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Role of floral strips and semi-natural habitats as enhancers of wild bee functional diversity in intensive agricultural landscapes

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Abstract

Installing patches of flowering plants is a commonly used strategy to enhance refuge and food resources for pollinators in intensive agricultural landscapes. Here, we evaluated how floral strips and semi-natural habitats impact the taxonomic and functional diversity of wild bees in intensively farmed sunflower fields. Pan traps were used to assess bee richness and functional diversity at 22 sampling sites (11 sites were positioned in sunflower fields with floral strips, and 11 control sites were adjacent to semi-natural habitats). Five sampling levels were established in each field, positioned at different distances from the flower strip or semi-natural habitat. Wild bee species richness and functional richness were significantly higher inside floral strips and semi-natural habitats compared to sunflower fields. Functional redundancy was significantly higher inside agricultural fields compared to inside floral strips and semi-natural habitats. Sunflower fields with floral strips had lower Rao values compared to sunflower fields adjacent to semi-natural habitats. The community-weighted mean (CWM) of intertegular distance (distance between where wings attach to body) of wild bees was significantly higher in sunflower fields adjacent to semi-natural habitats. In comparison, the CWM of wing length varied across sampling levels in sunflower fields with semi-natural habitats. Our results show it is essential to have semi-natural habitats within intensive agricultural landscapes to ensure the conservation of wild bee diversity, while the installation of floral strips offers a partial substitute to enhance wild bee diversity when semi-natural habitats are scarce or absent.

Keywords: Green infrastructure, pollinators, sunflower, traits, wild bees.

1. Introduction

Agricultural intensification has negatively impacted the abundance and diversity of wild bees through increased habitat fragmentation and limiting the availability of nesting sites and foraging resources (Kremen et al., 2002; Potts et al., 2005, 2003; Williams and Kremen, 2007; Wood et al., 2017). Both habitat connectivity and refuge availability for wild bees can be guaranteed by maintaining patches of semi-natural habitats already present in the landscape (i.e., field margins, hedgerows, fallows) (Altieri and Nicholls, 2012; Fischer et al., 2014). Furthermore, installing patches of flowering plants might also positively impact refuge and food resources for insect pollinators in agroecosystems (Benayas et al., 2015).

Thus, the European Union (EU) has adopted a biodiversity strategy that includes specific targets to enhance green infrastructure within the member states (European Commission 2012). The EU defined Green Infrastructure as “a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services” (European Commission 2012). Green Infrastructures (GIs) are considered important in biodiversity conservation because they contribute towards maintaining areas of wildlife-rich natural or semi-natural habitat that enhance landscape connectivity (Garmendia et al., 2016).

In particular, to counter the decline of pollinators within intensive agriculture landscapes, the EU biodiversity strategy recommends that different types of GI are established, such as sowing floral strips using a mixture of melliferous plants that are attractive to bees (Scheper et al., 2015). Floral strips provide critical refuges for bees and enhance the availability of floral resources, which is probably the most important limitation for bee communities

(Goulson, 2003; O'Toole and Gault, 1993). The existence of strips with wild vegetation enhances the taxonomic diversity of bee communities and pollination services in adjacent crops (Campbell et al., 2017; Hevia et al., 2016; Holzschuh et al., 2006; Jönsson et al., 2015). However, the importance of natural or semi-natural strips of wild vegetation on the functional diversity of bee communities within agroecosystems remains poorly understood (Hall et al., 2019; Papanikolaou et al., 2017).

Functional diversity (FD) reflects the value and range of the functional traits of organisms present in ecosystems (Díaz and Cabido, 2001). FD is widely recognized as a dimension of biological diversity that is closely linked to ecosystem processes (Gross et al., 2017; Hoehn et al., 2008; Tilman et al., 1997). It is also an essential tool for addressing and understanding many ecological questions (Carmona et al., 2016; Le Provost et al., 2020; Mason and de Bello, 2013). For example, differences in trait values among bee pollinator species determine how they are differently impacted by habitat loss in intensive agricultural landscapes (Warzecha et al., 2016). Hence, exploring the FD status of bee communities could advance our understanding of how the presence of natural or semi-natural vegetation patches within agroecosystems affects biodiversity and the provision of pollination services. Several morphological and behavioral characteristics of pollinators directly affect their capacity to provide pollination services. The distribution of these functional traits within a bee community has an essential role in pollination services, and can affect crop yields (Bartomeus et al., 2018; Hoehn et al., 2008; Woodcock et al., 2019). However, relatively few studies have evaluated how the potential loss of natural habitats could impact the functional diversity of bees (but see Geslin et al. 2016).

Drawing from the findings of an EU-funded Project that evaluated the effects of GIs on bee communities and pollination in sunflower fields, here we evaluated the effect of floral strips and semi-natural habitats on the taxonomic and functional diversity of bees in intensively farmed sunflower fields. Specifically, we tested the following hypotheses: (1) semi-natural habitats and floral strips serve as reservoirs of wild bees, and (2) taxonomic and functional diversity of wild bees in adjacent sunflower fields decreases with distance from semi-natural habitats and floral strips. Our results are expected to provide new insights on the role of floral strips and semi-natural habitats on wild bee communities in intensive sunflower landscapes.

2. Methods

2.1. Study area

The study area encompasses five municipalities in the Castilla-La Mancha region (Spain) (Fig. 1). This area is a flat plateau (830-900 m above sea level) characterized by a continental Mediterranean climate (mean annual temperature ca. 13 °C, mean annual rainfall ca. 550 mm, with severe summer drought). The landscape is dominated by oilseed sunflowers and non-irrigated cereals that are farmed intensively under an annual rotation regime.

2.2. Sampling design

We established 22 sampling sites, of which 11 were positioned in sunflower fields with floral strips installed, and 11 sites were positioned in sunflower fields without floral strips but were adjacent to semi-natural habitats. Floral strips consisted of a 120 m² area seeded with a mixture of 12 melliferous flowering species of herbaceous plants (Appendix A in Supplementary material). All floral strips were sown in March 2017 and resown in February 2018. Most of the melliferous species do not bloom for long, so we considered the succession of flowering by different plants to ensure that food resources for bees were present, at least, from March to September. In parallel, we selected sunflower fields adjacent to semi-natural habitats with native vegetation, covering an equivalent or larger area than that of the floral strips. These semi-natural habitats mainly consisted of basophilous scrub dominated by *Genista scorpius*, *Thymus vulgaris*, *Bupleurum fruticosum* and other low-growing woody plants, with a significant presence of species belonging to the Lamiaceae family (Appendix B in Supplementary material). All sampling sites were separated from each other by at least 500 m, because most solitary bees forage within this

range (Gathmann and Tschardtke, 2002; Zurbuchen et al., 2010). Although it is known that different sunflower cultivars might slightly differ in their potential attractiveness for wild bees, based on their nectar and pollen production, it was not possible for us to standardize the variety of sunflower cultivated on the study fields, given that cultivar selection highly varies depending on farmer preferences and seed availability in local stores (see Appendix C for consulting the nine varieties identified).

We used pan traps to survey the bee community at all sites. Pan traps are considered an efficient methodology for standardizing sampling effort, and have been widely used to quantitatively sample bee assemblages (Westphal et al., 2008). As any other sampling method, pan trapping has some limitations, especially regarding the understanding of real floral visitation of bees. Nevertheless, we chose pan trapping because our aim was to characterize the bee community rather than sample bee-flower interactions, and because we needed to standardize the sampling effort applied at each sampling site.

We established five sampling levels at each site, one in the floral strips or semi-natural habitat, and four within adjacent sunflower fields at 0, 15, 30, and 60 m from the floral strip/semi-natural habitat (Fig. 2). At each level, we set up two pan trap stations separated by 10 m. Each station consisted of a metal bar holding three plastic bowls painted with UV-reflective paint (white, yellow and blue) to attract flower-visiting insects (Toler et al. 2005, Westphal et al. 2008).

2.3. Data collection

All sites were sampled during the peak blooming period of sunflowers (between July 25 and August 22, 2018) on fair weather days. Bowls of each pan trap station were filled with soapy water and were operational from sunrise to sunset for two consecutive days.

Although honeybees are the dominant floral visitors in sunflower crops of our study area (Hevia et al., 2016), their abundance is highly dependent on the presence of local and transhumant hives, rather than environmental factors. We ensured that none of the fields sampled had beehives adjacent. However, honey bee hives were present throughout all the study area, as beehives from other parts of the country are customarily brought to the sunflower fields during the blooming season. Thus, we focused only on wild bee species, excluding *Apis mellifera* from our analyses. Taking into account that the number of honey bees captured was much higher than that of wild bees, we considered that including honey bees in the analysis of functional diversity would obscure the existing differences among wild bee communities (however, analyses including also *Apis mellifera* are provided in Appendix D for comparison).

Captured bees were identified to the species level by professional entomologists and were subsequently characterized according to three quantitative functional traits (Table 1): intertegular distance (ITD), wing length (WL), and hair length (HL) at the mesonotus. These traits were previously reported to be relevant for foraging activity and are correlated with susceptibility to land use change (Peters et al., 2016; Winfree et al., 2009). The three traits were measured in a random sample of 10 individuals per species. We did not include qualitative traits in our functional diversity indexes as we focused only on quantitative traits that vary within species. Further, we have tested the potential differences between semi-natural habitats and floral strips regarding social behavior of wild bees present, nesting site

preference and foraging specialization (polylectic versus oligolectic), finding no differences for any of these qualitative traits (see Appendix E).

2.4. Data analysis

2.4.1. Estimation of functional diversity

All traits were $\log+1$ transformed before any estimate of functional diversity was made. The three selected traits were strongly correlated, due to their inherent relationship with bee size; thus, we performed linear regressions of WL and HL, using ITD as a continuous predictor. We used the residuals of these regressions as the new values for WL and HL, respectively (Micó et al., 2020). Thus, the lengths represented by WL and HL are standardized with respect to the intertegular distance of each individual. We estimated the mean trait values for each species, which were used to estimate the community-weighted mean (CWM) of each trait, with the number of individuals of each species in each trap representing an indicator of abundance. CWM values indicated the trait values of the most abundant species in the trap.

Following Martello et al. (2018), we performed a PCA based on the average trait values of each species (Appendix F in Supplementary material). Then, we used the two first components of this PCA, which captured 77.4% of total variance, as the functional space to estimate different indicators of functional diversity. We estimated the position of individual bees in this functional space based on their trait values. This strategy allowed us to consider traits measured at the individual level, while giving equal weight to all species for the PCA, thus removing the effect of differing abundance across species in the dataset (Martello et al., 2018). We used the scores of the individuals in the functional space to estimate trait

probability density (TPD; Carmona et al., 2016) functions for each species using the TPD package (Carmona et al., 2019). The TPD function of a given species (TPDs) reflects how the individuals of that species are distributed within the functional space, effectively incorporating information on intraspecific variability in functional diversity analyses. The TPDs of different species could be combined to estimate the TPD function of a community (TPDc), which reflects the relative abundance of traits in an assemblage. TPDc can then be used to estimate different aspects of functional diversity (Carmona et al., 2019). We used the number of individuals of each species captured in the pan traps to estimate the TPDc of each pan trap.

Based on the TPDc of each individual trap, we estimated three indicators of functional diversity: functional richness (FRic), functional redundancy (FRed), and Rao's quadratic entropy (Rao). FRic reflects the amount of functional space occupied by the species present in each sample (Carmona et al., 2016), and represents the functional analogue of species richness. FRed indicates to what degree the removal of a random species from an assemblage would affect its functional structure. The removal of a random species in an assemblage with high redundancy should not strongly impact its functional structure, and vice versa (Carmona et al., 2020, 2017). Finally, we estimated Rao using the 'melodic' R function (de Bello et al., 2016). Rao represents the expected functional dissimilarity between two randomly chosen individuals from an assemblage by considering the relative abundance of each species (de Bello et al., 2016). For this, we estimated the functional dissimilarity between all pairs of species as 1 minus the overlap between their respective TPDs (Carmona et al., 2016).

2.4.2. Statistical analyses

We performed linear mixed models for each response variable at the trap level (species richness, CWM for each individual trait, FRic, FRed, and Rao), using sampling level (categorical variable reflecting the position of the trap with respect to the floral strip and semi-natural vegetation patch), vegetation type (semi-natural habitats and floral strips), and the interaction between them as fixed factors. We used the identity of the field as a random variable to account for the non-independence of traps from the same field. In cases where we detected a significant ($P < 0.05$) effect of trap position on the considered diversity index, we performed a Tukey HSD post-hoc test to detect differences between individual positions (Hevia et al., 2016). All analyses were performed using R (v 3.6.0, R Core Team, 2019).

3. Results

We collected 3028 wild bees from 46 species (Table 2). Wild bee species richness varied significantly among the five sampling levels, both in fields with floral strips and fields with semi-natural habitats ($F_{4,80} = 5.72$, $P < 0.001$). There were no significant differences between floral strips and semi-natural habitats ($F_{1,20} = 2.32$, $P = 0.144$), and the interaction was not significant ($F_{4,80} = 1.80$, $P = 0.137$). The highest species richness was found in traps located inside floral strips and semi-natural habitats (Fig. 3a).

The functional richness of wild bees varied across sampling levels in a similar way, both in sunflower fields with floral strips and semi-natural habitats (Sampling level: $F_{4,80} = 7.85$, $P < 0.001$; Interaction: $F_{4,80} = 0.15$, $P = 0.341$). Functional richness was higher inside the floral strips and semi-natural habitats (Fig. 3b).

Functional redundancy did not significantly differ between sunflower fields with floral strips and semi-natural habitats ($F_{1,20} = 1.29$, $P = 0.271$). However, functional redundancy did vary across sampling levels, both in sunflower fields with floral strips and those with semi-natural habitats, with higher values being documented inside agricultural fields ($F_{4,80} = 4.33$, $P = 0.003$) (Fig. 4a). Sunflower fields with floral strips had lower Rao values compared to those adjacent to semi-natural habitats ($F_{1,20} = 4.66$, $P = 0.043$). However, no differences were found across sampling levels in sunflower fields with floral strips or semi-natural habitats (Sampling level: $F_{4,80} = 2.25$, $P = 0.070$; Interaction: $F_{4,80} = 0.60$, $P = 0.665$; Fig. 4b).

CWM of wild bee ITD was significantly higher in sunflower fields with semi-natural habitats ($F_{1,20} = 10.37$, $P = 0.004$), but did not vary significantly among the five sampling

levels in sunflower fields with floral strips or semi-natural habitats (Sampling level: $F_{4,80} = 1.54$, $P = 0.198$; Interaction: $F_{4,80} = 0.99$, $P = 0.417$) (Fig. 5a).

CWM of wild bee WL varied across sampling levels in sunflower fields with semi-natural habitats ($F_{4,80} = 3.32$, $P = 0.014$). However, analysis of sampling level showed that the highest values differed between the two field types (Interaction: $F_{4,80} = 3.33$, $P = 0.014$) (Fig. 5b).

Finally, CWM of wild bee HL was marginally significantly higher in sunflower fields with floral strips ($F_{1,20} = 4.02$, $P = 0.059$), but did not vary significantly among the five sampling levels in sunflower fields with floral strips or semi-natural habitats (Sampling level: $F_{4,80} = 0.65$, $P = 0.626$; Interaction: $F_{4,80} = 0.64$, $P = 0.637$) (Fig. 5c).

4. Discussion

4.1 How do floral strips and semi-natural habitats affect wild bee diversity in sunflower landscapes?

Simplification of landscapes resulting from intensive management practices in agroecosystems could have consequences with respect to how many and which species persist (Potts et al., 2010; Williams et al., 2010). The presence of diverse pollinators offers multiple ecosystem services and functions, giving robustness and resilience to pollination networks (Jordano, 2016). However, in Mediterranean agricultural landscapes, these networks are usually disrupted, leading to the potential loss of ecosystem services and functions (Deguines et al., 2014; Kennedy et al., 2013).

Existing studies have explored the effects of field margins, hedgerows, flower strips, and road margins on conserving pollinators in monoculture landscapes (Albrecht et al., 2020). However, knowledge remains limited on how these types of habitats impact the functional diversity of wild bees on adjacent monocultures. Thus, it is important to understand the functional diversity of wild bees to elucidate the role of pollinators in agricultural systems (Frund et al., 2013; Hoehn et al., 2008).

Our study shows that wild bee assemblages in sunflower landscapes respond to the presence of floral strips and semi-natural habitats, both in taxonomic and functional terms. Wild bee species and functional richness were higher within both floral strips and patches of semi-natural habitats. Thus, we believe that these areas can act as biodiversity reservoirs, as they provide food and nesting resources during most part of the year. However, long-term studies of more than one year are necessary to verify this hypothesis. Our results also showed that wild bee assemblages in sunflower fields represent a poorer version of wild

bee assemblages in floral strips and semi-natural habitats, highlighting the importance of maintaining these “source” habitats, which provide consistent food resources for bees outside of the sunflower blooming season. This effect is particularly relevant in intensive agriculture environments, such as the sunflower landscape in our study. In areas where food resources and refugia are scarce, the presence of floral strips and semi-natural habitats fulfils an crucial role to maintain wild bee diversity (Maccagnani et al., 2020).

Our results show that the range of effects of semi-natural habitats and floral strips on species and functional richness seemed to be limited to the ecotonal strip, while functional redundancy peaked at 15 m. Yet, the Rao index showed homogeneous behavior across the entire extent of fields. Interestingly, this indicator showed consistently higher values for fields adjacent to semi-natural habitats; thus, these remnants are likely better reservoirs of wild bee functional diversity than floral strips. This effect could be the consequence of the greater stability and age of semi-natural fragments, which provide a reliable and relatively diverse reserve of floral resources (Appendix B in Supplementary material) and availability of nesting places. It is possible that the permanence of floral strips eventually generates similar effects over time (years). In any case, our results focusing on sunflower landscapes confirmed the importance of maintaining small habitat patches in highly transformed landscapes, both for conservation purposes (Volenec and Dobson, 2020; Wintle et al., 2019) and for increasing ecological resilience and ecosystem functioning at the landscape scale. This phenomenon was attributed to the dependence of these ecological properties on functional diversity (Gross et al., 2017; Hoehn et al., 2008; Tilman et al., 1997).

We found that the CWM of intertegular distance was higher in semi-natural habitats and adjacent sunflower fields compared with floral strips and adjacent fields. Intertegular

distance is correlated with body mass, tongue length, and foraging distance (Cariveau et al., 2016). Thus, contrarily to our expectations, the results indicate that wild bees are smaller on average when the floral strip is present. It is known that in habitats with abundant flower resources, small bee species may be able to obtain enough pollen-nectar resources within a small foraging radius because their low food requirements (Torné-Noguera et al., 2014). Thus, our results might be explained by our floral strips design (consisting only in a small patch of herbaceous melliferous plants), which might have mostly attracted bee species with smaller intertegular distances. However, due to the larger foraging distances of larger wild bee species (such as bumble bees), future research with long-distance sampling would be required to advance our understanding on the responses of large wild bee species.

Our results also showed that relative wing length tended to be smaller in semi-natural habitats compared to adjacent sunflower fields. If we assume that semi-natural habitats act as the main source of bees, the effect could be a consequence of the relationship between wing length and flying distance, so that larger-winged species are more likely to move into fields. In any case, the size of the effect was small, and it was only significant in the first two distances; thus, this result must be interpreted cautiously, with more research being required.

4.2 What are the implications for the management of sunflower landscapes?

Global concern over the loss of pollinators has led to the design and implementation of innovative agri-environmental measures to mitigate their decline (IPBES, 2016). For example, the European Union has adopted a biodiversity strategy that includes specific targets to promote green infrastructure by member states, including enhancing and maintaining ecosystem services in intensive agricultural landscapes (European

Commission, 2012). The installation of flower strips on the borders of agricultural fields is one such practice, which is intended to provide floral resources that attract enough insect pollinators to fulfil pollination demands in pollinator-dependent crops (Blaauw and Isaacs, 2014a, 2014b).

Our findings might have key implications for the management of intensive agricultural landscapes where pollinator-dependent crops are dominant. In the current context of agricultural intensification, maintaining functionally diverse wild bee communities is critical to ensure adequate pollination (Hevia et al., 2016; Kremen et al., 2002).

Specifically, successful pollination requires a bee community with complementary functional traits associated with foraging and resource use (Martins et al., 2015). Thus, spatial planning and management practices that increase both the abundance of pollinators and the functional diversity of the overall community represent an adequate approach to enhance crop production (Woodcock et al., 2019).

Our results were consistent with previous studies (Bartual et al., 2019) suggesting that the maintenance of semi-natural habitats might have important implications in preserving functionally diverse wild pollinator communities. The presence of floral strips might also be important in landscapes dominated by sunflower fields, which only provide valuable food resources for bees over a brief time period. Yet, our results suggest that floral strips only collect part of the wild bee community existing in semi-natural habitats, and are not that relevant. However, our findings should be taken with caution and applied only to the highly patched landscape predominant in our study area, comprising a matrix of agricultural fields and semi-natural habitats. In order to fully test the effect of floral strips

324 on wild bee diversity, future research is needed in agricultural landscapes where semi-
325 natural habitats are scarce or absent.

326 Further, it should be acknowledged that the floral strips installed in our study area have
327 only been maintained for two years; consequently, their effect on wild bee diversity over
328 time (years) has not been fully evaluated. The relevance of habitat stability over time has
329 been widely recognized as contributing to functional diversity in intensive agricultural
330 landscapes (Le Provost et al., 2020). Thus, future research with long-term sampling is
331 required to advance our knowledge on whether floral strips affect wild bee assemblages in a
332 similar way to semi-natural habitats after several years.

333

5. Conclusions

Our results provide novel evidence about the essential and irreplaceable role of semi-natural habitats within intensive agricultural landscapes and, therefore, the need to preserve them to ensure the conservation of wild bee taxonomic and functional diversity. Nevertheless, the installation of green infrastructure, such as floral strips, adjacent to sunflower fields might offer a partial substitute to enhance the diversity of bee communities in places where semi-natural habitats are scarce or absent.

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References

- Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R., Campbell, A.J., Dainese, M., Drummond, F.A., Entling, M.H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., Jonsson, M., Knop, E., Kremen, C., Landis, D.A., Loeb, G.M., Marini, L., McKerchar, M., Morandin, L., Pfister, S.C., Potts, S.G., Rundlöf, M., Sardiñas, H., Sciligo, A., Thies, C., Tscharnke, T., Venturini, E., Veromann, E., Vollhardt, I.M.G., Wäckers, F., Ward, K., Wilby, A., Woltz, M., Wratten, S., Sutter, L., 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecol. Lett.* 23, 1488–1498. <https://doi.org/10.1111/ele.13576>
- Altieri, M.A., Nicholls, C.I., 2012. *Agroecology Scaling Up for Food Sovereignty and Resiliency*. pp. 1–29. https://doi.org/10.1007/978-94-007-5449-2_1
- Bartomeus, I., Cariveau, D.P., Harrison, T., Winfree, R., 2018. On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. *Oikos* 127, 306–315. <https://doi.org/10.1111/oik.04507>
- Bartual, A.M., Sutter, L., Bocci, G., Moonen, A.C., Cresswell, J., Entling, M., Giffard, B., Jacot, K., Jeanneret, P., Holland, J., Pfister, S., Pintér, O., Veromann, E., Winkler, K., Albrecht, M., 2019. The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. *Agric. Ecosyst. Environ.* 279, 43–52. <https://doi.org/10.1016/j.agee.2019.04.009>
- Benayas, J., Landscapes, J.B.-R.E., 2015, U., 2015. *Rewilding European Landscapes*.

372 oapen.org. <https://doi.org/10.1007/978-3-319-12039-3>

373 Blaauw, B.R., Isaacs, R., 2014a. Flower plantings increase wild bee abundance and the
374 pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.* 51, n/a-
375 n/a. <https://doi.org/10.1111/1365-2664.12257>

376 Blaauw, B.R., Isaacs, R., 2014b. Larger patches of diverse floral resources increase insect
377 pollinator density, diversity, and their pollination of native wildflowers. *Basic Appl.*
378 *Ecol.* <https://doi.org/10.1016/j.baae.2014.10.001>

379 Campbell, A.J., Wilby, A., Sutton, P., Wäckers, F.L., 2017. Do sown flower strips boost
380 wild pollinator abundance and pollination services in a spring-flowering crop? A case
381 study from UK cider apple orchards. *Agric. Ecosyst. Environ.* 239, 20–29.
382 <https://doi.org/10.1016/j.agee.2017.01.005>

383 Cariveau, D.P., Nayak, G.K., Bartomeus, I., Zientek, J., Ascher, J.S., Gibbs, J., Winfree, R.,
384 2016. The Allometry of Bee Proboscis Length and Its Uses in Ecology. *PLoS One* 11,
385 e0151482. <https://doi.org/10.1371/journal.pone.0151482>

386 Carmona, C., De Bello, F., Mason, N.W.H., Lepš, J., 2016. Traits Without Borders:
387 Integrating Functional Diversity Across Scales. 382 *Trends Ecol. Evol.* 31.
388 <https://doi.org/10.1016/j.tree.2016.02.003>

389 Carmona, C.P., Bello, F., Mason, N.W.H., Lepš, J., 2019. Trait probability density (TPD):
390 measuring functional diversity across scales based on TPD with R. *Ecology* 1–8.
391 <https://doi.org/10.1002/ecy.2876>

392 Carmona, C.P., de Bello, F., Mason, N.W.H., Lepš, J., 2016. Traits Without Borders:

393 Integrating Functional Diversity Across Scales. *Trends Ecol. Evol.*
 394 <https://doi.org/10.1016/j.tree.2016.02.003>

395 Carmona, C.P., Guerrero, I., Morales, M.B., Oñate, J.J., Peco, B., 2017. Assessing
 396 vulnerability of functional diversity to species loss: a case study in Mediterranean
 397 agricultural systems. *Funct. Ecol.* 31, 427–435. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2435.12709)
 398 2435.12709

399 Carmona, C.P., Guerrero, I., Peco, B., Morales, M.B., Oñate, J.J., Pärt, T., Tscharnke, T.,
 400 Liira, J., Aavik, T., Emmerson, M., Berendse, F., Ceryngier, P., Bretagnolle, V.,
 401 Weisser, W.W., Bengtsson, J., 2020. Agriculture intensification reduces plant
 402 taxonomic and functional diversity across European arable systems. *Funct. Ecol.* 34,
 403 1448–1460. <https://doi.org/10.1111/1365-2435.13608>

404 de Bello, F., Carmona, C.P., Lepš, J., Szava-Kovats, R., Pärtel, M., 2016. Functional
 405 diversity through the mean trait dissimilarity: resolving shortcomings with existing
 406 paradigms and algorithms. *Oecologia* 180, 933–940. [https://doi.org/10.1007/s00442-](https://doi.org/10.1007/s00442-016-3546-0)
 407 016-3546-0

408 Deguines, N., Jono, C., Baude, M., Henry, M., Julliard, R., Fontaine, C., 2014. Large-scale
 409 trade-off between agricultural intensification and crop pollination services. *Front.*
 410 *Ecol. Environ.* 12, 212–217. <https://doi.org/10.1890/130054>

411 Díaz, S., Cabido, M., 2001. Vive la différence: Plant functional diversity matters to
 412 ecosystem processes. *Trends Ecol. Evol.* [https://doi.org/10.1016/S0169-](https://doi.org/10.1016/S0169-5347(01)02283-2)
 413 5347(01)02283-2

414 Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle,
415 T., Smith, H.G., von Wehrden, H., 2014. Land Sparing Versus Land Sharing: Moving
416 Forward. *Conserv. Lett.* 7, 149–157. <https://doi.org/10.1111/conl.12084>

417 Frund, J., Dormann, C.F., Holzschuh, A., Tschardtke, T., 2013. Bee diversity effects on
418 pollination depend on functional complementarity and niche shifts. *Ecology* 94, 2042–
419 2054. <https://doi.org/10.1890/12-1620.1>

420 Garmendia, E., Apostolopoulou, E., Adams, W.M., Bormpoudakis, D., 2016. Biodiversity
421 and Green Infrastructure in Europe: Boundary object or ecological trap? *Land use*
422 *policy* 56, 315–319. <https://doi.org/10.1016/j.landusepol.2016.04.003>

423 Gathmann, A., Tschardtke, T., 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* 71,
424 757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>

425 Geslin, B., Oddie, M., Folschweiller, M., Legras, G., Seymour, C.L., van Veen, F.J.F.,
426 Thébault, E., 2016. Spatiotemporal changes in flying insect abundance and their
427 functional diversity as a function of distance to natural habitats in a mass flowering
428 crop. *Agric. Ecosyst. Environ.* 229, 21–29. <https://doi.org/10.1016/j.agee.2016.05.010>

429 Goulson, D., 2003. Effects of Introduced Bees on Native Ecosystems. *Annu. Rev. Ecol.*
430 *Evol. Syst.* 34, 1–26. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132355>

431 Gross, N., Bagousse-Pinguet, Y. Le, Liancourt, P., Berdugo, M., Gotelli, N.J., Maestre,
432 F.T., 2017. Functional trait diversity maximizes ecosystem multifunctionality. *Nat.*
433 *Ecol. Evol.* 1, 1–9. <https://doi.org/10.1038/s41559-017-0132>

434 Hall, M.A., Nimmo, D.G., Cunningham, S.A., Walker, K., Bennett, A.F., 2019. The

435 response of wild bees to tree cover and rural land use is mediated by species' traits.
 436 Biol. Conserv. 231, 1–12. <https://doi.org/10.1016/j.biocon.2018.12.032>

437 Hevia, V., Bosch, J., Azcárate, F.M., Fernández, E., Rodrigo, A., Barril-Graells, H.,
 438 González, J.A., 2016. Bee diversity and abundance in a livestock drove road and its
 439 impact on pollination and seed set in adjacent sunflower fields. Agric. Ecosyst.
 440 Environ. 232, 336–344. <https://doi.org/10.1016/j.agee.2016.08.021>

441 Hevia, V., Bosch, J., Azcárate, F.M., Fernández, E., Rodrigo, A., Barril-Graells, H.,
 442 González, J.A., 2016. Bee diversity and abundance in a livestock drove road and its
 443 impact on pollination and seed set in adjacent sunflower fields. Agric. Ecosyst.
 444 Environ. 232. <https://doi.org/10.1016/j.agee.2016.08.021>

445 Hevia, V., Bosch, J., Azcárate, F.M., Fernández, E., Rodrigo, A., Barril-Graells, H.,
 446 González, J.A., 2016. Bee diversity and abundance in a livestock drove road and its
 447 impact on pollination and seed set in adjacent sunflower fields. Agric. Ecosyst.
 448 Environ. 232, 336–344. <https://doi.org/10.1016/J.AGEE.2016.08.021>

449 Hoehn, P., Tscharntke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group
 450 diversity of bee pollinators increases crop yield. Proc. R. Soc. B Biol. Sci. 275, 2283–
 451 2291. <https://doi.org/10.1098/rspb.2008.0405>

452 Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tscharntke, T., 2006. Diversity of flower-
 453 visiting bees in cereal fields: effects of farming system, landscape composition and
 454 regional context. J. Appl. Ecol. 44, 41–49. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2664.2006.01259.x)
 455 2664.2006.01259.x

456 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, I.,
 457 2016. Assessment Report on Pollinators, Pollination and Food Production.
 458 <https://doi.org/10.5281/ZENODO.3402857>

459 Jönsson, A.M., Ekroos, J., Dänhardt, J., Andersson, G.K.S., Olsson, O., Smith, H.G., 2015.
 460 Sown flower strips in southern Sweden increase abundances of wild bees and
 461 hoverflies in the wider landscape. *Biol. Conserv.* 184, 51–58.
 462 <https://doi.org/10.1016/j.biocon.2014.12.027>

463 Jordano, P., 2016. Natural history matters: how biological constraints shape diversified
 464 interactions in pollination networks. *J. Anim. Ecol.* 85, 1423–1426.
 465 <https://doi.org/10.1111/1365-2656.12584>

466 Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R.,
 467 Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalho, L.G., Chacoff,
 468 N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R.,
 469 Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein,
 470 A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A.,
 471 Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki,
 472 H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A
 473 global quantitative synthesis of local and landscape effects on wild bee pollinators in
 474 agroecosystems. *Ecol. Lett.* 16, 584–99. <https://doi.org/10.1111/ele.12082>

475 Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk
 476 from agricultural intensification. *Proc. Natl. Acad. Sci. U. S. A.* 99, 16812–6.
 477 <https://doi.org/10.1073/pnas.262413599>

478 Le Provost, G., Badenhauer, I., Le Bagousse-Pinguet, Y., Clough, Y., Henckel, L.,
 479 Violle, C., Bretagnolle, V., Roncoroni, M., Manning, P., Gross, N., 2020. Land-use
 480 history impacts functional diversity across multiple trophic groups. *Proc. Natl. Acad.*
 481 *Sci. U. S. A.* 117, 1573–1579. <https://doi.org/10.1073/pnas.1910023117>

482 Maccagnani, B., Veromann, E., Ferrari, R., Boriani, L., Boecking, O., 2020.
 483 Agroecosystem design supports the activity of pollinator networks, in:
 484 Entomovectoring for Precision Biocontrol and Enhanced Pollination of Crops.
 485 Springer International Publishing, pp. 1–17. [https://doi.org/10.1007/978-3-030-18917-](https://doi.org/10.1007/978-3-030-18917-4_1)
 486 [4_1](https://doi.org/10.1007/978-3-030-18917-4_1)

487 Martello, F., De Bello, F., De Castro Morini, M.S., Silva, R.R., De Souza-Campana, D.R.,
 488 Ribeiro, M.C., Carmona, C.P., 2018. Homogenization and impoverishment of
 489 taxonomic and functional diversity of ants in Eucalyptus plantations. *Sci. Rep.* 8, 1–
 490 11. <https://doi.org/10.1038/s41598-018-20823-1>

491 Martins, K.T., Gonzalez, A., Lechowicz, M.J., 2015. Pollination services are mediated by
 492 bee functional diversity and landscape context. *Agric. Ecosyst. Environ.* 200, 12–20.
 493 <https://doi.org/10.1016/j.agee.2014.10.018>

494 Mason, N.W.H., de Bello, F., 2013. Functional diversity: a tool for answering challenging
 495 ecological questions. *J. Veg. Sci.* 24, 777–780. <https://doi.org/10.1111/jvs.12097>

496 Micó, E., Ramilo, P., Thorn, S., Müller, J., Galante, E., Carmona, C.P., 2020. Contrasting
 497 functional structure of saproxylic beetle assemblages associated to different
 498 microhabitats. *Sci. Rep.* 10, 10. <https://doi.org/10.1038/s41598-020-58408-6>

499 O'Toole, C., Gauld, I.J., 1993. Diversity of native bees and agroecosystems. Hymenoptera
500 and biodiversity., in: LaSalle, I.J., Gauld, D. (Eds.), CAB Internationalnational.
501 Wallingford, pp. 169–196.

502 Papanikolaou, A.D., Kühn, I., Frenzel, M., Kuhlmann, M., Poschlod, P., Potts, S.G.,
503 Roberts, S.P.M., Schweiger, O., 2017. Wild bee and floral diversity co-vary in
504 response to the direct and indirect impacts of land use. *Ecosphere* 8, e02008.
505 <https://doi.org/10.1002/ecs2.2008>

506 Peters, M.K., Peisker, J., Steffan-Dewenter, I., Hoiss, B., 2016. Morphological traits are
507 linked to the cold performance and distribution of bees along elevational gradients. *J.*
508 *Biogeogr.* 43, 2040–2049. <https://doi.org/10.1111/jbi.12768>

509 Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010.
510 Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–53.
511 <https://doi.org/10.1016/j.tree.2010.01.007>

512 Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., Willmer, P., 2003. Linking bees and
513 flowers: how do floral communities structure pollinator communities? *Ecology* 84,
514 2628–2642. <https://doi.org/10.1890/02-0136>

515 Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., Willmer, P.,
516 2005. Role of nesting resources in organising diverse bee communities in a
517 Mediterranean landscape. *Ecol. Entomol.* 30, 78–85. [https://doi.org/10.1111/j.0307-](https://doi.org/10.1111/j.0307-6946.2005.00662.x)
518 [6946.2005.00662.x](https://doi.org/10.1111/j.0307-6946.2005.00662.x)

519 Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M.,

520 Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleijn,
 521 D., 2015. Local and landscape-level floral resources explain effects of wildflower
 522 strips on wild bees across four European countries. *J. Appl. Ecol.* 52, 1165–1175.
 523 <https://doi.org/10.1111/1365-2664.12479>

524 Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The Influence
 525 of Functional Diversity and Composition on Ecosystem Processes. *Science* (80-.).
 526 277, 1300–1302. <https://doi.org/10.1126/science.277.5330.1300>

527 Torné-Noguera, A., Rodrigo, A., Arnan, X., Osorio, S., Barril-Graells, H., da Rocha-Filho,
 528 L.C., Bosch, J., 2014. Determinants of Spatial Distribution in a Bee Community:
 529 Nesting Resources, Flower Resources, and Body Size. *PLoS One* 9, e97255.
 530 <https://doi.org/10.1371/journal.pone.0097255>

531 Volenec, Z.M., Dobson, A.P., 2020. Conservation value of small reserves. *Conserv. Biol.*
 532 34, 66–79. <https://doi.org/10.1111/cobi.13308>

533 Warzecha, D., Diekötter, T., Wolters, V., Jauker, F., 2016. Intraspecific body size increases
 534 with habitat fragmentation in wild bee pollinators. *Landsc. Ecol.* 31, 1449–1455.
 535 <https://doi.org/10.1007/s10980-016-0349-y>

536 Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts,
 537 S.G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E.,
 538 Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I.,
 539 2008. Measuring bee diversity in different European habitats and biogeographical
 540 regions. *Ecol. Monogr.* 78, 653–671. <https://doi.org/10.1890/07-1292.1>

541 Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L., Potts, S.G., 2010.
 542 Ecological and life-history traits predict bee species responses to environmental
 543 disturbances. *Biol. Conserv.* 143, 2280–2291.
 544 <https://doi.org/10.1016/j.biocon.2010.03.024>

545 Williams, N.M., Kremen, C., 2007. Resource distributions among habitats determine
 546 solitary bee offspring production in a mosaic landscape. *Ecol. Appl.* 17, 910–921.
 547 <https://doi.org/10.1890/06-0269>

548 Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., Aizen, M.A., 2009. A meta-analysis
 549 of bees' responses to anthropogenic disturbance. *Ecology* 90, 2068–2076.
 550 <https://doi.org/10.1890/08-1245.1>

551 Wintle, B.A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen,
 552 A., Gordon, A., Lentini, P.E., Cadenhead, N.C.R., Bekessy, S.A., 2019. Global
 553 synthesis of conservation studies reveals the importance of small habitat patches for
 554 biodiversity. *Proc. Natl. Acad. Sci. U. S. A.* 116, 909–914.
 555 <https://doi.org/10.1073/pnas.1813051115>

556 Wood, T.J., Holland, J.M., Goulson, D., 2017. Providing foraging resources for solitary
 557 bees on farmland: current schemes for pollinators benefit a limited suite of species. *J.*
 558 *Appl. Ecol.* 54, 323–333. <https://doi.org/10.1111/1365-2664.12718>

559 Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J.,
 560 Lindström, S.A.M., Stanley, D., Ouvrard, P., Edwards, M.E., Jauker, F., McCracken,
 561 M.E., Zou, Y., Potts, S.G., Rundlöf, M., Noriega, J.A., Greenop, A., Smith, H.G.,
 562 Bommarco, R., van der Werf, W., Stout, J.C., Steffan-Dewenter, I., Morandin, L.,

563 Bullock, J.M., Pywell, R.F., 2019. Meta-analysis reveals that pollinator functional
564 diversity and abundance enhance crop pollination and yield. *Nat. Commun.* 10, 1–10.
565 <https://doi.org/10.1038/s41467-019-09393-6>

566 Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum
567 foraging ranges in solitary bees: only few individuals have the capability to cover long
568 foraging distances. *Biol. Conserv.* 143, 669–676.
569 <https://doi.org/10.1016/j.biocon.2009.12.003>

570

Highlights:

- Semi-natural habitats act as reservoirs of wild bees in agricultural landscapes
- Floral strips offer a partial substitute to enhance wild bee diversity
- Floral strips and semi-natural habitats enhance wild bee functional diversity
- Maintaining semi-natural habitats is essential in sunflower landscapes

Table 1. List of the functional traits of bees included in the analysis.

Trait	Description	Range
Intertegular distance (ITD)	Distance between the nearest edges of the tegulae (plates covering the wing bases).	7.710-0.518 mm
Wing length (WL)	Length of forewings.	21.323-2.193 mm
Hair length at mesonotus (HL)	Maximum hair length at mesonotus.	2.282-0.031 mm

Table 2. Wild bee species found on the floral strips (FS) and semi-natural habitats (SN); and at 0, 15, 30 and 60 m from both in adjacent sunflower fields.

Species	Fields with flower strip					Fields adjacent to semi-natural habitat				
	Inside FS	0m	15m	30m	60m	Inside SN	0m	15m	30m	60m
<i>Amegilla</i> (<i>Amegilla</i>) <i>quadrifasciata</i>	X	X	X	X		X				X
<i>Andrena</i> (<i>Holandrena</i>) <i>variabilis</i>	X	X				X				
<i>Andrena</i> (<i>Melandrena</i>) <i>albopunctata</i>	X	X		X	X	X	X			
<i>Andrena</i> (<i>Zonandrena</i>) <i>flavipes</i>		X			X	X	X	X	X	
<i>Anthidium</i> (<i>Anthidium</i>) <i>cingulatum</i>						X	X			
<i>Bombus</i> (<i>Bombus</i>) <i>terrestris</i>	X	X		X	X		X			X
<i>Ceratina</i> (<i>Ceratina</i>) <i>cucurbitina</i>	X	X							X	
<i>Ceratina</i> (<i>Euceratina</i>) <i>chalybea</i>		X								
<i>Ceratina</i> (<i>Euceratina</i>) <i>dallatorreana</i>		X					X			
<i>Ceratina</i> (<i>Euceratina</i>) <i>nigrolabiata</i>	X			X						
<i>Colletes eous</i>				X	X					
<i>Colletes nigricans</i>										X
<i>Halictus</i> (<i>Halictus</i>) <i>brunnescens</i>				X						
<i>Halictus</i> (<i>Halictus</i>) <i>crenicornis</i>	X	X	X	X	X	X	X	X	X	X
<i>Halictus</i> (<i>Halictus</i>) <i>quadricinctus</i>	X	X			X	X	X	X	X	X
<i>Halictus</i> (<i>Halictus</i>) <i>scabiosae</i>	X	X			X	X	X	X		X
<i>Halictus</i> (<i>Seladonia</i>) <i>smaragdulus</i>	X	X	X			X	X	X		X
<i>Halictus</i> (<i>Seladonia</i>) <i>subauratus</i>										X
<i>Halictus</i> (<i>Vestitohalictus</i>) <i>vestitus</i>	X		X	X	X	X		X	X	X
<i>Halictus</i> (<i>Seladonia</i>) <i>gemmeus</i>	X	X	X	X	X	X	X	X	X	X
<i>Hoplitis</i> (<i>Anthocopa</i>) <i>cristatula</i>			X			X				
<i>Lasioglossum</i> (<i>Dialictus</i>) <i>morio</i>							X			
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>brevicorne</i>	X	X	X	X	X	X	X	X	X	X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>corvinum</i>	X	X	X	X	X	X	X	X	X	X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>crassepunctatum</i>	X	X	X	X	X	X	X	X	X	X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>glabriusculum</i>	X	X	X	X	X	X	X	X	X	X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>griseolum</i>	X	X	X	X			X			X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>interruptum</i>	X	X	X	X	X	X	X	X	X	X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>malachurum</i>	X	X	X	X	X	X	X	X	X	X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>mediterraneum</i>				X	X	X				
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>pauperatum</i>	X	X	X	X	X	X	X	X	X	X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>pauxillum</i>					X	X				X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>politum</i>						X		X		X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>puncticolle</i>	X	X		X		X				X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>subhirtum</i>	X	X	X	X	X	X		X	X	X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>transitorium</i>	X									
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>truncaticolle</i>						X				X
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>villosulum</i>	X	X	X	X	X	X	X	X	X	X
<i>Lasioglossum</i> (<i>Lasioglossum</i>) <i>albocinctum</i>	X	X			X					X
<i>Lasioglossum</i> (<i>Lasioglossum</i>) <i>discum</i>	X	X	X	X	X	X	X	X	X	X
<i>Megachile</i> (<i>Eutricharaea</i>) <i>cf. concinna</i>	X					X				
<i>Megachile</i> (<i>Eutricharaea</i>) <i>pilidens</i>				X		X	X			
<i>Megachile</i> (<i>Eutricharaea</i>) <i>sp.</i>	X								X	
<i>Sphecodes alternatus</i>				X						
<i>Tetraloniella</i> (<i>Tetraloniella</i>) <i>julliani</i>				X		X			X	
<i>Xylocopa iris</i>		X				X		X	X	

Figure captions

Figure 1. Location map of the study area showing sampling sites located on sunflower fields adjacent to semi-natural habitats (blue points; photograph A) and on sunflower fields with floral strips installed (green points; photograph B).

Figure 2. Schematic representation of the sampling design in sunflower fields with floral strips (A), and plots on sunflower fields adjacent to semi-natural habitats (B).

Figure 3. Boxplots showing the effect of floral strips (FS) and semi-natural habitats (SN) on species richness (a) and functional richness (b) for the five sampling levels. Bars represent the mean \pm standard error of the mean. Different letters indicate significant differences ($P < 0.05$).

Figure 4. Boxplots showing the effect of floral strips (FS) and semi-natural habitats (SN) on functional redundancy (a) and Rao index (b) for the five sampling levels. Bars represent the mean \pm standard error of the mean. Different letters indicate significant differences ($P < 0.05$).

Figure 5. Boxplots showing the effect of floral strips (FS) and semi-natural habitats (SN) on the community-weighted mean (CWM) of intertegular distance (a), CWM of wing length (b), and CWM of hair length (c) for the five sampling levels. Bars represent the mean \pm standard error of the mean. Different letters indicate significant differences ($P < 0.05$).

Figure 1

[Click here to access/download;Figure;Fig.1.jpg](#)

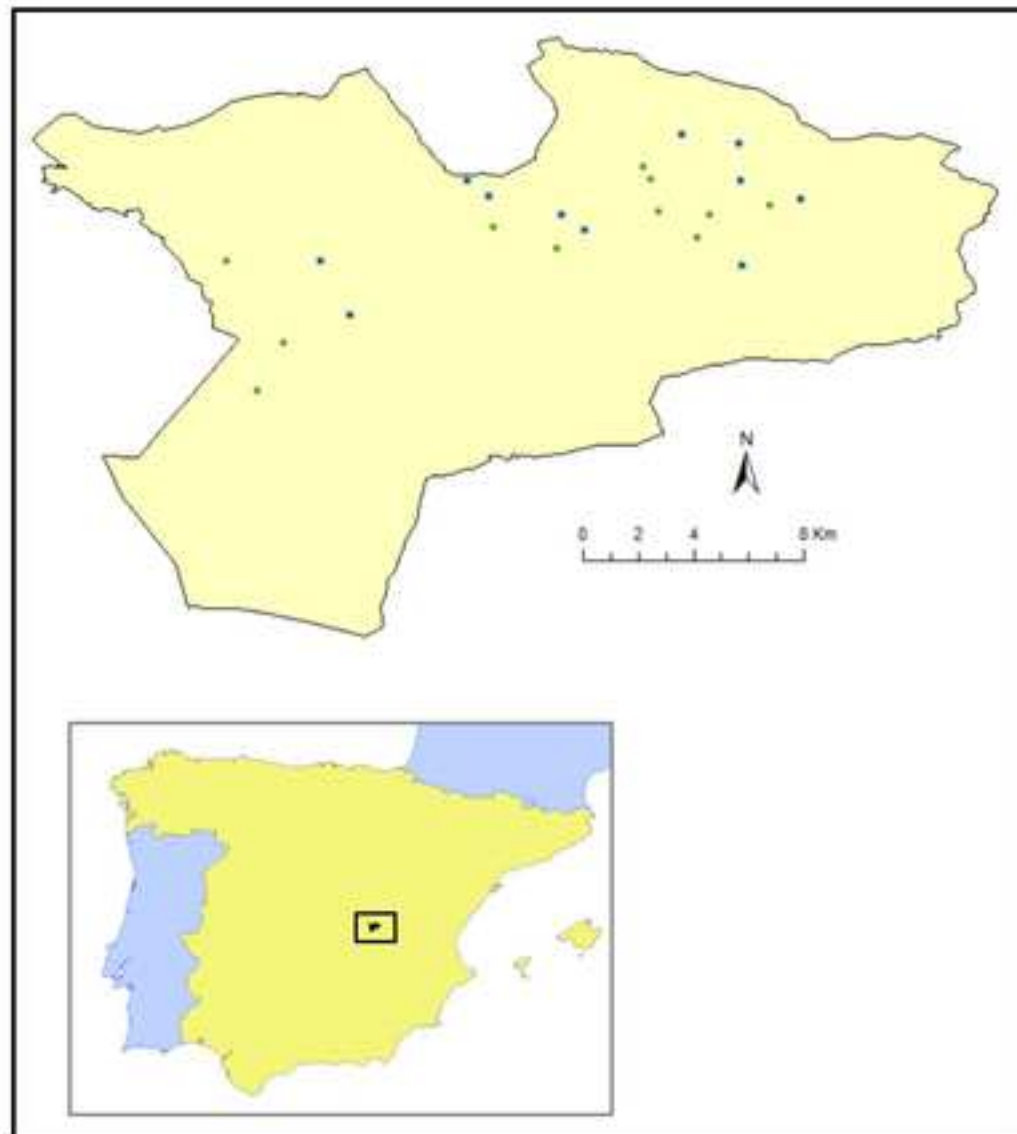
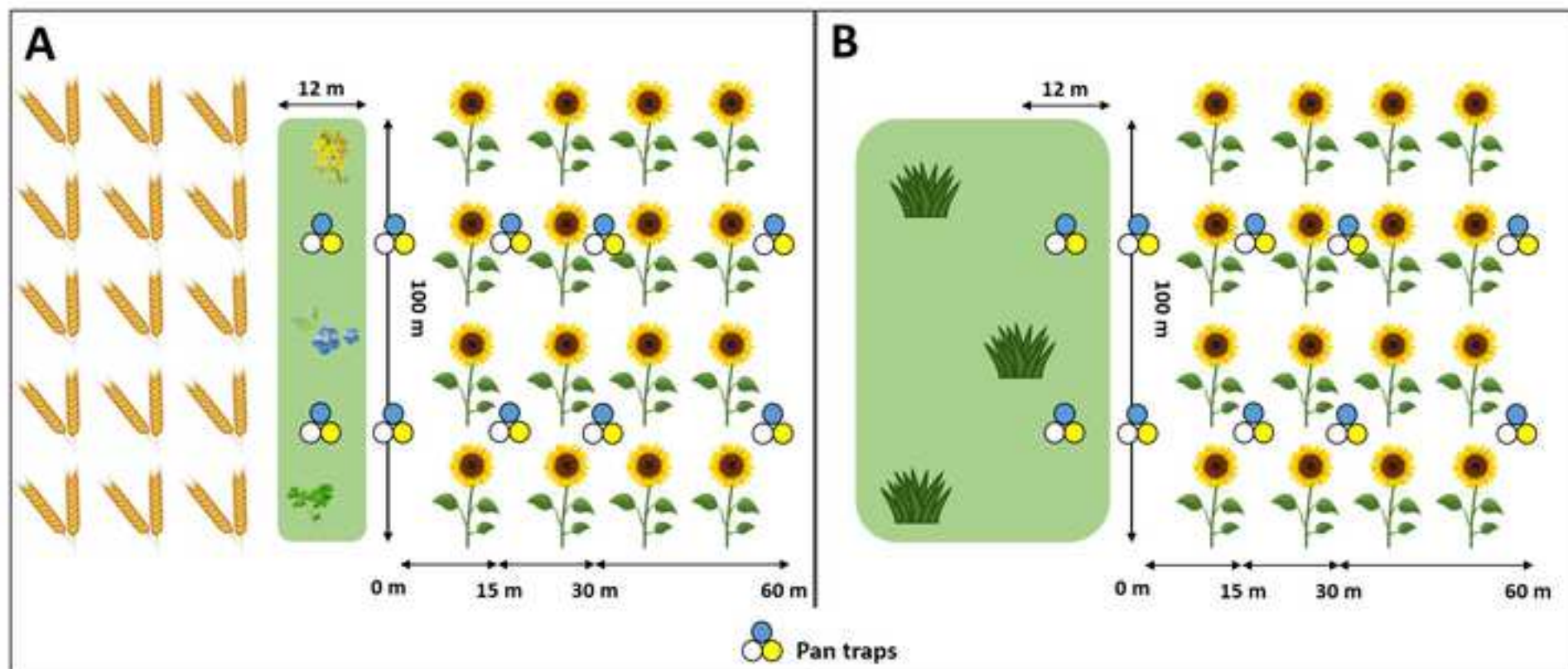


Figure 2

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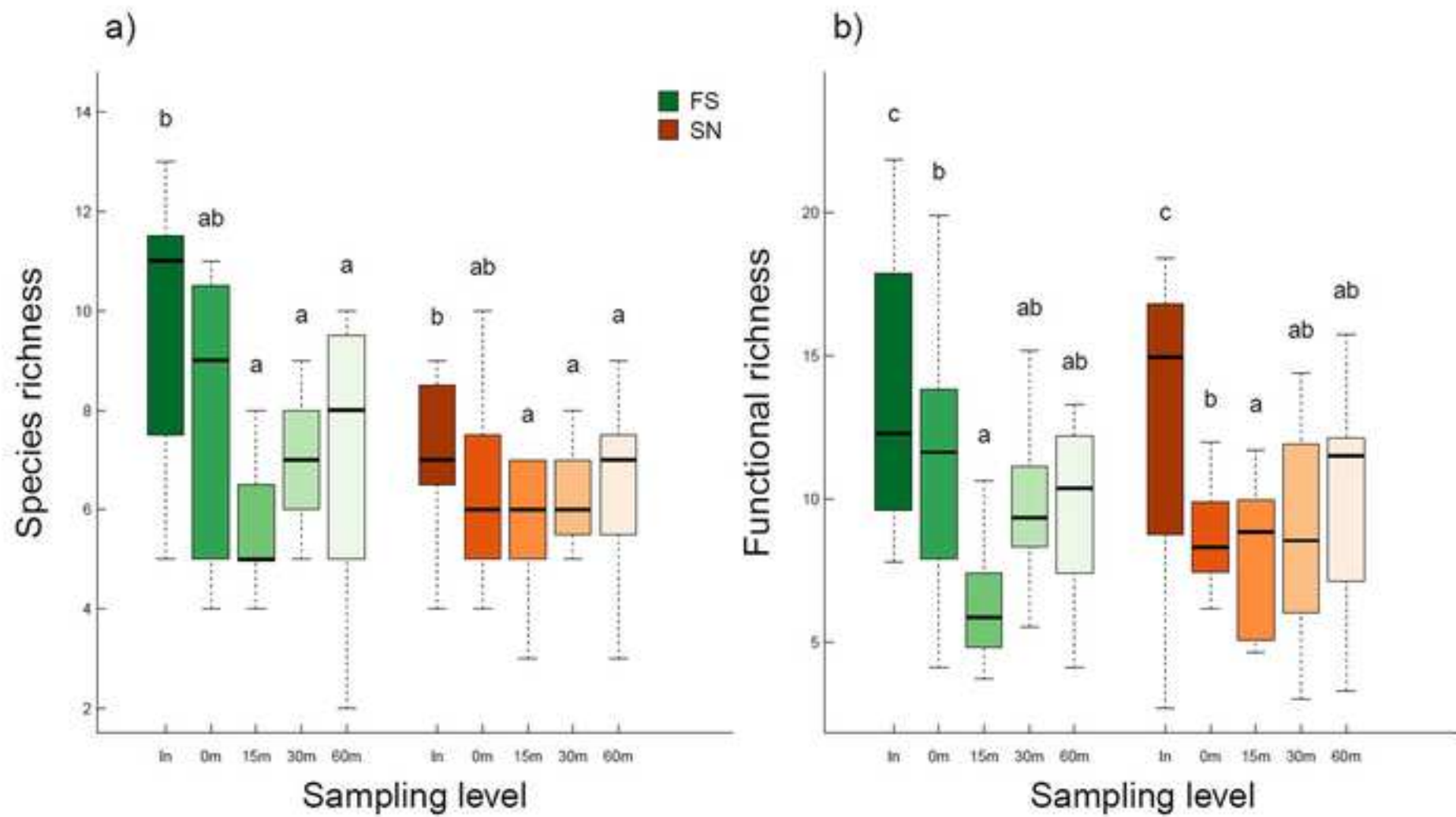


Figure 4

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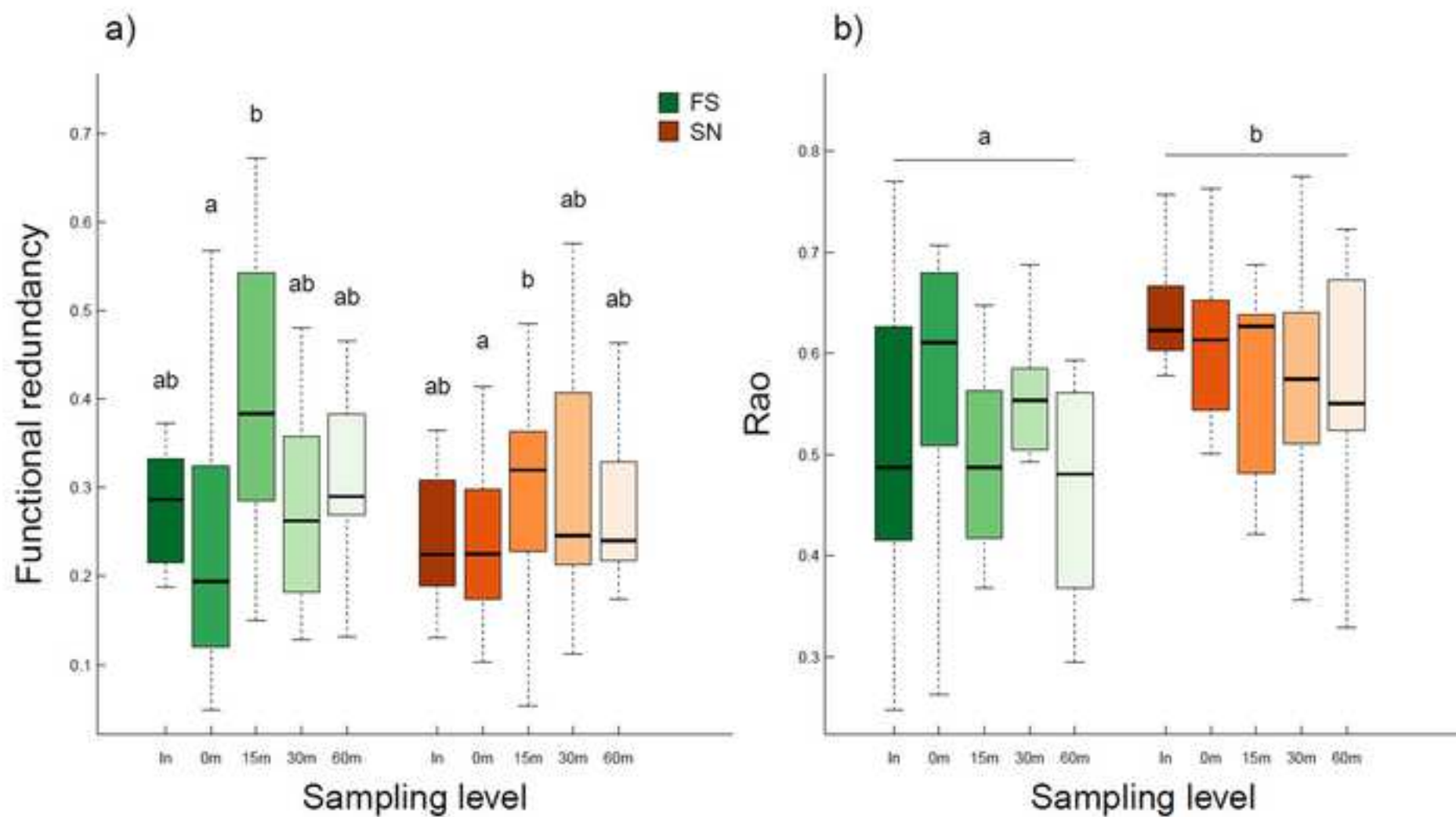
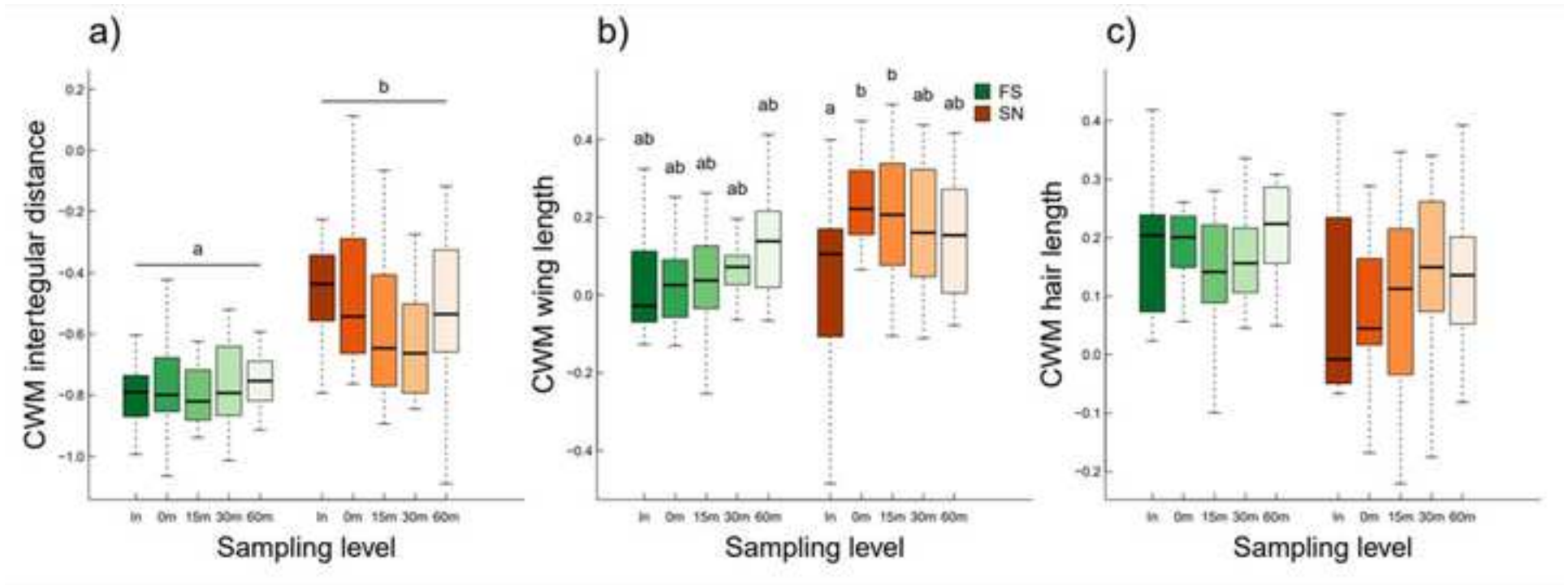


Figure 5



Appendix A

List of the melliferous species of herbaceous plants sown in the floral strips.

Species	Family	Flowering season	Flower color
<i>Borago officinalis</i> L.	Boraginaceae	May-September	Blue
<i>Calendula arvensis</i> L.	Asteraceae	June- September	Yellow
<i>Coriandrum sativum</i> L.	Apiaceae	May-June	White
<i>Salvia pratensis</i>	Lamiaceae (Labiatae)	May-August	Blue-violet
<i>Melilotus officinalis</i>	Fabaceae	April- September	White/yellow
<i>Diplotaxis erucoides</i>	Brassicaceae	January-December	White
<i>Echium plantagineum</i>	Boraginaceae	February-July	Violet
<i>Silene vulgaris</i>	Caryophyllaceae	April-June	White
<i>Vicia sativa</i>	Fabaceae (Leguminosae)	March-June	Purple
<i>Nigella damascena</i>	Ranunculaceae	April-June	Numerous
<i>Sinapis alba</i> L.	Cruciferae	March-May	Yellow
<i>Medicago sativa</i> L.	Fabaceae	May-September	Violet

Appendix B

List of the most common species present in the semi-natural habitats adjacent to sunflower fields.

Species	Family	Flowering season	Flower color
<i>Alyssum serpyllifolium</i> Desf.	Brassicaceae	April-July	Yellow
<i>Argyrolobium zanonii</i> (Turra) P. W. Ball	Fabaceae	April-July	Yellow
<i>Bupleurum fruticosum</i> L.	Umbelliferae	May-October	Yellow
<i>Catananche caerulea</i> L.	Asteraceae	May-June	Blue / Purple
<i>Centaurium quadrifolium</i>	Gentianaceae	April-August	Pink / Purple
<i>Cephalaria leucantha</i> (L.) Roemer & Schultes	Dipsacaceae	July-October	White / Yellow
<i>Coris monspeliensis</i> L.	Primulaceae	April-July	Pink / Purple
<i>Coronilla minima</i> L.	Fabaceae	March-July	Yellow
<i>Dorycnium pentaphyllum</i> L.	Fabaceae	April-July	White / Pink
<i>Euphorbia nicaensis</i> All	Euphorbiaceae	May-August	Green / Yellow
<i>Fumana ericoides</i> (Cav.) Gand. In Magnier	Cistaceae	March-August	Yellow
<i>Fumana procumbens</i> (Dunal) Gren. & Godr.	Cistaceae	June-August	Yellow
<i>Genista scorpius</i> L.	Fabaceae	March-July	Yellow
<i>Helianthemum asperum</i> Lag. ex Dunal	Cistaceae	March-June	White
<i>Helianthemum cinereum</i> (Cav.) Pers.	Cistaceae	April-June	Yellow
<i>Helichrysum stoechas</i> (L.) Moench	Asteraceae	April-August	Yellow
<i>Hippocrepis commutata</i> Pau	Fabaceae	March-July	Yellow
<i>Lavandula latifolia</i> Medik.	Labiatae	June-November	Purple
<i>Linum suffruticosum</i> L.	Linaceae	May-July	White
<i>Linum narbonense</i> L.	Linaceae	May-June	Blue
<i>Lithodora fruticosa</i> (L.) Griseb.	Boraginaceae	February-July	Blue / Purple
<i>Ononis spinosa</i> L.	Fabaceae	April-September	White / Pink
<i>Phlomis herba-venti</i> L.	Labiatae	March-June	Pink / Purple
<i>Phlomis lychnitis</i> L.	Labiatae	March-August	Yellow
<i>Polygala rupestris</i> Pourret	Polygalaceae	February-August	Pink / Purple
<i>Quercus coccifera</i> L.	Fagaceae	March-June	(unconspicuous)
<i>Rhamnus alaternus</i> L.	Rhamnaceae	January-April	Yellow
<i>Rhaponticum coniferum</i> (L.) Greuter	Asteraceae	May-July	Pink / Purple
<i>Santolina chamaecyparissus</i> L.	Asteraceae	February-August	Yellow
<i>Salvia lavandulifolia</i> Vahl	Labiatae	May-July	Pink / Blue / Purple
<i>Sideritis hirsuta</i> L.	Labiatae	March-October	White
<i>Sideritis incana</i> L.	Labiatae	April-August	Yellow
<i>Stachelina dubia</i> L.	Asteraceae	May-August	Pink / Purple
<i>Stipa atlantica</i> P.A. Smirn.	Poaceae	April-July	(unconspicuous)
<i>Teucrium capitatum</i> L.	Labiatae	March-August	White
<i>Teucrium chamaedrys</i> L.	Labiatae	March-September	Purple
<i>Teucrium polium</i> L.	Labiatae	June-July	White
<i>Teucrium pseudochamaepitys</i> L.	Labiatae	March-August	White / Pink
<i>Thymus lacaitae</i> Pau	Labiatae	May-July	White

<i>Thymus vulgaris</i> L.	Labiatae	March-August	White / Pink /Purple
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Appendix C

List of sunflower varieties cultivated on the study fields.

Euralis ES ARTIC

Koipesol Napoli

Koipesol Oleko

Koipesol Subaro

Koipesol SY Arco

Maisadour MAS 87.OL High Oleic

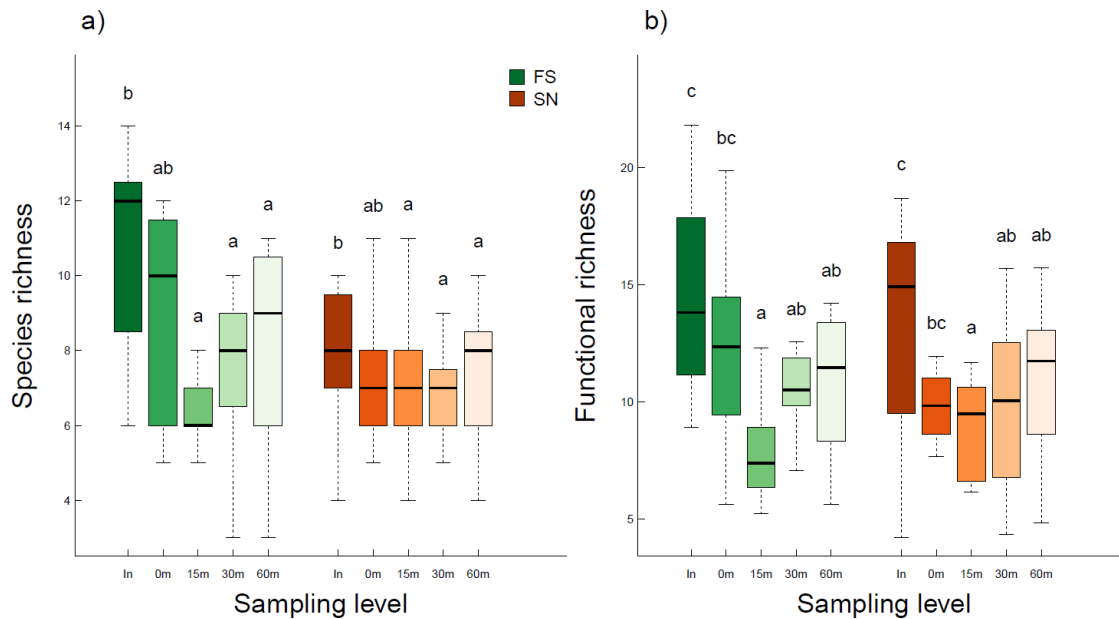
Pioneer P64LE19

Pioneer P64HE118 High Oleic

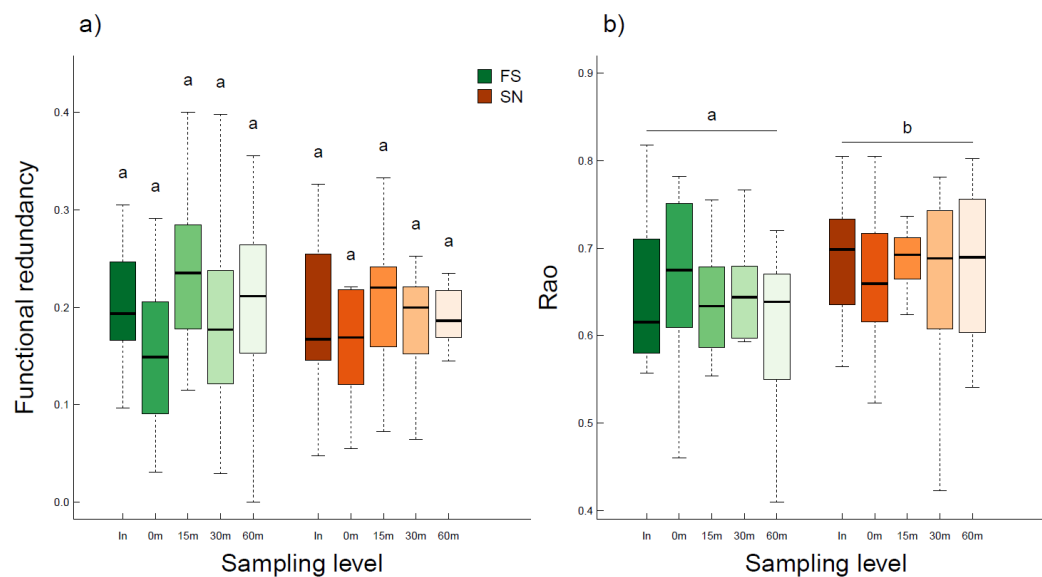
Romy

Appendix D

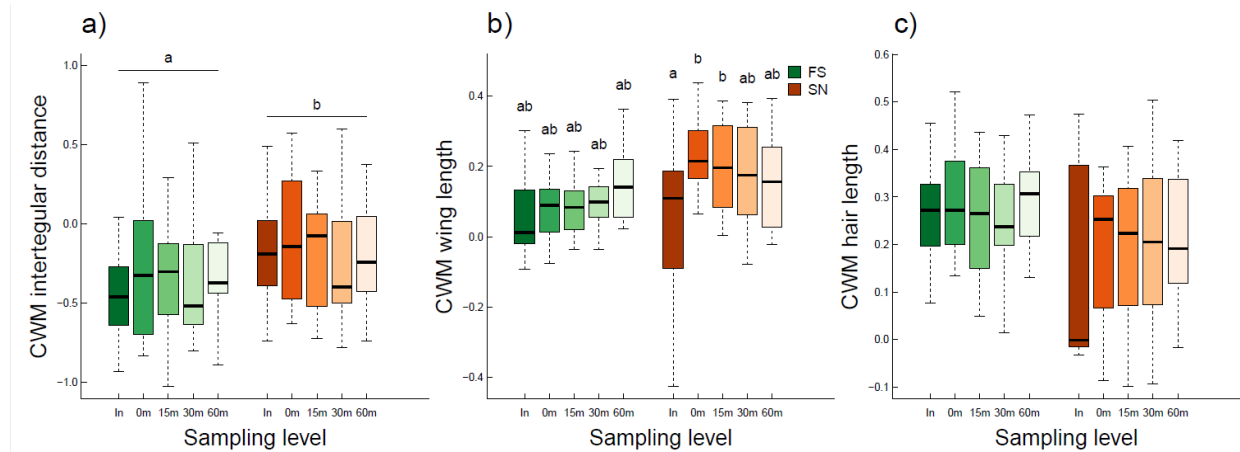
Boxplots showing the effect of floral strips (FS) and semi-natural habitats (SN) on species richness (a) and functional richness (b) for the five sampling levels, incorporating the *Apis mellifera* data. Bars represent the mean \pm standard error of the mean. Different letters indicate significant differences ($P < 0.05$).



Boxplots showing the effect of floral strips (FS) and semi-natural habitats (SN) on functional redundancy (a) and Rao index (b) for the five sampling levels, incorporating the *Apis mellifera* data. Bars represent the mean \pm standard error of the mean. Different letters indicate significant differences ($P < 0.05$).



Boxplots showing the effect of floral strips (FS) and semi-natural habitats (SN) on the community-weighted mean (CWM) of intertegular distance (a), CWM of wing length (b), and CWM of hair length (c) for the five sampling levels, incorporating the *Apis mellifera* data. Bars represent the mean \pm standard error of the mean. Different letters indicate significant differences ($P < 0.05$).



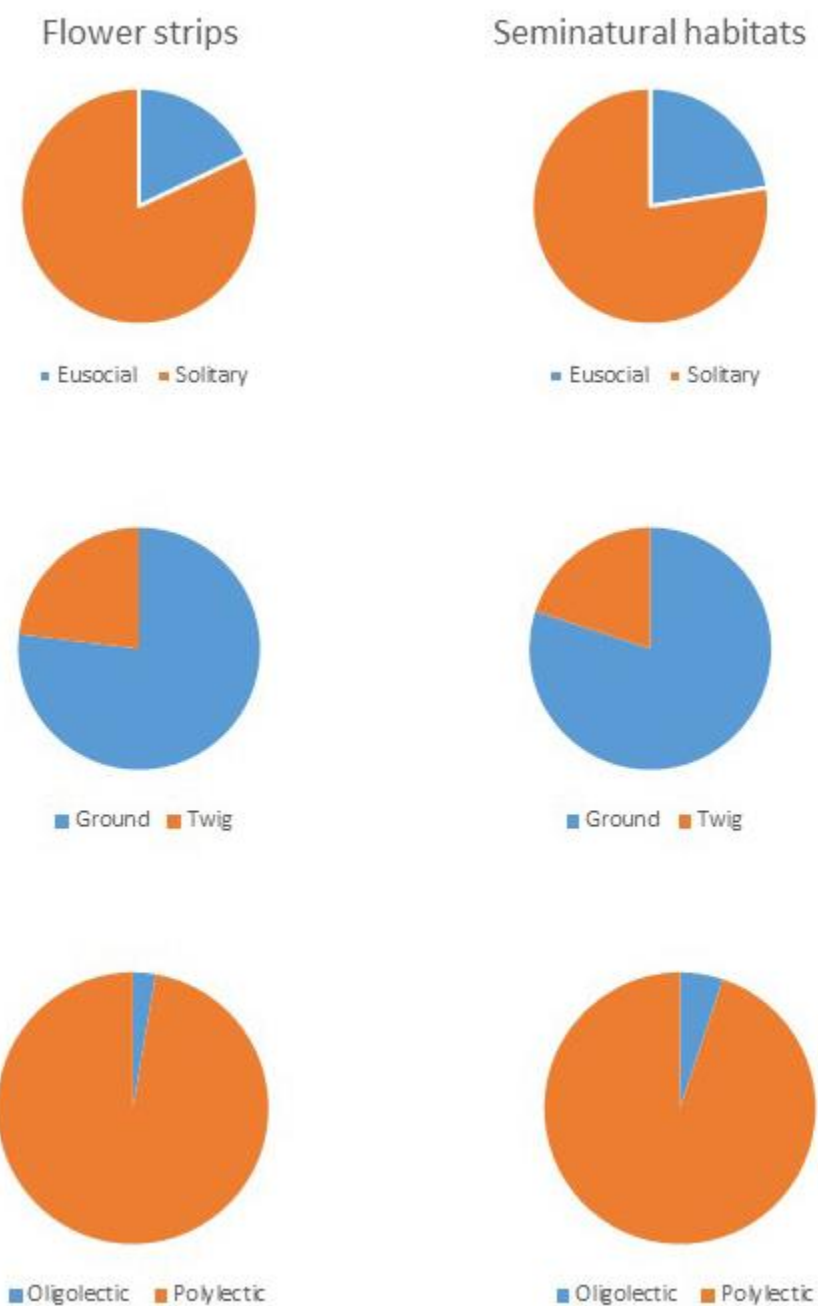
Appendix E

Characteristics of sociality, nest location (ground or above-ground) and foraging specialization (polylectic versus oligolectic) of wild bee species sampled.

Species	Social / Solitary	Ground nesting / Twig nesting	Polylectic / Oligolectic
<i>Amegilla</i> (<i>Amegilla</i>) <i>quadrifasciata</i>	Solitary	Ground	Polylectic
<i>Andrena</i> (<i>Holandrena</i>) <i>variabialis</i>	Solitary	Ground	Polylectic
<i>Andrena</i> (<i>Melandrena</i>) <i>albopunctata</i>	Solitary	Ground	Polylectic
<i>Andrena</i> (<i>Zonandrena</i>) <i>flavipes</i>	Solitary	Ground	Polylectic
<i>Anthidium</i> (<i>Anthidium</i>) <i>cingulatum</i>	Solitary	Twigs-cavities	Oligolectic
<i>Bombus</i> (<i>Bombus</i>) <i>terrestris</i>	Social	Ground	Polylectic
<i>Ceratina</i> (<i>Ceratina</i>) <i>cucurbitina</i>	Solitary	Twigs	Polylectic
<i>Ceratina</i> (<i>Euceratina</i>) <i>chalybea</i>	Solitary	Twigs	Polylectic
<i>Ceratina</i> (<i>Euceratina</i>) <i>dallatorreana</i>	Solitary	Twigs	Polylectic
<i>Ceratina</i> (<i>Euceratina</i>) <i>nigrolabiata</i>	Solitary	Twigs	Polylectic
<i>Colletes eous</i>	Solitary	Ground	NA
<i>Colletes nigricans</i>	Solitary	Ground	Polylectic
<i>Halictus</i> (<i>Halictus</i>) <i>brunnescens</i>	Solitary	Ground	Polylectic
<i>Halictus</i> (<i>Halictus</i>) <i>crenicornis</i>	Solitary	Ground	Polylectic
<i>Halictus</i> (<i>Halictus</i>) <i>quadricinctus</i>	Eusocial	Ground	Polylectic
<i>Halictus</i> (<i>Halictus</i>) <i>scabiosae</i>	Eusocial	Ground	Polylectic
<i>Halictus</i> (<i>Seladonia</i>) <i>smaragdulus</i>	Solitary	Ground	Polylectic
<i>Halictus</i> (<i>Seladonia</i>) <i>subauratus</i>	Eusocial	Ground	Polylectic
<i>Halictus</i> (<i>Vestitohalictus</i>) <i>vestitus</i>	Solitary	Ground	Polylectic
<i>Halictus</i> _(<i>Seladonia</i>) <i>gemmeus</i>	Solitary	Ground	Polylectic
<i>Hoplitis</i> (<i>Anthocopa</i>) <i>cristatula</i>	Solitary	Twigs	Polylectic
<i>Lasioglossum</i> (<i>Dialictus</i>) <i>morio</i>	Solitary	Ground	Polylectic
<i>Lasioglossum</i> (<i>Evylaeus</i>) <i>brevicorne</i>	Solitary	Ground	Polylectic

<i>Lasioglossum(Evylaeus) corvinum</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Evylaeus) crassepunctatum</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Evylaeus) glabriusculum</i>	Eusocial	Ground	Polylectic
<i>Lasioglossum(Evylaeus) griseolum</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Evylaeus) interruptum</i>	Eusocial	Ground	Polylectic
<i>Lasioglossum(Evylaeus) malachurum</i>	Eusocial	Ground	Polylectic
<i>Lasioglossum(Evylaeus) mediterraneum</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Evylaeus) pauperatum</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Evylaeus) pauxillum</i>	Eusocial	Ground	Polylectic
<i>Lasioglossum(Evylaeus) politum</i>	Eusocial	Ground	Polylectic
<i>Lasioglossum(Evylaeus) puncticolle</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Evylaeus) subhirtum</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Evylaeus) transitorium</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Evylaeus) truncaticolle</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Evylaeus) villosulum</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Lasioglossum) albocinctum</i>	Solitary	Ground	Polylectic
<i>Lasioglossum(Lasioglossum) discum</i>	Solitary	Ground	Polylectic
<i>Megachile(Eutricharaea) cf. concinna</i>	Solitary	Twigs	Polylectic
<i>Megachile(Eutricharaea) pilidens</i>	Solitary	Twigs	Oligolectic
<i>Megachile(Eutricharaea) sp.</i>	Solitary	Twigs	Polylectic
<i>Sphecodes alternatus</i>	Solitary	Ground	Polylectic
<i>Tetraloniella(Tetraloniella) julliani</i>	Solitary	Ground	NA
<i>Xylocopa iris</i>	Solitary	Twigs	Polylectic

Percentage of wild bee species recorded in flower strips and semi-natural habitats, according to their sociality, nest location preference (ground or above-ground) and foraging specialization (polylectic versus oligolectic).



Appendix F

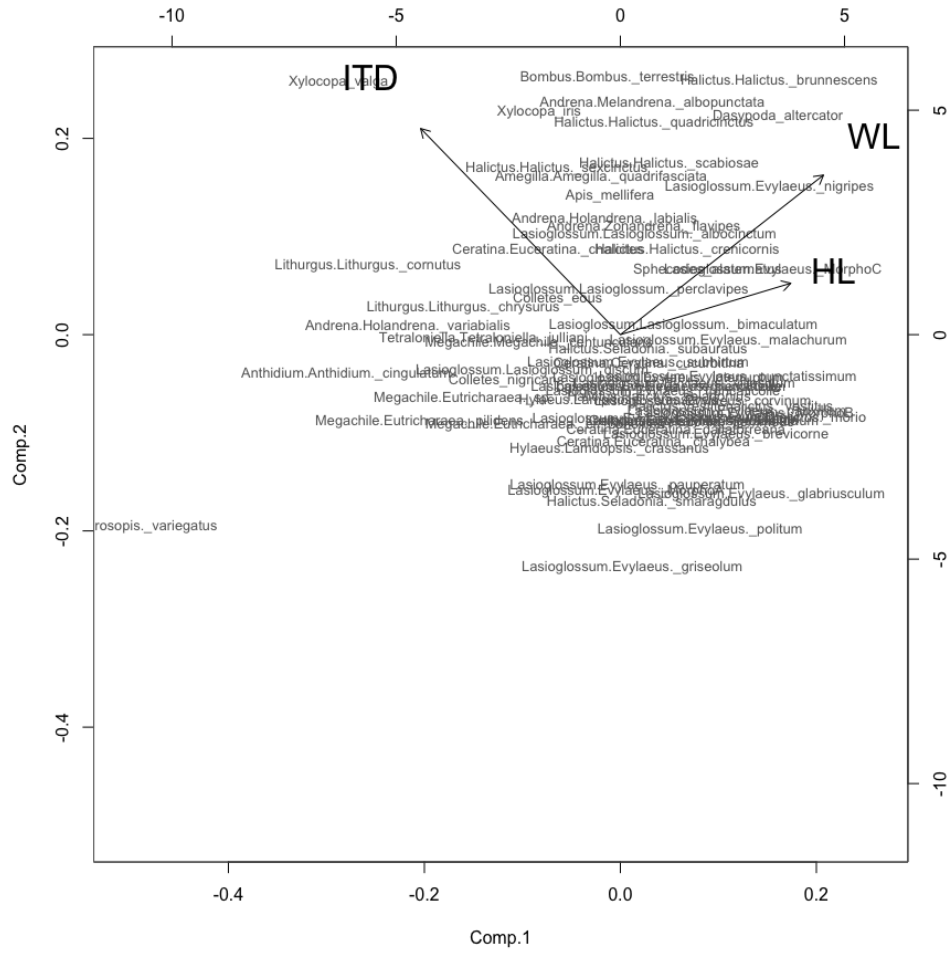
Results of the PCA based on the average trait values of each species

Loadings:

	Comp.1	Comp.2	Comp.3
WL	0.612	0.601	0.515
HL	0.513	0.194	-0.836
ITD	-0.602	0.776	-0.190

Importance of components:

	Comp.1	Comp.2	Comp.3
Standard deviation	1.1481609	0.9178109	0.7938896
Proportion of Variance	0.4723452	0.3018286	0.2258261
Cumulative Proportion	0.4723452	0.7741739	1.0000000



Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: