



Effect of land-use intensity and adjacent semi-natural habitats on wild and honey bees of meadows

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Abstract – Most terrestrial ecosystems are shaped by the pollination service provided by insects, foremost bees. As bees are also important pollinators of crop plants, they are key for both the pollination of wild plants and for agricultural production. Meadows and semi-natural habitats (SNHs) are important habitats for bees. However, there is limited knowledge on how land-use intensity of meadows affects wild bees and managed Western honey bees. Further, it is unknown whether SNHs adjacent to meadows affect bees in meadows. Here, we examined in a landscape dominated by grasslands, the effects of land-use intensity (nitrogen input, grazing intensity, mowing frequency), flower availability and adjacent SNHs on bee communities in meadows. We recorded more than 5000 individuals of 87 species of bees and found no effect of land-use intensity on wild and honey bees. Flowering plant species richness had a positive effect on bee species richness in one study year. Though we recorded more bee species in SNHs than meadows, overall and specifically in ecologically specialized bee species (e.g. parasitic bees, oligoleges), the availability of adjacent SNHs did not affect bee abundance and richness in meadows. We discuss why land-use intensity and SNHs adjacent to meadows did not affect bees in meadows and conclude that SNHs are important in sustaining functionally diverse bee communities in landscapes dominated by grasslands.

biodiversity / grassland / land-use intensity / meadows / semi-natural habitats / wild and honey bees

1. INTRODUCTION

Most angiosperms are pollinated by insects (Ollerton et al. 2011), and insect pollination is a main factor shaping terrestrial ecosystems. Given that insects also pollinate various crop plants (Klein et al. 2007), insect pollination additionally has an enormous economic value, estimated to €153 billion per year (Gallai et al. 2009). Bees are the most dominant pollinators of both crop (Klein et al. 2007) and non-crop (Ollerton 2017) plants. There is evidence of regional mass losses

in managed *Apis mellifera* (Western honey bee) and declines in wild bee abundance and species richness (Potts et al. 2010), with negative implications for agricultural production (Bartomeus et al. 2014; Blaauw and Isaacs 2014; Stein et al. 2017) and the functioning of terrestrial ecosystems (Biesmeijer et al. 2006).

Bees need appropriate nesting sites and host plants in close proximity (Gathmann and Tschardt 2002; Kreyer et al. 2004; Zurbuchen and Müller 2012). In the temperate zone, semi-natural habitats (SNH) and agricultural areas (Mandelik et al. 2012; Westrich 2018; Zurbuchen and Müller 2012) fulfilled these criteria and harboured a high number of species until mid of the twentieth century. Traditional extensive

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and manifold land use by subsistence farmers produced a small-scale and diverse landscape over most countries of Central Europe, offering suitable habitats with continuous flower supply and nesting sites for many bee species. For more than 100 years, but increasingly in the last 50 years, specialization, intensification and industrialisation of agriculture have taken place (Dallimer et al. 2009). As a result, field sizes and the amounts of applied agrochemicals (e.g. pesticides, inorganic fertiliser) have increased. Additionally, semi-natural habitats such as field margins, waysides, hedgerows and structured forest edges have been destroyed to a large extent, as machines grew bigger and land-use diversity and crop diversity declined (D'Aquino et al. 2002; Matson et al. 1997). This finally resulted in parallel declines of plants (Wesche et al. 2012) and bee species richness and abundance (Biesmeijer et al. 2006; Le Féon et al. 2010; Zattara and Aizen 2021).

Agricultural intensification not only affected arable land but also grassland, an important habitat of bees (Westrich 2018). The intensified management of grassland was mostly associated with the introduction of silage production or artificial hay drying and took place in many areas that were not suitable for intensive crop production (Oenema et al. 2014). In grassland areas of Central Europe, intensification resulted in an increase in mowing frequency, from mostly two cuttings per year to four to six or even more cuttings, and an increase in nitrogen fertilisation (Isselstein et al. 2005), both mainly with the aim to harvest protein-rich young grass for maximizing milk production (Kuoppala et al. 2008). Also, wet soils were drained, and stocking rates were increased (Isselstein et al. 2005). This intensification in grassland management shifted species-rich grassland to highly productive meadows and pastures (Isselstein et al. 2005), accompanied by large losses in plant species richness (Isselstein et al. 2005; Wesche et al. 2012). Interestingly, losses were especially evident in insect-pollinated herbs (Wesche et al. 2012), many of which are used as food sources by bees.

Intensification in grassland management can be expected to also affect bee communities

(especially flower specialists, i.e. oligoleges; Westrich 2018). Indeed, bee species richness was shown to be higher in less intensively managed meadows (Meyer et al. 2017; Weiner et al. 2011), though such effects were sometimes only evident at regional and not at site-specific scales (Ekroos et al. 2020; van Klink et al. 2019), and only for some but not other bee groups (Kimoto et al. 2012). Similarly, bee abundance and alpha diversity were sometimes shown to be independent of land-use intensity (Weiner et al. 2011), but other studies found them to be affected by management intensity (Kimoto et al. 2012). Some of these variations in the research outcomes might be due to methodological differences among the studies, such as whether to include the Western honey bee (Weiner et al. 2011), which has other ecological requirements than wild bees (Sørensen et al. 2020), or to exclude it (Ekroos et al. 2020; Kimoto et al. 2012). Another reason may be that the different studies considered different management factors (e.g. nitrogen input by Ekroos et al. 2020; grazing intensity by Kimoto et al. 2012). Mowing frequency, grazing intensity and nitrogen input are the most important management factors in grasslands (Blüthgen et al. 2012); however, the combined effects of these factors on bees (e.g. community composition) in grasslands are not well understood (Allan et al. 2014; De Palma et al. 2015).

Though it is known (based on studies in arable crops) that SNHs have positive effects on bee abundance and diversity (e.g. Millard et al. 2021; Raderschall et al. 2021; Aguilera et al. 2020), there is limited knowledge about the effect of adjacent SNHs on bees in grasslands at local scale (Papanikolaou et al. 2017). Though grasslands provide, at least temporarily, food sources for bees (e.g. in meadows before mowing events), bees might rely on semi-natural habitats (SNHs) for foraging, especially after mowing and grazing when no or only a small number of plant species with flowers are available on meadows and pastures, respectively. Also, given that highly productive grasslands do typically not provide nesting sites for both below and above-ground nesting

bees (Westrich 2018), including parasitic species, bees foraging in grasslands might depend on SNHs for nesting.

Here, we tested in a landscape dominated by grasslands the effects of land-use intensity, flower supply and flower species richness, as well as availability of SNHs on abundance, species richness and composition of bee communities in grasslands, and whether wild and honey bees respond differently to these factors. We hypothesize that (i) an increase in land-use intensity has a negative impact on bee abundance and species richness, while (ii) flower density, flower species richness and adjacent semi-natural habitats have a positive influence on bee abundance and species richness in grasslands; (iii) different bee species (wild bees, honey bee) respond differently to management intensity and flower supply; thus, management intensity also affects bee community composition, and (iv) grasslands harbour only a subset of the species found at semi-natural habitats.

2. MATERIAL AND METHODS

2.1. Study sites

The study was conducted in the alpine foothills of Austria, the Mondseerland in Upper Austria, in 2017 and 2018. In this region, precipitation is between 1100 and 1600 mm per year (DORIS 2023; Pils 1994), clayey soils are widespread (BFW 2019), and with very few exceptions, meadows have been drained several decades ago. In the last 50 years, mixed production systems of arable fields (cereals) and grasslands were replaced by increasingly intensive grassland farming. We sampled 23 meadows, of which six (Online Resource I) had an adjacent semi-natural habitat (SNH), whereas the others were embedded in other meadows. The SNHs were three sun-exposed shrubby forest edges, a sparsely overgrown site with about 60% plant coverage, a ruderal area and an unpaved road with areas free of vegetation, thus, habitats known to be of high value (as foraging and/or nesting sites) to bees (Westrich 2018). The six

SNHs and their adjacent meadows were sampled only in 2018. From the remaining 17 meadows, six were sampled in both years and eleven were sampled only in 2017 (Online Resource I).

3. SAMPLING AND IDENTIFICATION OF BEES

Each meadow/SNH was visited three times per year, the meadows before mowing events, from April to September. The SNHs were sampled on the same days as the adjacent meadows. The protocol of sampling varied among years and/or habitat types (Online Resource II). In 2017, bees were sampled (independent of the size of the meadow) at each survey for 2 h following a targeted netting approach. In 2018, bees were collected in the meadows along transects of a length of 90 m, for 1 h per survey. Bees within 1.5 m to each side of a transect were considered. In meadows with adjacent SNH, bees were not surveyed in a 30-m-wide buffer zone between the meadow and SNH, and the transects were placed at a 90° angle to the border of the meadows, from the SNHs in the direction of the centres of the meadows. In meadows without SNH, a similar buffer zone to neighbouring grasslands was established, also to avoid possible border effects. Similar to the meadows in 2018, the SNHs were also sampled for 1 h. Given that most of the SNHs had a size of just a few square meters to 30 m², it was not possible to fit a transect of 90 m; thus, the SNHs were sampled for 1 h per survey by the targeted netting approach.

Independent of the approach used, bees were collected via sweep netting or identified to species level in the field (primarily *Bombus* spp and *Apis mellifera*). Collected bees were identified in the lab using various identification keys (Amiet 1996; Amiet et al. 1999, 2001a, b, 2007, 2010; Bogusch and Straka 2012; Ebmer 1969, 1970, 1971, 1973; Gokcezade et al. 2015; Mauss 1987; Scheuchl 1995, 2006; Schmid-Egger and Scheuchl 1997; Straka and Bogusch 2011). Information on the biology and ecology of bees (see Results) is based on Scheuchl and Willner (2016) and Westrich (2018).

4. PLANT DIVERSITY MEASURE

In addition to the bee surveys, we recorded the flowering of non-grass plant species and estimated flower coverage in the meadows three times per year, at the same time as the bee surveys. In 2017, these data were recorded as a measure for a whole meadow, and in 2018, for the sampled transects only. Plant species were determined using established determination literature (Schmeil and Fitschen 2011).

5. CALCULATION OF LAND USE INTENSITY INDEX

For all 23 meadows, we gathered information about mowing, grazing and fertilisation (for meadows used both in 2017 and 2018, land use did not change between), and calculated the land-use intensity index developed by Blüthgen et al. (2012) for grasslands as $L_i' = \sqrt{\frac{F_i}{F_r} + \frac{M_i}{M_r} + \frac{G_i}{G_r}}$. Meadows were mown (M_i) between one and five times per year (mean, 3), and eleven of the 23 meadows were additionally grazed by cattle. Grazing intensity (G_i) ranged from 108 to 1080 livestock unit days/(ha × year) (mean, 423) (Online Resource I). Ungrazed meadows were on average mown three times and grazed meadows two times. With two exceptions, all meadows were fertilised (F_i), by an application of 16 kg nitrogen/ (ha × year) to 340 kg nitrogen/ (ha × year) (mean, 114).

6. STATISTICS

For each sampling year separately (because of the difference in sampling methods between years), we used linear mixed models (function lme in library nlme) in R version 4.3.1 (R Core team 2023), with meadow identity as a random effect, to test for effects of SNH presence (only 2018), Li', mean flower coverage and flowering plant species richness on species richness of bees, abundance of honey bees and on abundance of wild bees. All variables were log-transformed

except flowering plant species richness, which was square root-transformed. Fitting bee abundance as a covariate in the species richness models did not change the results, and this variable was not further used in the models. To test for effects of SNH presence (only 2018), Li', mean flower coverage and flowering plant species richness on bee community composition we ran, again separately for the 2 study years but pooled across sampling dates within 1 year, PerMANOVAs (permutational analysis of variance, based on pairwise Bray–Curtis dissimilarities on abundances of bees, 9999 permutations) using R, and graphically displayed the results in non-metric multidimensional scaling plots using PRIMER (Clarke and Gorley 2006).

7. RESULTS

During the 2 study years, 5374 bee individuals of 87 species were recorded, from which 66% of the individuals were honey bees, 17% were bumblebees and 17% were other wild bees of 17 genera. The most species-rich genera were *Andrena* (19 species), followed by *Bombus* (14), *Lasioglossum* (13), *Nomada* (10) and *Sphecodes* (6) (Online Resource III). Overall, 75% of the recorded bee species were nest-building bees and 25% were parasitic bees. Among the 65 nest-building bee species were 11 (17%) oligoleges (Online Resource III).

8. EFFECT OF LAND-USE INTENSITY AND ADJACENT SEMI-NATURAL HABITATS ON BEES IN MEADOWS

In neither of the study years, land-use intensity, the presence of an SNH next to the meadow and mean flower coverage had effects on bee species richness and abundance of wild and honey bees in meadows (Online Resource IV, Figure 1). The species richness of flowering plants had positive effects on the species richness of bees in one of the study years (Online Resource IV), but neither on honey

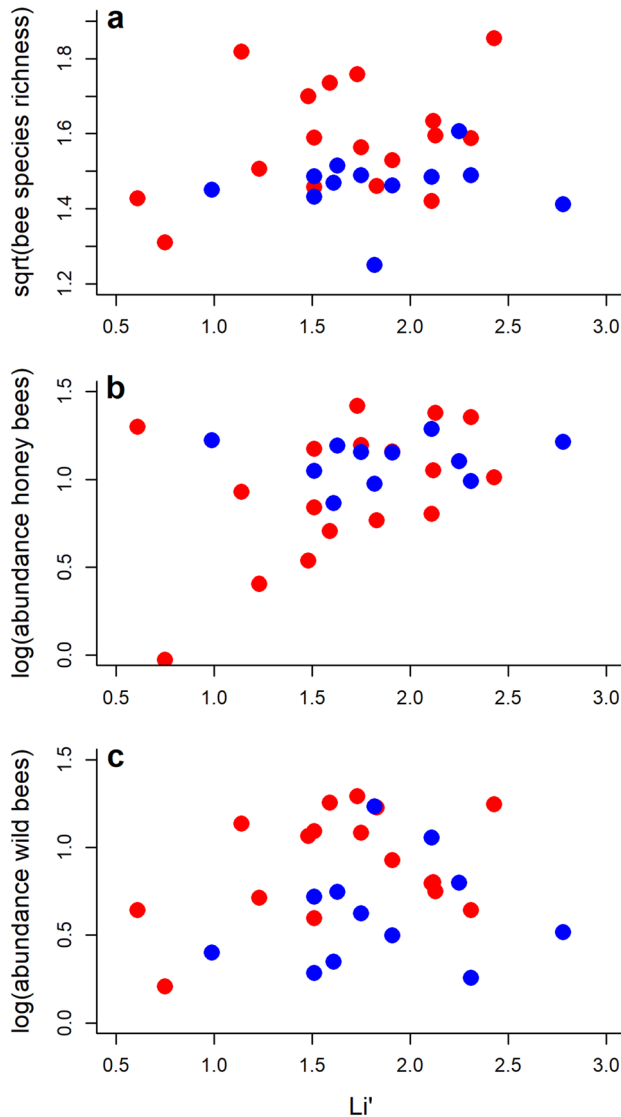


Figure 1. Relationship between land-use intensity (Li') and species richness of bees (a), abundance of honey bees (b), and abundance of wild bees (c). Data are presented (and were analysed) separately for the two study years (2017, red; 2018, blue). For graphical display, bee data were pooled among the three surveys per meadow and year. Land-use intensity did not explain any of the bee data according to linear mixed models ($p > 0.05$ each).

nor wild bee abundances in any of the years (Online Resource IV). We found no effects of land-use intensity (Figure 2), the presence of SNHs (data only for 2018), flower coverage or flowering plant species richness on bee community composition in meadows (Online Resource V).

9. BEES IN MEADOWS AND SEMI-NATURAL HABITATS (SNHS)

In total, we observed 739 and 1034 individuals of honey and wild bees in the six SNHs and the adjacent meadows, respectively. In the SNHs,

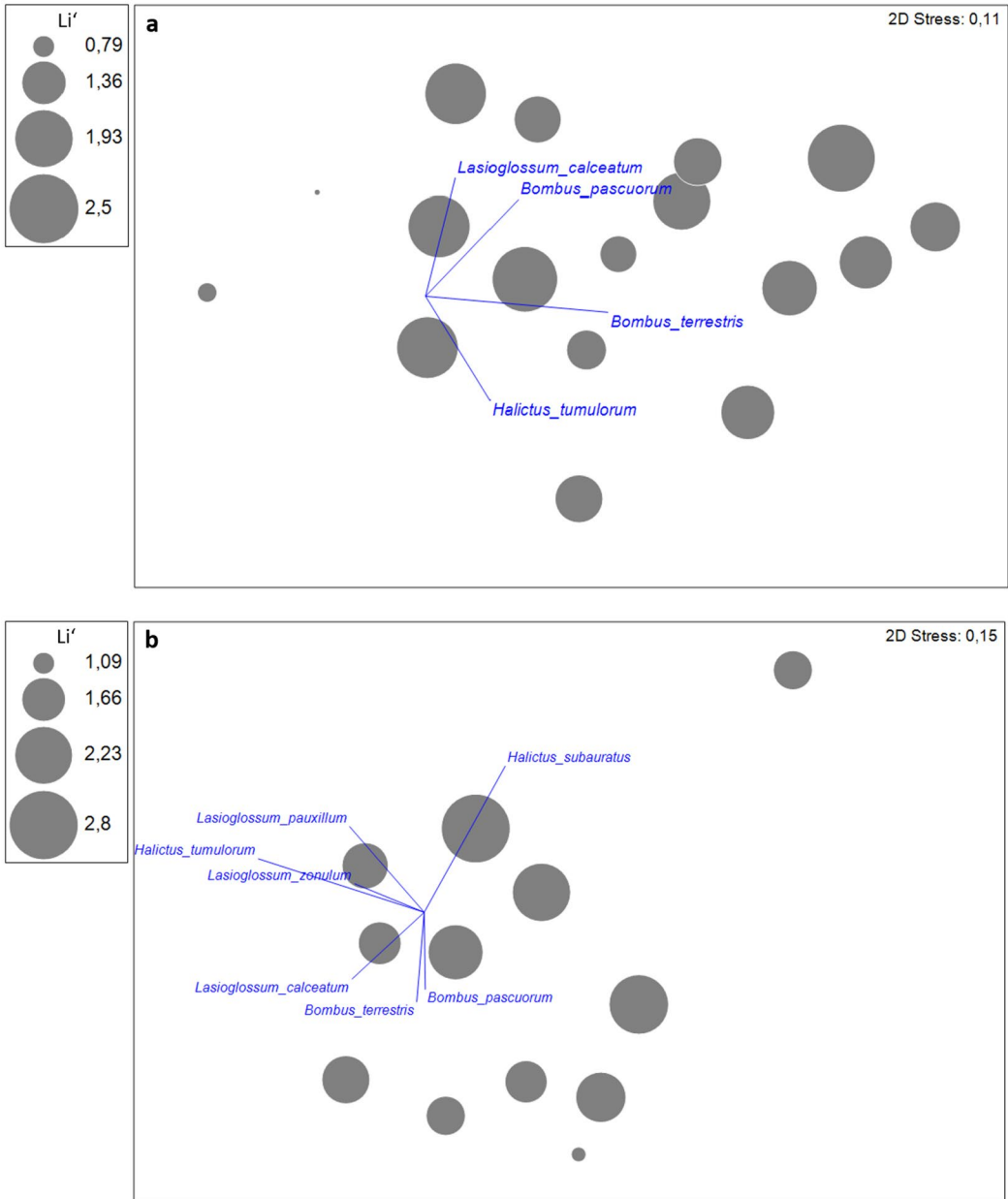


Figure 2. Non-metric multidimensional scaling based on pairwise Bray–Curtis dissimilarity matrices of wild bee communities of the studied meadows in 2017 (a) and 2018 (b). The symbols for the meadows vary in size according to their land-use intensity (Li'), i.e., the larger the symbol the higher the land-use intensity. The vectors represent bee species that correlated best ($r > 0.3$) with the axes.

40% (293) of the observed bees were wild bees, whereas in the meadows, only 19% (200) of the observed bees were wild bees.

In the six SNHs and their adjacent meadows, we recorded overall 57 bee species, thereof 49 in the SNHs and 27 in the meadows (Figure 3, Online Resource III). Thirty species were exclusively detected in the SNHs, eight species were exclusively recorded in the meadows adjacent to the SNHs, and 19 species occurred overall both in the six SNHs and the six meadows adjacent to the SNHs (Figure 3, Online Resource III). The SNHs hosted in the median 15 species, the meadows 10. On

average, about two-thirds (62%) of the bee species observed in a specific meadow were also found in the adjacent SNH, whereas only 39% of the bees recorded in a specific SNH were also found in the adjacent meadow.

Of the nest-building bees, 18 species were found in both SNHs and adjacent meadows, 17 only in SNHs, and seven only in meadows (Online Resource III). Among the parasitic bee species, only one each was found in meadows only (*Nomada sexfasciata*) and in both, SNHs and meadows (*Sphecodes monilicornis*), whereas most species (13; e.g. *Nomada bifasciata*, *N. flava*, *N. moeschleri*, *Sphecodes puncticeps*,

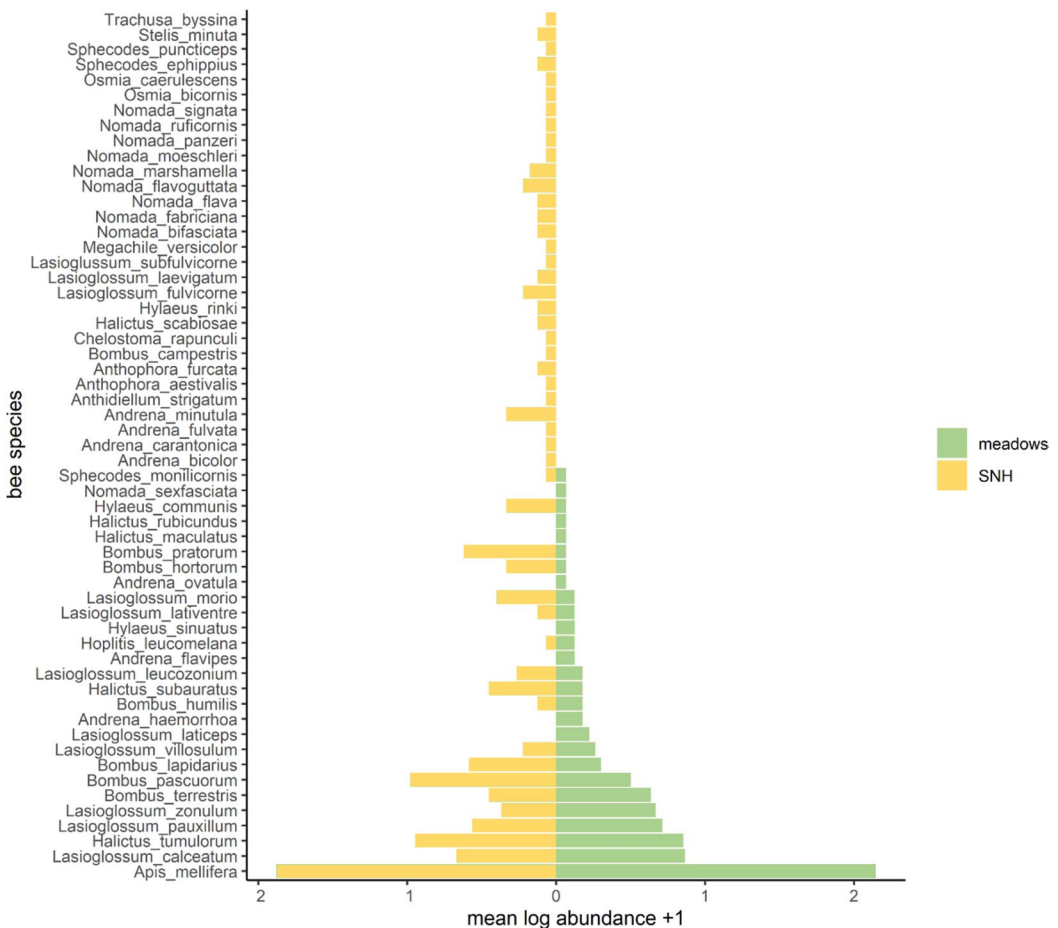


Figure 3. The Bi-bar plot of the log-transformed mean abundances of recorded bee species in the six semi-natural habitats (SNHs) and their adjacent meadows. Species were sorted according to their mean abundances in meadows, whereas SNH-specific bee species were sorted alphabetically.

Stelis minuta) were exclusively recorded in SNHs.

Oligoleges were all only recorded in SNHs (Online Resource III): *Anthophora furcata* (specialized on Lamiaceae), *Chelostoma rapunculi* (specialized on *Campanula*), and *Trachusa byssina* (specialized on Fabaceae).

10. DISCUSSION

In our study, we recorded more than 5000 individuals of 87 species of bees and did not find effects of land-use intensity, the presence/absence of adjacent semi-natural habitats (SNHs) and flower coverage on wild and honey bee abundances, bee community composition, and species richness of wild bees in meadows. Similarly, the species richness of flowering plants had no effects on wild and honey bee abundances and bee community composition. However, species richness of flowering plants had a positive effect on bee species richness. We found relatively more wild bees than honey bees in SNHs than in meadows adjacent to SNHs and recorded more bee species in SNHs than in meadows. Most pronounced differences were observed in parasitic bees and oligoleges: most parasites and all oligoleges were SNH-specific.

Our finding that wild bees in grasslands were not affected by an increasing land-use intensity was surprising, given that other studies found that wild bees are more species rich in extensively managed meadows (Ekroos et al. 2020; Weiner et al. 2011) and in less intensively mown urban lawns (Lerman et al. 2018) than in intensively managed grasslands. In grasslands, wild bee species richness mainly depends on flowering plant species richness and flower supply (Blaauw and Isaacs 2014; Blüthgen et al. 2012; Ollerton 2017; Sutter et al. 2017), which, in our study showed no relationships with land-use intensity (Schlager et al., unpubl. Data). We did not find a relationship between flower supply and bees but detected a positive influence of flowering plant species richness on bee species richness in 1 year. Anyhow, due to the missing relationship between land-use intensity and

flower supply, it seems plausible that wild bees were largely independent of land-use intensity in our study. Kruse et al. (2016) studied plant communities of meadows and pastures on drained clayey soils in Central Europe, similar to the soils in our study (BFW 2019), and also found that management is not a major driver of plant species richness. Instead, plant species richness was mainly explained by soil properties, with most species-rich sites having dry sandy or wet soils. In our study region, dry meadows are rare because of high precipitation and soil conditions, whereas wet meadows are rare due to drainage and mainly persisted in protected grasslands around bogs and lakes (Pils 1994). In the long term, the rarity of plant species-rich habitats is suspected to result in species-poor seedbanks (Kruse et al. 2016), and in consequence, management extensification does not necessarily have positive effects on plant communities, as also suggested in our study. A second reason why meadows and pastures with low Li' were not more plant species rich than more intensely used grasslands might be nitrogen import via the atmosphere (Engardt et al. 2017; Fowler et al. 2015), that is ca. 20 kg/h/a in our study region (Zechmeister et al. 2016). This input influences the nitrogen balance especially in nutrient-poor habitats. Another reason, why bees did not profit from low land-use intensity, besides the species richness of food resources, might be that grasslands do not provide appropriate nesting sites for many bee species. Indeed, nesting sites are often found in SNHs (Kennedy et al. 2013; Rivers-Moore et al. 2020, see also below), which is also suggested by our data. Except for two species, we recorded all parasitic bee species in SNHs only, likely because they were looking for host bee species that built their nests in these habitats.

We were surprised that the meadows with adjacent SNHs did not have a higher species richness and abundance of bees or a different bee community composition than meadows without adjacent meadows. One reason why the SNHs did not influence bees in meadows might have been their size. The SNHs were very small (maximum 30 m²) and probably too small to have measurable effects on the large

meadows. While almost two-thirds of the bee species recorded in meadows were also recorded in adjacent semi-natural habitats, the majority of the SNH bees could not be found in adjacent meadows. For many bees that occur in SNHs, meadows likely do not provide appropriate resources, and the species-rich bee communities in SNHs thus seem to have only limited effects on bee communities in adjacent meadows. In contrast, bees in meadows are dependent on the SNHs as food sources. Especially after mowing, meadows are practically devoid of resources for bees, and in cases in which meadows in specific regions are mown simultaneously, bees cannot use other meadows. Thus, in a landscape dominated by grasslands, as in our study area, bees using meadows as foraging sites will then depend on nearby semi-natural habitats for foraging. When the first flowers are showing up again after mowing, bees might remigrate into the meadows. Overall, the management of meadows likely results in a push-and-pull effect driving bee distribution in meadows and adjacent SNHs, but further studies in this direction are needed to confirm this hypothesis.

Our finding that SNHs are more species rich than grasslands is consistent with other studies (Duelli and Obrist 2003; Rivers-Moore et al. 2020). In agreement with literature (Westrich 2018) is also that especially generalist species were recorded at both the six SNHs and their adjacent meadows (e.g. *Apis mellifera*, all non-parasitic *Bombus* species, *Halictus tumulorum*, *Lasioglossum calceatum*) or only at the adjacent meadows (e.g. *Andrena haemorrhoa*, *Lasioglossum laticeps*). In contrast, the vast majority of parasitic bee species (e.g. *Nomada* spp., *Sphecodes* spp., *Stelis minuta*), that depend on nests of specific host bees, and oligolectic species, that depend on a specific subset of flowering plants (e.g. *Campanula*, Lamiaceae), were only found at the SNHs. Meadows rarely provide appropriate nesting sites for bees, given that they are densely covered with vegetation and do not provide, e.g. sparsely overgrown areas, (cavities in) dead wood, appropriate plant shoots or empty shells of snails, making SNHs, which often have such structures, important nesting

sites for nest-building bees, and in consequence also for parasitic bees (Bihaly et al. 2021). Similarly, as meadows typically have fewer flowering plant species than SNHs (Cranmer et al. 2012; Lindborg and Eriksson 2004; Pykäkä et al. 2005), oligolectic bees are dependent on SNHs as foraging sites (Forrest et al. 2015; Westrich 2018).

The few flowering plant species occurring in meadows, such as *Taraxacum officinale* or *Trifolium repens*, are often characterized by mass flowering, making these habitats highly attractive to honey bees and possibly contributing to a lower proportion of wild bees in meadows than SNHs. Wild bees might avoid foraging in such meadows to avoid competition for nectar and pollen with honey bees (Angelella et al. 2021; Herbertsson et al. 2016). Overall, SNHs are highly important habitats for bees in landscapes dominated by agriculturally used grasslands from an ecological point of view, and also for conservation purposes, given that oligolectic and parasitic bees are among the most threatened bee species (e.g. Voith et al. 2021).

11. CONCLUSIONS

To conclude, we found only minor effects of changes in land-use intensity on bee communities, which might have to do with the landscape dominated by grassland and edaphic factors in the study area, both of which possibly limit the potential positive effects of extensification on flowering plant communities. In addition, the magnitude of change in land-use intensity might have been too small to result in measurable effects on bee communities. Indeed, preliminary data of an ongoing study suggest that a strong reduction in land-use intensity (abandonment of fertilisation; mowing only once per year) has positive effects on bee species richness and abundance in our study region (Neumayer, Schlager et al., unpubl. data; see also Meyer et al. 2017; Weiner et al. 2011). Semi-natural habitats, which have become rare in the last few decades in the study region, as is generally true across most of Europe (European Environmental

Agency 2021; Krauss et al. 2010; Mihók et al. 2017), were overall more species rich than meadows and, thus, may be playing a highly important role in sustaining diverse bee communities even though our design could not detect it statistically. A further loss of SNHs in the landscape could still result in a loss of bee diversity, given that they provide habitats for various species (e.g. parasitic bees and oligoleges) that do not find appropriate resources in meadows. On the contrary, if SNHs are abundantly available, land-use extensification in meadows is expected to have positive effects on wild bee communities, given the higher availability of wild bees and seeds in the landscape, likely increasing plant and bee species richness in meadows in the long term (Carrié et al. 2017; Duelli and Obrist 2003).

SUPPLEMENTARY INFORMATION

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AUTHOR CONTRIBUTION

SD and JN conceived and conceptualized the study. MS collected the data, analysed them together with JP and SD, and wrote the first draft of the manuscript. All authors contributed to the final manuscript and approved the submitted version.

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DATA AVAILABILITY

All data generated or analysed during this study are included in this published article and its supplementary information files.

CODE AVAILABILITY

Not applicable.

DECLARATIONS

Ethics approval This study was performed in line with the principles of the Declaration of Helsinki.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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