly in orchards, *B. terrestris* pollen diet can include mainly fruit tree species but also include other co-flowering resources (Jaumejoan et al., 2023). The low percentage of apple pollen collected by *B. terrestris* in some of our sites may therefore reflect the high abundance of more preferred pollen plant species in the surrounding landscape.

Osmia bicornis did not collect abundant apple or rapeseed pollen. The pollen collected by *O. bicornis* consisted mainly of Fagaceae (*Quercus* sp.)

pollen while Rosaceae and Brassicaceae pollen only reached 10 and 19 % of the pollen sampled in apple orchards and rapeseed crops, respectively. We confirmed previous studies that showed already these preferences in orchards and rapeseed fields (Splitt et al., 2021; Bednarska et al., 2022; Knauer et al., 2024). This limited affinity for Rosaceae and Brassicaceae pollen reflects the diet of wild *Osmia bicornis* (Haider et al., 2014). However, this highlights a potential lack of suitable pollen for wild populations in agricultural landscapes. In extensive monocultures of rapeseed fields or apple orchards, *O. bicornis* and other native species may therefore struggle to find diverse and suitable pollen resources essential for their survival. These results contrast with other managed mason bee species (all from the subgenus *Osmia*) that are known to have a high affinity for orchard species pollen and to be

excellent orchard pollinators (*e.g.*, *O. cornuta*, *O. cornifrons*, *O. lignaria*; Torchio, 1976; Russo and Danforth, 2017; Osterman et al., 2021; Knauer et al., 2024). For example, in European orchards*, O. cornuta* collects mainly on Rosaceae, up to 92 % of fruit tree pollen (Jaumejoan et al., 2023). Comparisons of the two European species *O. cornuta* and *O. bicornis* showed that *O. cornuta* efficacy was not driven by the availability of co-flowering species (Jaumejoan et al., 2023; Knauer et al., 2024), while *O. bicornis* tends to bypass crop species to other species with similar flowering phenology (Russo and Danforth, 2017). Different flight periods and larvae physiological requirements are likely the cause of this divergence in pollen-collecting behaviour (Sedivy et al., 2011). Alternatively, although unlikely in agroecosystems with abundant floral resources, *O. bicornis* may have shifted to wild plant species due to competition with other managed bee species (Hudewenz and Klein, 2015). Ultimately, while *O. bicornis* has been used as a managed pollinator of fruit tree orchards and rapeseed crops since the 1970s (Steffan-Dewenter, 2003; Gruber et al., 2011; Sedivy and Dorn, 2014), our results contradict their affinity for apple and rapeseed pollen. The use of *O. bicornis* as managed pollinators of apple orchards and rapeseed crops should be reconsidered in favour of other commercially available mason bees such as *O. cornuta* (Hansted et al., 2014).

4.3. Intraspecific variation of pollen diet across biogeographic regions and landscapes

This first continent-level investigation of managed bee affinity for apple and rapeseed pollen highlighted discrepancies in pollen diets across European biogeographic regions. In apple orchards, biogeographic regions only had impacts on *O. bicornis* affinity for apple pollen, which decreased in the Boreal and Mediterranean regions in favour of various wild trees and herbaceous plants (*e.g.*, *Quercus* spp., *Papaver* spp.). In rapeseed fields, all three species' affinity for rapeseed pollen depended on biogeographic regions. *Apis mellifera* and *B. terrestris* exhibited a higher affinity for rapeseed pollen in the Continental and Atlantic regions, respectively, while *O. bicornis* displayed reduced rapeseed pollen collection in the Mediterranean region, diverting foraging mainly towards oaks and Papaveraceae. These results may be explained by variations in plant richness and flora composition across biogeographic regions (Mutke and Barthlott, 2005; Thuiller et al., 2005; Ronk et al., 2015). Understanding how biogeographic regions are responsible for such changes requires further continental-level analysis of general flora, which are poorly available, complex to implement and highly context-dependent. However, these initial results at the European scale already suggest that affinity for focal crop pollen varies across Europe, especially in rapeseed fields, and that regions should be considered when addressing managed bee suitability. Another explanation for this effect could be that biogeographic regions vary in crop size or occurrence of the landscape, with lower collection of cultivated species potentially reflecting the high availability of alternative crops and other habitats within the surrounding landscape. To investigate the role of landscape composition around the studied sites on pollen diet, the effect of land cover was also examined. Contrary to our initial hypothesis, while land covers can influence pollinator populations including bees, they had minimal impact on the percentage of focal crop pollen collected by the studied bee species (Bottero et al., 2023). Regarding *A. mellifera*, landscape composition can affect its foraging behaviour and pollen affinity for focal crop species (Garbuzov et al., 2015; Danner et al., 2016). However, honey bees often show a high affinity for rapeseed and apple pollen, despite co-flowering species or even co-flowering crops in the landscape (Grab et al., 2017; Bänsch et al., 2020). The lack of impact of land covers is therefore likely the result of *A. mellifera* strong affinity for the studied crop species as well as its tendency to forage on dominant floral resources in the landscape (Hung et al., 2019; Raimets et al., 2020). Conversely, *B. terrestris* and *O. bicornis* foraged more on co-flowering species, and we expected a stronger effect of the landscape on their pollen diets. While few studies

addressed this question, *B. terrestris* and *O. bicornis* pollen richness can be affected by landscape composition (Eckerter et al., 2022; Jaumejoan et al., 2023; Misiewicz et al., 2023). A first explanation for this lack of impact could be that co-flowering species used by managed bee species do not occur in alternative non-cultivated landscapes (woodlands, grasslands, and urban habitats) but rather within fields and orchards. For example, the ground cover of apple orchards can contain numerous wild co-flowering plant species that attract wild and managed bees and may limit the influence of other habitats in the landscape (Brown et al., 2022). An alternative hypothesis could be that environmental factors affecting pollen diet are not occurring at the landscape level (*i.e.*, land covers) but rather at a more local level within microhabitat conditions (Everaars et al., 2011; Cusser et al., 2019). Indeed, several studies have highlighted that *O. bicornis* pollen diet was mainly driven by the availability of suitable pollen sources nearby (*i.e.*, *Ranunculus* spp. and *Quercus* spp.) that could not always be related to landscape factors (Everaars et al., 2011; Coudrain et al., 2016; Bednarska et al., 2022; Eckerter et al., 2022). Management protocols aiming to limit managed bee species from shifting to wild co-flowering species should therefore consider the availability of alternative preferred food resources in the crop surroundings rather than landscape composition.

4.4. Selection of managed bee species for crop pollination

Our results suggest that *A. mellifera* and both *A. mellifera* and *B. terrestris* have the highest affinity with rapeseed and apple pollen, respectively. However, species selection for crop pollination must also consider other parameters including management costs and ecological impact of managed bee species. For instance, honey bee hives benefit from an efficient social system with numerous individuals resulting in lower cost per individual but also from longer activity periods and simpler handling compared to bumblebee colonies or mason bee populations (Bosch and Kemp, 2002; Velthuis and Van Doorn, 2006; Sperandio et al., 2019). Nonetheless, the negative impact of honey bees on wild bee communities can be significant when they compete for limited resources, act as vectors for parasites, cause reproductive disruption, and modify plant communities (Stout and Morales, 2009; Iwasaki and Hogendoorn, 2022; Tourbez et al., 2025). Moreover, while it is of high importance, one must not consider that pollinator efficacy is solely driven by species pollen affinity. Pollination efficacy depends on numerous factors including pollinator species abundance, visitation rates, stigma pollen deposition during pollen or nectar foraging visits, quality and heterogeneity of deposited pollen and amount of pollen grain carried (King et al., 2013; Stanley et al., 2013). For instance, corbiculate bees (*i.e.*, honey, bumble, stingless and orchid bees), carry pollen mixed with nectar in specific structures on hind legs (*i.e.*, corbicula) making the pollen less available for plant pollination (Michener, 2000). Consequently, a single visit of honey and bumble bees is usually less efficient than a single visit of mason bees showing loose scopa with dry pollen (Parker et al., 2015).

Overall, in apple orchards, mason bees show better stigma contact and pollen deposition compared to bumblebees and honey bees, making them the preferable choice (Bosch and Kemp, 2002; Thomson and Goodell, 2001; Roquer-Beni et al., 2022). Additionally, *O. bicornis* may forage on apple and rapeseed flowers for nectar rather than pollen, yet still act as pollinators for these species. While *O. bicornis* may still be a good pollinator despite its low affinity for apple and rapeseed pollen, other mason bees, such as the commercially available *O. cornuta*, which exhibit both high affinity and high pollen deposition, are likely the most efficient pollinators for apple orchards. In rapeseed crops, the three species are known to promote crop yield (Jauker et al., 2012; Lindström et al., 2016). However, *A. mellifera* has a higher affinity for rapeseed pollen (Stanley et al., 2013). At similar densities, *O. bicornis* is likely a more efficient rapeseed pollinator than *A. mellifera* thanks to its high pollen deposition (Jauker et al., 2012), but it also has a lower affinity for rapeseed pollen. Therefore, considering bee affinity and practical

difficulties in handling big populations of mason bees compared to honey bees, we conclude that *A. mellifera* is likely the easiest and most efficient pollinator of rapeseed crops. Finally, while this study assesses the suitability of three managed bee species for crop pollination, it does not advocate for the exclusive reliance on any single species. It is essential to recognize the significant contribution of wild bees and other pollinators to crop pollination processes (Garibaldi et al., 2013). Additionally, using multiple managed pollinators can lead to synergistic effects on crop yields, as interactions among pollinators can enhance their pollination activity (Sapir et al., 2017; Eeraerts et al., 2020). Therefore, an optimal approach to crop pollination management may involve the use of multiple managed bee species while concurrently supporting the presence of wild pollinators to leverage the synergistic interactions among diverse pollinator species (Garibaldi et al., 2014).

5. Conclusion

This study marks, to our knowledge, the first continent-level comparison of pollen foraging behaviour in three widely used managed bee species within European agroecosystems. Our findings provide clear evidence that *A. mellifera*, *B. terrestris*, and *O. bicornis* exhibit distinct pollen diet profiles as well as distinct preferences for apple and rapeseed pollen. Additionally, we have identified variations in crop pollen collection across different European biogeographic regions but only minimal impact from the landscape composition. These results have economic implications since the affinity of managed pollinators directly impacts their effectiveness in pollinating focal crop species. Therefore, our findings aid in the selection of the most suitable managed pollinators for specific agricultural contexts. By shedding light on the foraging behaviour of managed pollinators in these agroecosystems, our study introduces new understanding of their affinity for focal crops that can enhance field yields, addressing the ongoing global resource crisis.

CRediT authorship contribution statement

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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.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109518.

Data availability

Data will be made available on request.

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