Changes in the wild bee community (Apoidea: Hymenoptera) over 100 years in relation to land use: A case study in a protected steppe habitat in Eastern Austria

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Abstract

The wild bee community of a sand steppe habitat in Eastern Austria was surveyed in the years 2018 and 2019, complemented with historical data from over 100 years, and analyzed in relation to land use change. The mapping of land use categories was based on historical aerial photographs and orthophotos. Changes in bee community composition were analyzed by a multivariate statistical approach and took ecological traits into account. In total, 310 bee species were recorded in the area, with the oldest records dating back to 1882. The bee species composition differed significantly among four defined timespans. Across the two most intensively sampled time periods (1931–1966 vs. 2001–2021), a decline in species richness of more than 50% was observed. We observed a disproportionately high decline of steppe and sand-associated species, and a distinct shift from ground nesting species to above ground nesting species. The area covered with woods increased from 1966 to 2018, while the total area covered with grassland and fallows decreased slightly between 1966 and 1994. The oligolectic species assemblage was specialized on Dipsacaceae, Brassicaceae and Fabaceae in the two earlier periods, and on Asteraceae and specifically on Carduoideae during the two later ones. Implications for insect conservation: Our results indicate that the shift from grazing to mowing as land management is a major factor in the decline of species diversity in the studied nature reserve and its surrounding. Particular attention should be given to measures that facilitate the re-establishment of steppe species.

Introduction

Wild bees are among the most important pollinators of insect-pollinated wild and cultivated plants (Klein et al. 2007; Ollerton et al. 2011). Their protection and successful conservation are of paramount importance to ensure human well-being (Vanbergen et al. 2013) and biodiversity of organisms in other trophic levels (Potts et al. 2010). The close and often highly specialized relationships between bees and plants also imply a risk of cascading extinctions with severe consequences for the resilience of ecosystem functions (Potts et al. 2010; Vanbergen et al. 2013; IPBES 2016).

Habitat destruction, fragmentation, and degradation, along with land use change and intensive land management practices have been identified as main drivers of pollinator decline on a global scale (Goulson et al. 2015; IPBES 2016; Sánchez-Bayo and Wyckhuys 2019). In Europe, natural and semi-natural grasslands, which had traditionally been used for livestock grazing a century ago, have been subject to a dramatic loss in area since then (Dengler et al. 2014), with a reduction of the area to less than one fifth since 1960 in Austria (1960: 289.809ha, 2020: 53.171ha; Grüner Bericht 2022). Especially natural steppes and semi-dry grasslands are highly endangered through transformation into arable fields, afforestation, abandonment, eutrophication or biotic invasion (Vrahnakis et al. 2013). In Central Europe these habitats, on which many endangered xerothermic bee species are critically depending, have been reduced to small protected sites by now (Wiesbauer 2008; WallisDeVries and van Swaay 2009; Dengler et al. 2014; Nieto et al. 2014; Wiesbauer 2020).

The drifting sand areas in the eastern Marchfeld are the last remnants of a once extensive dune landscape formed during the last ice age and at the beginning of the postglacial period. During this period the water level decreased and extensive gravel and sand banks dried out, allowing the wind to spread large quantities of fine sediment in the landscape (Küster 1999; Wiesbauer and Mazzucco 1997). Today, non-forested sand areas are only found very locally in Lower Austria. "Pannonic inland dunes" are among the most endangered habitats in Austria and home to a unique fauna and flora. For several plant and animal species specialized on sandy soil, the study site "Sandberge Oberweiden" is or has been the last occurrence in Austria (Kasy 1957; Wiesbauer and Mazzucco 1997; Rabitsch 2002). Thus, the "Pannonic inland dunes" are priority habitats according to the Fauna-Flora-Habitat Directive and therefore under special protection (European Council 2007).

In the present contribution we survey the nature reserve "Sandberge Oberweiden", a 126-hectare large sand steppe habitat in Eastern Austria, which is protected since 1961 (Wiesbauer 2002a). The unique steppe fauna and flora of Oberweiden is known already since the end of the 19th century (Kasy 1957). The oldest bee records are specimens collected by the Austrian entomologists Josef Kolazy and Anton Handlirsch in 1882, followed by records from Hans Zerny around 1915 (specimens in Coll. NHMW), while the most comprehensive historical data go back to the Austrian bee researchers Bruno Pittioni and Stefan Schmidt in the 1930ies and 1940ies (Pittioni and Schmidt 1942; Pittioni and Schmidt 1943; Funnell 2022). In the 1950ies and 1960ies the site was occasionally studied by hymenopterologists from Upper Austria, foremost Andreas W. Ebmer and Josef Gusenleitner (ZOBODAT 2021).

In this article, we investigate historical and recent data on a wild bee community by (i) defining four time periods representing major collection efforts, (ii) analyzing the alterations in the community in relation to ecological traits, (iii) discussing these changes
integrating landscape development trends and (iv) analyzing community composition changes and their associated drivers.

Material And Methods

Study area

The study area (Fig. 1A; N 48°17’13", E 16°49’43") is located in Lower Austria, south of the village Oberweiden. It is part of the Natura 2000 protected area "March-Thaya-Auen" and the protected habitat "Pannonic Inland Dunes" (European Environment Agency 2022).

For the apidological survey (2018–2019), the 126-hectare large area was divided into four study plots (Fig. 1B) representing differently structured parts of the landscape: The Hills in the northern part of the reserve (HG), the Old Area south of the Hills (AF), the New Area which has only recently been set under protection (NF) and is adjacent to the Old Area to the northwest, and a former horse racing track, which occupies a large area to the south (RB). Important foraging plants were qualitatively (i.e. not systematically) surveyed in the area to improve the definition of the four study plots.

Hills. The hills in the northern area provide a suitable habitat for many plant rarities, such as the common gypsophila (Gypsophila paniculata), the late carnation (Dianthus serotinus), and the immortelle (Helichrysum arenarium). Other flowering plants of interest to wild bees here include knapweed (Centaurea spp.), eld eryngo (Eryngium campestris), and Odontites luteus. In the southern area, where the hills gradually transition into the flat, steppe-like meadow, the ground is sparsely vegetated. The open, sandy areas serve as nesting habitat for various species of wild bees and wasps. Prickly saltwort (Kali turgidum) grows on the open, sparsely vegetated soil patches.

Former horse racing course. An extensive steppe-like area is surrounded by the track of a former horse racing course. The edges of the race course form a low, sandy slope towards the meadow and are partially overgrown with flowering plants such as thyme (Thymus sp.), hoary alyssum (Berteroa incana), yellow scabious (Scabiosa ochroleuca), and knapweed (Centaurea spp.). Hoary alyssum seems to be particularly attractive to various wild bee species, blooming in large numbers especially in the southeast corner of the horse track. Very early in the year, sand cinquefoil (Potentilla incana) blooms in large number.

Old Area. The Old Area is a meadow west of the hills, crossed with several sandy paths. Flowering plant species include knapweed (Centaurea spp.), thorny knapweed (Ononis spinosa), and resede (Reseda sp.).

New Area. North of the old area and the hills is another meadow that has only recently become part of the nature preserve. Many flowering plants grow here, such as thorny knapweed (Ononis spinosa), yellow scabiosia (Scabiosa ochroleuca), knapweed (Centaurea spp.) and sage (Salvia sp.).

Due to imprecise locality on the specimen labels until the 1960ies, it must be assumed that until the 1960ies records labelled as "Oberweiden" are not restricted to the protected area today, but could also include the area between the steppe and the train station in the village in a few kilometres distance, where entomologists arrived (Fig. 1A). Thus, the entire area was considered in the analysis of the landscape changes.

Today, the protected area is managed by mowing. Though as a result of an EU LIFE-project (Wiesbauer 2002b) staggered mowing with a certain proportion of the area left standing each year was foreseen, own- and third-party observations (e.g. M. Lödl pers. comm.) have shown that the entire area is actually mowed in one go by selecting the overlapping time window for mowing that is open for all sub-areas in accordance with the management contract. The non-use areas should be rotated annually so that scrub encroachment due to long-term fallow is prevented, which is not the case. The management plan is currently being revised (pers. comm. Department of Nature Conservation, State Government of Lower Austria).

Field work. Surveys were conducted by visual collecting with a hand net from April until September 2018 and from April until August 2019 (for dates see Online Resource 1). For the determination of the species Amiet et al. (1999, 2001), Dathe et al. (2016), Ebmer (1969–1973), Scheuchl (1995, 1996), Schmid-Egger and Scheuchl (1997), as well as the Collections of the Natural History Museum Vienna (NHMW), Sabine Schoder and Herbert Zettel were used.

A complete list of the collected specimens including specimen-IDs and GPS coordinates is given as supplementary material (Online Resource 1).
Bumblebees (Bombus spp.) were not considered in the most recent survey (2018–2019). However, historical bumblebee records are included in Online Resource 2, but not further evaluated and discussed in comparison with recent data.

**Nomeclature.** Nomenclature follows Scheuchl and Willner (2016), with the following exceptions: classification of Eucera s.l. follows Dorchin et al. (2018); *Andrena afzeliiella* is understood following Praz et al. (2022).

**Databases, literature and Collection data.** The data from the current survey were complemented by historical data from the Collection of the Natural History Museum Vienna (NHMW Coll.), the Collection of the Landesmuseum Burgenland (Coll. Bgl.), the database of the Natural History Museum Vienna (NHMW-DB), the Global Biodiversity Information Facility (GBIF 2022), the Zobodat specimen database (Zobodat 2022), and the private database of Herbert Zettel (HZ-DB in Online Resource 2), as well as for selected species the bee database Apidat owned by the Biologiezentrum Linz, and finally the Pittioni Bee Collection Index Cards held at and digitized by the Natural History Museum, London (Pittioni Index Cards, Funnell 2022) and a comprehensive literature search using the Zobodat literature database (Zobodat 2022). All literature references used for compiling the species list in Online Resource 2 are listed in Online Resource 2.

Bruno Pittioni and Stefan Schmidt (1942, 1943) published an extensive survey of the bee fauna from Eastern Austria. For many species they listed all known records, but for more common species the localities were listed without reference to specific records. In cases in which such records were found in the Pittioni Index Cards, these were listed preferably. The high number of recorded species in the year 1942 is due to records published by Bruno Pittioni (1942) without a year date; these records were assigned the year of publication, but may have been collected in a foregoing years.

**Assignment of ecological traits.** The ecological traits, specifically feeding preferences (i.e. lecty: polylectic, oligolectic), preferred plant taxa of oligolectic species, nesting type (ground nesting vs. above ground nesting species; above ground includes nesting in dead wood, plant stems, beetle tunnels, cavities, snail shells and freely suspended), parasitism (nest-building- vs. parasitic species), host associations for parasitic species, habitat requirement (open land, forest edge, ubiquitous) and strong dependence on sand or steppe-like habitats were assigned following Scheuchl and Willner (2016) and Wiesbauer (2020). Additionally, the flight period was assessed: Species recorded as flying until July were coded as spring species, species flying from May onwards or later as summer-associated species, such flying from April or earlier until August or later were classified as species with a long flight period, and those starting in August as autumn species.

**Landscape Study**

To correlate changes in wild bee community composition with temporal land use change we mapped land use categories (Table 1) from historical aerial photos and recent orthophotos. Historical aerial photos were georeferenced before mapping. Georeferencing and landscape mapping was done with ArcGis Pro 2.8 (ESRI 2021). Historical aerial photos/orthophotos were retrieved from the Austrian Federal Office of Metrology and Surveying (BEV, Bundesamt für Eich- und Vermessungswesen) and were available for 1966, 1994 and 2000. The most recent orthophoto when conducting the study was from 2018 (basemap.at s.a.). The land use categories were defined based on habitat requirements of wild bees, preliminary mapping of the 1966 aerial photo and expert discussion within the author team. Because of the above-mentioned uncertainty of location of specimen records until the 1960ies, the geographical frame for landscape mapping was extended from the protected area northwards to include the train station of Oberweiden (Fig. 1A).
Table 1
Land use categories for landscape mapping of historical (1966, 1994, 2000) and recent (2018) aerial photos/orthophotos of the study area in Oberweiden (Lower Austria) including total covered area (ha) per year. Definitions based on habitat requirements of wild bees, preliminary mapping (1966 aerial photo) and expert discussion.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Land use category</th>
<th>Definition</th>
<th>Total hectare per year</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>1966</td>
</tr>
<tr>
<td>CW</td>
<td>Closed wood</td>
<td>Tree cover 100–50%</td>
<td>85.89</td>
</tr>
<tr>
<td>MOW</td>
<td>Medium open wood</td>
<td>Tree cover 50–20%</td>
<td>8.77</td>
</tr>
<tr>
<td>SW</td>
<td>Sparsely wooded</td>
<td>Tree cover &lt; 20%</td>
<td>29.83</td>
</tr>
<tr>
<td>GL</td>
<td>Grassland</td>
<td>Open habitat without agricultural use (e.g. fallow fields, meadows)</td>
<td>78.50</td>
</tr>
<tr>
<td>DRnonV</td>
<td>Dirt road without central vegetation</td>
<td>Dirt road without vegetation in the middle of the track</td>
<td>3.61</td>
</tr>
<tr>
<td>DRwithV</td>
<td>Dirt road with central vegetation</td>
<td>Dirt road with vegetation in the middle of the track</td>
<td>3.74</td>
</tr>
<tr>
<td>FM</td>
<td>Field margin</td>
<td>Field edges, Road margins, infrequently used dirt roads (e.g. through a meadow)</td>
<td>4.41</td>
</tr>
<tr>
<td>BG</td>
<td>Bare ground</td>
<td>Areas without vegetation</td>
<td>7.39</td>
</tr>
<tr>
<td>Agri</td>
<td>Agricultural field</td>
<td>Areas for crop cultivation</td>
<td>651.51</td>
</tr>
<tr>
<td>TR</td>
<td>Tree row</td>
<td>Row of trees</td>
<td>3.35</td>
</tr>
<tr>
<td>Str</td>
<td>Street</td>
<td>Streets and roads with impervious surface</td>
<td>3.52</td>
</tr>
<tr>
<td>Anthr</td>
<td>Anthropogenic entity</td>
<td>Villages, buildings incl. gardens, industrial sites</td>
<td>2.62</td>
</tr>
</tbody>
</table>

Data analysis

All data analyses were done using the software R version 4.1.2 (R Core Team 2021). All wild bee data were analyzed as presence-absence data. The proportion of coverage per landscape category per year (1966, 1994, 2000, 2018) was calculated in ArcGis Pro 2.8. Changes of wild bee species richness per trait and land use changes between the mapped years were visualized with a stacked area chart with the R-package ggplot2 (Wickham 2016). To provide a measure for species turnover across all time periods, the Sørensen index was calculated in the R package vegan (Oksanen 2013; Oksanen et al. 2020).

The wild bee data from periods with approximately complete sampling (1931–1966 and 2000–2021) are compared descriptively. Due to very sparse wild bee data availability in some observation years, specifically between 1885 and 1930 as well as between the 1950ies and the 2010s these data were pooled (Table 2) for statistical analysis. To show differences of the wild bee community over time and relations to land use change, the data were attributed to time periods (before 1930, 1931–1966, 1967–2000, 2000–2021) in accordance with the available historical aerial photos/orthophotos (Table 2). Since the relation of wild bee data before 1950 with a landscape situation from 1966 (earliest aerial photo available for the region) seemed inadequate, no landscape data were attributed to wild bee data before 1950 (Table 2).

To analyze changes in wild bee community composition, traits and related land use change, a multivariate statistical approach was chosen. We performed a NMDS (non-metric multidimensional scaling) with the R package vegan (Oksanen et al. 2020) using a binary bray-curtis distance matrix to show differences in the wild bee community among the defined time periods (Table 2). To analyze how ecological traits were associated over time, community weighted means (CWM) per observation (year or aggregated observation years; Table 2) were calculated with the R package FD (Laliberté et al. 2014; Laliberté and Legendre 2020) using the ecological traits nesting type, lecty, parasitism, flight period and habitat requirements. The CMWs and the proportion per land use category were fitted onto the NMDS using the function “envfit” of the R package vegan (Oksanen et al. 2020). Some traits appeared to be dominant over time (nest building vs. parasitism, nesting type; Table 2), thus these CWM had to be excluded from this fitting step. Due to significant heterogeneity of the wild bee community among the timespans (Permutation test in vegan: 999 permutations, p = 0.001) we did not perform an ADONIS to assess significant variation among the timespans, but instead we included the timespans in the vector fitting.
Table 2
Information about observation year and data pooling, attributed time period, associated land use data, community weighted means (CWM) and species richness for analyzing the wild bee community in Oberweiden over 100 years. Abbreviations: pl = polylectic, ol = oligolectic, OL Steppe = species requiring open land and steppe habitat, OL Sand = species requiring open land and sandy habitat, OL Sand & Steppe = species requiring open land and sandy steppe habitat.

<table>
<thead>
<tr>
<th>Observation year incl. aggregation</th>
<th>Time period</th>
<th>Land use aerial photo/orthophoto</th>
<th>Lecty</th>
<th>Parasitism</th>
<th>Habitat requirements</th>
<th>Nesting type</th>
<th>Flight period/Main activity</th>
<th>Species richness</th>
</tr>
</thead>
<tbody>
<tr>
<td>1882</td>
<td>Before 1930</td>
<td>No data available</td>
<td>PI nest_building</td>
<td>Ubiquist</td>
<td>Ground nesting</td>
<td>Two or more Seasons</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>1883</td>
<td>Before 1930</td>
<td>No data available</td>
<td>PI nest_building</td>
<td>OL Steppe</td>
<td>Ground nesting</td>
<td>Two or more Seasons</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>1885</td>
<td>Before 1930</td>
<td>No data available</td>
<td>PI nest_building</td>
<td>OL Sand</td>
<td>Ground nesting</td>
<td>Two or more Seasons</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>1908–1930</td>
<td>Before 1930</td>
<td>No data available</td>
<td>PI nest_building</td>
<td>Forestedge</td>
<td>Ground nesting</td>
<td>Two or more Seasons</td>
<td>57</td>
<td></td>
</tr>
<tr>
<td>1931</td>
<td>1931–1966</td>
<td>No data available</td>
<td>PI nest_building</td>
<td>OL Sand &amp; Steppe</td>
<td>Ground nesting</td>
<td>Two or more Seasons</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>1932</td>
<td>1931–1966</td>
<td>No data available</td>
<td>PI nest_building</td>
<td>OL Sand</td>
<td>Ground nesting</td>
<td>Summer</td>
<td>5</td>
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<tr>
<td>1933</td>
<td>1931–1966</td>
<td>No data available</td>
<td>PI nest_building</td>
<td>Forestedge</td>
<td>Ground nesting</td>
<td>Spring</td>
<td>13</td>
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<tr>
<td>1934</td>
<td>1931–1966</td>
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<td>Ground nesting</td>
<td>Spring</td>
<td>41</td>
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<tr>
<td>1935</td>
<td>1931–1966</td>
<td>No data available</td>
<td>PI nest_building</td>
<td>Open land</td>
<td>Ground nesting</td>
<td>Spring</td>
<td>56</td>
<td></td>
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<tr>
<td>1936</td>
<td>1931–1966</td>
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<td>Open land</td>
<td>Ground nesting</td>
<td>Summer</td>
<td>31</td>
<td></td>
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<tr>
<td>1937</td>
<td>1931–1966</td>
<td>No data available</td>
<td>PI nest_building</td>
<td>Open land</td>
<td>Ground nesting</td>
<td>Summer</td>
<td>43</td>
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<tr>
<td>1938</td>
<td>1931–1966</td>
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<td>Open land</td>
<td>Ground nesting</td>
<td>Summer</td>
<td>35</td>
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<tr>
<td>1939–1941</td>
<td>1931–1966</td>
<td>No data available</td>
<td>Ol nest_building</td>
<td>OL Sand &amp; Steppe</td>
<td>Ground nesting</td>
<td>Summer</td>
<td>11</td>
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<td>1931–1966</td>
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<td>Spring</td>
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<td>Two or more Seasons</td>
<td>4</td>
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<tr>
<td>1948</td>
<td>1931–1966</td>
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<td>Ol nest_building</td>
<td>Open land</td>
<td>Ground nesting</td>
<td>Summer</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Observation year incl. aggregation</td>
<td>Time period</td>
<td>Land use aerial photo/orthophoto</td>
<td>Lecty</td>
<td>Parasitism</td>
<td>Habitat requirements</td>
<td>Nesting type</td>
<td>Flight period/Main activity</td>
<td>Species richness</td>
</tr>
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<td>----------------------------------</td>
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<tr>
<td>2018</td>
<td>2001_2021</td>
<td>2018</td>
<td>PI</td>
<td>nest_building</td>
<td>Open land</td>
<td>Ground nesting</td>
<td>Summer</td>
<td>52</td>
</tr>
<tr>
<td>2019</td>
<td>2001_2021</td>
<td>2018</td>
<td>PI</td>
<td>nest_building</td>
<td>Forestedge</td>
<td>Ground nesting</td>
<td>Summer</td>
<td>87</td>
</tr>
</tbody>
</table>

### Results

#### 3.1 Distribution and composition of species records

Altogether 310 wild bee species representing 41 genera were recorded in and around the nature preserve Oberweiden until now (Online Resource 2). The oldest records date back to the year 1882. According to collecting efforts, the data are distributed unequally, with more than 15 species recorded for the years 1885 (17 spp.), 1911 (33 spp.), 1934–1938 (45 spp., 59 spp., 34 spp., 48 spp., 38 spp.), 1942–1943 (115 spp., 37 spp.), 1952 (16 spp.), 1959 (35 spp.), 1967 (23 spp.) and 2018–2020 (52 spp., 87 spp., 28 spp.). 99 species were recorded during the recent survey (2018–2019) by DZ and SS. Across the entire time span of the dataset a high species turnover (Sørensen index = 0.88) was detected.

Across the four time spans and excluding the 21 documented bumblebee species (*Bombus* spp.), 79 of 289 species were recorded before 1930, 246 in the period 1931–1966, 34 between 1967 and 2000, and 119 between 2001 and 2021. After 1966, 160 of the 289 species were not recorded again. Eight species were recorded in all four analyzed time periods: *Colletes chengtehensis*, *Dasypoda hirtipes*, *Halictus semitectus*, *Lasioglossum calceatum*, *L. discum*, *L. lucidulum*, *L. sexnotatum* and *Melitta tricincta*, of which four species can be characterized as sand-ane and three as steppe-associated species. Over the whole studied time period, 155 species (53.6%) were polylectic, 75 species (26%) oligolectic and 59 parasitic (20.4%), 47 species (16.3%) were sand-ane and 58 (20%) highly depend on steppe-like habitats.

#### 3.2. Comparison Of Wild Bee Species Richness And Ecological Traits Across Timespans

Across the two periods with approximately complete samples (1931–1966 vs. 2000–2021), 283 of the 289 species were recorded, with an overlap of 82 species, while 164 species occurred only in the earlier period, and 37 species only in the later one. The total species richness decreased over 50% between the two periods, from 246 to 119 species. Taking all time periods into account, 28 species were recorded from the site for the first time after 2001.

**Lecty.** The data from the two periods with approximately complete samples showed an increase of oligolectic species from 23.5% (58 of 246 spp.) in 1931–1966 to 28.5% (34 of 119 spp.) in 2001–2021. This pattern was even more pronounced, comparing species documented only in 1931–1966 with a relative amount of 23.8% oligolecty, to species documented only in 2001–2021 with 40.5% oligolecty. Changes in lecty were similar across the four timespans, which include all wild bee data (Fig. 2A).

**Parasitic species.** The proportion of total parasitic species decreased from 22% (54 of 246 spp.) in 1931–1966 to 18.5% (22 of 119 spp.) in 2001–2021. Again, this pattern was even clearer comparing species that occurred only in 1931–1966 with 22.5% parasitic ones versus 13.5% in the species which occurred only in 2001–2021.
**Nesting type.** While 91.5% (174 of 190 spp.) of the species occurring in 1931–1966 were ground nesting (dig into soil for nest construction), the proportion decreased to 69.3% (67 of 97 spp.) in 2001–2021. Instead, the number of above ground nesting species showed a reversed picture: Species nesting in wooden structures or shrubs increased from 6% (12 of 190 nest-building spp.) in 1931–1966 to 24% (24 of 97 nest-building spp.) in 2000–2021. Specifically, species nesting in dead wood elements increased from 2.2–4.7%, species nesting in pre-existing cavities associated to tunnels created by wood-boring beetles increased from 3.8–8.2% and such species nesting in dead twigs or plant stems increased from 5.5–10.8%. The proportion of species nesting in snail shells increased from 1–3%. Changes in the proportion of species with different nesting type were similar across the four timespans (Fig. 2B).

**Habitat requirements.** The proportion of sand-affine species decreased from 18.3% (45 of 246 spp.) in 1931–1966 to 13.4% (16 of 119 spp.) in 2001–2021. Similarly, the proportion of steppe-associated species decreased from 21.1% (52 of 246 spp.) in 1931–1966 to 15.1% (18 of 119 spp.) in 2001–2021. The proportion of ubiquitous species increased slightly from 21.5% (53 of 246 spp.) in 1931–1966 to 22.7% (27 of 119 spp.) in 2001–2021. Species adapted to open land habitats decreased from 54% (133 of 246 spp.) in 1931–1966 to 47% (56 of 119 spp.) in 2001–2021. Species requiring forest edges and related habitats increased relative to the absolute number of species recorded in the respective time period from 24.4% (60 of 246 spp.) in 1931–1966 to 30.3% (36 of 119 spp.) in 2001–2021. Looking specifically at the species recorded exclusively in one of the time periods, 54.9% open land species and 25% edge species were recorded in the time period 1931–1966 versus 35% open land species and 45.9% edge species in 2001–2021. The proportional changes of species with different habitat requirements were similar across the four time periods (Fig. 2C).

**Flight period.** Species with their main flight period in spring decreased from 30.9% (75 of 246 spp.) in 1931–1966 to 21% (25 of 119 spp.) in 2001–2021, while species mainly flying during summer increased from 33.3% (82 of 246 spp.) to 45.4% (54 of 119 spp.). Species with a later or long flight period did not change as much (2% vs. 3.4%, 33.7% vs. 30.3%). The proportional changes of species with different flight periods were similar across all time periods (Fig. 2D). The nesting preferences differ with the flight period, with 91.7% of all non-parasitic spring species being ground nesting (55 of 60 spp.), 70.5% of the summer species (62 of 88 spp.), 100% of the autumn species (6 spp.) and 90.7% of the species with a long flight period (69 of 76 spp.).

### 3.3. Land use change
In total an 883.125 ha area per year (1966, 1994, 2000, 2018) were mapped from historical aerial photographs and orthophotos (Table 1). The landscape was dominated by agricultural areas across all periods (Fig. 3A–D). Grassland, fallows and woods with different proportions of canopy cover were characteristic semi-natural habitats in the study area (Fig. 3A–D).

While the total agricultural area in the study area stayed relatively equal over time (Fig. 4A), the area covered with woods increased from 1966 (124.49 ha) to 2018 (174.75 ha). Specifically, areas characterized by medium and sparse wood cover increased, while woods with continuous canopy cover increased from 1966 to 1994, but afterwards decreased between 2000 and 2018 (Fig. 4B; Table 1). Further, the total area covered with grassland and fallows decreased slightly between 1966 and 1994 and stayed equal afterwards (Fig. 4B). The total area with anthropogenic entities such as villages, buildings or industrial sites also increased steadily from 1966 to 2018.

### 3.4. Changes in wild bee community composition
The whole wild bee community (Fig. 5A; $r^2 = 0.66; p = 0.02$) as well as the community including only sand and steppe specialists (Fig. 5C; $r^2 = 0.007$) were significantly different among the four time periods. Vector fitting revealed that the bee community in the period 1967–2000 (Fig. 5A) was significantly associated with the area of closed woods ($r^2 = 0.78; p = 0.03$), bare ground patches ($r^2 = 0.9; p = 0.001$) and field margins ($r^2 = 0.93; p = 0.001$). Across all time periods, the CWMs for lecty were significantly ($r^2 = 0.15; p = 0.023$) associated with the NMDS (Fig. 5A). Results from vector fitting indicated on the one hand, that oligolectic species were characteristic for the late 1930ies and early 1940ies, but on the other hand oligolectic species may also benefitted from the increasing area of field margins after 1966 (Fig. 5A).

When specifically analyzing the oligolectic bee community (Fig. 5B) the vector fitting reveals that dependence on different plant taxa were significantly associated to the wild bee community of the different time periods ($r^2 = 0.42; p = 0.045$). In the two earlier periods the oligolectic species assemblage was specialized on Dipsacaceae, Brassicaceae and Fabaceae. Also, parasitic species depending
on oligolectic hosts were associated to these periods. During the two later periods the oligolectic wild bee community was characterized by species specialized on Asteraceae or specifically on Carduoideae.

The wild bee community including only species depending on sand and steppe habitats (Fig. 5C) and for the most recent time period (2001–2021) was significantly associated with grassland ($r^2 = 0.78; p = 0.03$), medium ($r^2 = 0.77; p = 0.04$) and sparsely wooded areas ($r^2 = 0.78; p = 0.04$) as well as anthropogenic entities ($r^2 = 0.78; p = 0.05$). The sand and steppe bee community during the earlier time period (1967–2000) showed a tendential relation with closed woods ($r^2 = 0.77; p = 0.04$) and bare ground patches ($r^2 = 0.79; p = 0.04$).

**Discussion**

An increasing number of studies dealing with biodiversity change have been demonstrating worldwide concerning trends in biodiversity and biomass loss, but also illustrated considerable variation in these trends, and the need to address these complexities with detailed studies on realm-, region- and taxa-specific trends over time (Dornelas and Daskalova 2020). Among the existing studies, there is only a small amount addressing a longer time period; e.g. in the biodiversity database BioTIME only 1.4% of the time series reach back over 50 years (Dornelas et al. 2018).

In the wild bee community in the steppe habitat Oberweiden we found a high species turnover and a dramatic decline of species richness since the period 1931–1966. Only 82 of the 283 wild bee species (excl. bumblebees) recorded altogether in the two intensively studied time periods 1931–1966 and 2001–2021, occurred in both, while 28 species were only recorded in the most recent period. The decline in species richness of more than 50% between the two time periods indicates, that the area has significantly lost quality as a habitat for bees in the last 100 years. Similar trends have been documented in other European countries, as Belgium, the Netherlands and Great Britain, where a strong decline of wild bee species between the 1950ies and 1990 was observed, along with a biotic homogenization driven by an expansion of common bee species (Jauker et al. 2009; Carvalheiro et al. 2013). A gradual community turnover resulting in temporal and spatial biotic homogenization was also revealed by a comprehensive e-DNA study of plant-associated arthropod communities from leaf material archived over a period of 30 years (Krehenwinkel et al. 2022).

Fifteen of 33 species which are regionally extinct in Austria (Kratschmer et al. 2021) and endangered at the European level (Nieto et al. 2014), have been recorded from the site before 1966, with a high proportion adapted to steppe and sand habitats. Specifically, these are *Amegilla quadrifasciata*, *Andrena hungarica*, *A. morio*, *A. transitoria*, *Bombus armeniacus*, *B. fragrans*, *B. laeus*, *Colletes albomaculatus*, *C. punctatus*, *Dasypoda braccata*, *D. suripes*, *Nomada melathoracica*, *Pseudapis femoralis* and *Eucera (Tetraloniella) pollinosa*. Among the newly recorded species, seven currently expand their distribution from warmer, more southern and eastern regions to Austria, probably as a response to climatic warming (*Ceratina nigrolabiata*, *Icteranthidium laterale*, *Lithurgus chrysurus*, *L. cornutus*, *Osmia bidentata*, *O. spinulosa*, *Pseudapis diversipes*, and its parasite *Pasites maculatus*: Zettel et al. 2019, Pachinger et al. 2019).

We have studied the changes in landscapes and found correlations with the bee community (Fig. 5). However, land use changes detectable on aerial images affect only a small portion of the entire area. Changes in land management (e.g. mowing regime, grazing, use as a horse track) might have had a greater impact on changes in the bee fauna, similar to Cousins et al. (2015) who describe the influence of the changing character of land use due to management changes on biodiversity. Such qualitative changes could not be considered in the statistical analysis, because of lacking data, but is useful for the interpretation of the results. Additionally, digitization of polygons from aerial photos/orthophotos has several limitations compared to field mapping, as structures and cover may not always be clearly detectable (e.g. agricultural field and fallow). Further, picture quality differed between the years, which made assignability of land use categories sometimes difficult. For example, the 1966 aerial photo was only available in black and white, and the 1994 photo was available only in lower resolution than the one from 2000 or 2018. Other studies summarized the methodological drawbacks of digitization procedures of historical maps and pictures, though concluding it is still the best way of gathering information of historical land use (Geri et al. 2010).

**Shift from ground to above ground nesting species**

The decrease of the proportion of ground nesting species of over 20% (91.5–69.3%) shows a distinct shift towards above-ground nesting species since the 1930ies (Fig. 2B). The shift from spring to summer species observed on the site (Fig. 2D) contrasts with the results of other recent studies, showing increased extinction vulnerability of late-summer active bee species in Central Europe.
The shift observed in Oberweiden was likely correlated with the decrease of ground-nesters, as they make up a much higher proportion of the spring compared with the summer species (91.7% vs. 70.5%). While no landscape data were available for the time period 1930–1966, changes in the bee community of 1967–2000 significantly correlated with changes in forest structures (Fig. 5A), specifically with "closed wood". This can be explained by increased loose tree structures (medium open wood, sparsely wooded) accompanying the decrease of closed wood area. Especially above-ground nesting bee species, which likewise proportionally increased in that time period (Fig. 2B), benefitted from open woody structures, as they provide a variety of nesting structures.

Despite measures to remove woody plants implemented in 2004 as part of an EU-LIFE project (Wiesbauer 2002b), the total amount of open grassland decreased since 1966, while the sparsely wooded area increased (Fig. 4). This trend was also depicted by the analysis of the wild bee community including only species depending on sand and steppe habitats, because the decrease of grassland area and the increase of medium to sparsely wooded area significantly related to the sand and steppe bee community during the most recent time period 2001–2021 (Fig. 5C). Similar results were found in a study of several steppe-associated bee species in the Czech Republic, which documented an increase in above-ground nesting bee species and a decrease in ground nesting species during 1990–2017 compared to 1930–1990 (Bogusch et al. 2020).

Besides the succession of grassland to sparsely wooded land, also the successional shift from steppe grassland to a dense meadow and shrubs was possibly affecting the ground nesting bee community. The extent of open ground patches, flower abundance and diversity are often reduced in later successional stages through competitive exclusion by increasingly dominant grasses, affecting the quality as nesting habitat for ground nesting bees (Albrecht et al. 2021). Such changes might have been fostered by three factors:

1. The shift from traditional sheep grazing to mowing: Low-intensity grazing is likely to be more beneficial for the bee community than the homogenizing regime of mowing (Tonietto and Larkin 2018), as it creates small-scale heterogeneity through varying grazing, and small open ground patches through the trampling. Though localized eutrophication from defecation is possible, it contributes to nutrient removal in the long term, especially if the animals are kept in a barn during the night (Wiesbauer and Mazzucco 1997).

2. Plantings of windbreaks: The formerly open sandy areas used to be regularly moved by strong winds in the area and accumulated as dunes. To make the land usable, a close-meshed network of windbreaks has been planted since the 18th century, reducing the wind speed and thus promoting advanced succession of sandy grasslands (Wiesbauer 2002b).

3. Nitrification has been documented to greatly influence plant and insect communities (WallisDeVries and van Swaay 2017; Wagner 2020; Raven and Wagner 2021), and is particularly likely to have affected the specialized steppe plant community of the site negatively by promoting fast-growing grasses and woody plants.

The amount of floral resources is a key factor driving wild bee diversity and its loss (Potts et al. 2003; Scheper et al. 2014). Besides the strong decline of species recorded on the site to less than 50% compared with the time period 1931–1966, also the decrease of the proportion of parasitic species is an indicator of decreasing or strongly fluctuating population sizes of host bee species (Sheffield et al. 2013) and may corroborate changes in the availability and reliability of floral resources. The management of the conservation area with mowing of nearly the entire area in mid-June (Wiesbauer 2002b; pers. comm. M. Lödl and pers. obs.) might represent one of the factors negatively affecting the quality of the habitat. Mowing represents a serious intervention on bee populations, as it leads to immediate decrease of floral resources needed for survival and reproduction.

Of particular interest in this context are bee species specialized in the pollen of teasel family (Dipsacaceae), as they are particularly endangered in Europe (Nieto et al. 2014, Potts et al. 2015) and may become the focus of a European Action Plan for pollinator conservation (Hochkirch et al. 2021). The vector fitting of CWMs of the oligolectic species and their specific host plants revealed a specialization on Dipsacaceae only in the two earlier periods. Two bee species in the focus of the European Action Plan are both endangered at the European level (Nieto et al. 2014), and regionally extinct in Austria, with the last records from 1940 in the study area (Kratshmer et al. 2021). Specifically, these are the Dark Pantaloone Bee Dasyboda braccata, oligolectic on Scabiosa ochroleuca in Austria (Praz et al. 2008), and the Swollen Pantaloone Bee Dasypoda suripes, specialized on Knautia arvensis and Scabiosa species. Likewise, the near threatened Silvery Pantaloone Bee Dasypoda argentata, also specialized on S. ochroleuca, was observed at the site in 1959 for the last time (Online Resource 2). One reason for the disappearance of these bee species from the study area is a
likely reduction of the abundance of their host plant species. These Dipsacaceae species must have been common previously in the study area, as a large number of flowers seems to be necessary for a population to survive. It has been calculated for *Andrena hattorfiana*, a bee species of comparable large body size, that a medium-sized population of 50 females needs pollen of 924 plants of *K. arvensis* to be self-sustaining (Larsson and Franzen 2007; Zurbuchen and Müller 2012). While still sparsely distributed plants of *K. arvensis* and *S. ochroleuca* are found in the area today (pers. obs.), their quantity is likely not enough to meet the requirements of one or more relatively large bee species. A study of the reproductive success of *S. ochroleuca* under a future climatic scenario with drier summers and wetter springs and falls showed an increased seed production in summer. The drought-tolerant species is more affected by competition than by water availability and in the contrary seems to benefit from a lower competitor biomass in drier summers (Andrzejak et al. 2022). A strong effect of competition on the abundance of *S. ochroleuca* has been shown under abandonment of grazing under varying densities of the grass *Festuca rupicola* (Partzsch et al. 2017). This suggests that the disappearance of bee species oligolectic on Dipsacaceae might be related with a qualitative successional shift from steppe grassland to a denser grass-dominated meadow.

**Conclusions**

Our study corroborates the bad conservation status of habitats and species of Pannonic inland dunes compared to the favourable status described in the Habitats Directive, as assessed in Austria in the evaluation 2013–2018 by the European Environment Agency (2022). Altogether, our results indicate that land management, the most important driver of pollinator decline in Europe (Dicks et al. 2021), is also the major factor in the decline of species diversity in the studied protected area and its surrounding. A stronger reference to historic land management practices and decoupling from economic factors would be desirable to restore the value of the area for many bee species which have become regionally extinct in the last 100 years. Additionally, climatic changes in the last 20 years are reflected in a relative reduction of early flying spring species and a considerably number of new species records in the last 20 years, which are mostly xerothermophilic species immigrating from warmer Eastern and Southern regions.

**Declarations**

**Funding.** The survey of the bee species in the years 2018 and 2019 by DZ and SS was funded by the initiative „Give bees a chance“ (Arcotel Hotels). The respective collecting permits are deposited at the NHMW.

**Conflicts of interest.** The authors have no competing interests to declare. The authors have no relevant financial or non-financial interests to disclose. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The authors have no financial or proprietary interests in any material discussed in this article.

**Ethics approval.** No ethics approval is required to study bees.

**Availability of data and material.** The datasets used for analyses will be made available via a data repository after acceptance.

**Consent for publication.** The authors consent to participate in the review process and to transfer the copyright if the manuscript is accepted.

**Author contributions.** Dominique Zimmermann and Sophie Kratschmer contributed to the study conception and design. Collection, preparation, and determination of the bees in the recent survey (2018-2019) was performed mainly by Sabine Schoder, and to a minor extent by Dominique Zimmermann. Herbert Zettel contributed recent bee records from his collection and checked determinations of species which were difficult to determine. Christa Hainz-Renetzeder and Sophie Kratschmer mapped and analyzed the landscape data and Sophie Kratschmer did the statistical analyses. The manuscript was written by Dominique Zimmermann (introduction, discussion, bee data) and Sophie Kratschmer (landscape data and analyses), and all authors commented on the text.

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References


Tables

Table 1 and 2 are available in the Supplementary Files section.

Figures

Figure 1

The study site “Sandberge Oberweiden” (A) location of the study site; protected areas are marked in green, the transect of the landscape study is marked by a red square, and the village Oberweiden by a star symbol, (B) overview of study plots, abbreviations: HG: hills, RB: former horse racing course, AF: old area, NF: new area (data source hillshade: basemap.at, Nature conservation areas: Abteilung RU5 - Naturschutz / Amt der NÖ Landesregierung - http://www.noe.gv.at/, municipal boundaries: Abteilung BD1 - GIS Support / Amt der NÖ Landesregierung - http://www.noe.gv.at/)
Figure 2

Proportional changes of ecological traits of the recorded bee species over all surveyed time periods in and around the nature preserve Oberweiden. (A) lecty, (B) nesting type, (C) habitat requirements, (D) flight period.
Figure 3

Land use cover in and around the nature preservation area in Oberweiden (Lower Austria) in (A) 1966, (B) 1994, (C) 2000 and (D) 2018 mapped using historical and recent aerial photographs/orthophotos.
Figure 4

Land use change (ha) in and around the nature preservation area in Oberweiden (Lower Austria) between 1966 and 2018 including (A) agricultural area and (B) without agricultural area.
Figure 5

Non-metric Multidimensional Scaling and significant ($p \leq 0.05$) results from vector fitting of land use change (data fitted for period 1966 to 2020), and community weighted means of (A) the whole wild bee community, (B) oligolectic wild bee species and (C) wild bee species specialized on sand and steppe habitats in and around the nature preservation area in Oberweiden (Lower Austria) between 1882 and 2020. Ellipses show clustering of wild bee communities among different time periods. Abbreviations – Land use categories: Anthr = Anthropogenic entity, BG = Bare ground patches, CW = Closed woods, DRwithV = Dirt road with central vegetation, DRnonV = Dirt road without central vegetation, FM = Field margin, GL = Grassland, MOW = Medium open wood, SW = Sparsely wooded. Abbreviation – Traits: pl = polylectic, ol = oligolectic.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Table1.xlsx
- Table2.xlsx
- SupplMat2.xlsx
- SupplMat1.xlsx