



The loss of forest gaps, changes of vegetation and wild bee communities from 1975 to 2020 – increasing numbers of endangered wild bee species despite negative habitat trends in the Danube valley

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ARTICLE INFO

Keywords:

Forest gap
Open forest
Forest ecosystem
Pollinator
Wild bee

ABSTRACT

This study investigated how structural changes of a historical traditionally used forest landscape in Central Europe have affected traits of vegetation and wild bee communities. We compared the extent of gaps in the forest using aerial photographs between 1945 and 2020. And we found historic vegetation and bee surveys from 1975 and 1990, which we repeated in 2010 and 2020. We characterised the vegetation of the closed forest, the forest gaps and the small-scale meadows adjacent to the forest as well as the wild bee community by traits and investigated trait changes with Kruskal-Wallis tests. By NMDS we characterised sample plots and transect walks of timepoints with traits and species. Area of forest gaps decreased by 88% from 1945 to 2020 and by 74% from 1975 to 2020. In the traits of vegetation, Ellenberg Indicator Values (EIV) for moisture and soil nutrients significantly increased in closed forest, forest gaps and meadows adjacent to forest. The EIVs for light and temperature, and the number of red list species decreased. The number of wild bee species that specialise in visiting flowers with long tubes and hylophilic species declined. The number of eremophilic species, species with longer phenologies, and recently Red list species increased. In the NMDS figure of forest gaps and of adjacent meadows, different species and traits characterised more recent and older sample plots of vegetation and confirm the results of the Kruskal Wallis tests. Wild bee communities of 2010 and 2020 were characterised by frequent species, while those of 1975 and 1990 were not characterised by any species. The traits characterised the wild bee communities of the older and younger transect walks in accordance with the results of the Kruskal Wallis tests. In addition, oligolectic bees characterised the older transect walks. The loss of forest gaps represents a direct loss of habitat for many plant and wild bee species. In addition, the qualitative changes in vegetation indicate a deterioration in habitat quality for plants of open forests and wild bees. Among wild bees, specialists were negatively affected by the changes described. These developments were reflected in the initial downward trend in Red List bee species. The increase in bee species with longer phenology, in eremophilic species, the decrease in hylophilic species, and the recent increase in red-listed species can indicate climate change. Therefore, this study underlines the importance of the preservation and development of ecologically valuable forest gaps, particularly in historical traditionally used forests with a typical species composition.

1. Introduction

Pollination is a finely tuned interaction between animals and plants, and one of the most important services of natural ecosystems for both humans and the ecosystems themselves. Therefore, interest in pollinators by researchers and the public has increased in recent years (IPBES 2019; Sanches-Bayo and Wyckhuys 2019). Among the most important

pollinators in Central Europe are wild bees (Williams et al., 1991; Jauker et al., 2012; Guntern et al., 2014), which are typically found in open landscapes. Forested areas are historically not considered important habitats for wild bees (Sobek et al., 2009; Westrich, 2018). However, both earlier and more recent studies have shown that open forests and forest gaps are of great importance for wild bees (Haeseler, 1972; Fuhrmann, 2007; Eckerter et al., 2022). The entire cultural landscape of

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<https://doi.org/10.1016/j.foreco.2024.121968>

Received 8 January 2024; Received in revised form 30 April 2024; Accepted 2 May 2024

Available online 11 May 2024

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Central Europe has undergone fundamental changes, and forests have shown the effects of these, which are largely related to changes in use (Warren and Key 1989; Bürgi, 1998; Poschlod, 2017). The traditional uses of forests in Central Europe, such as coppicing, forest pasture, forest litter removal, leaf-fodder harvest, and wood collection, directly lead to forest gaps and nutrient depletion, which has helped to maintain the open character of the forests (Rupp, 2013; Regierung von Mittelfranken, 2016; Kamp, 2022). However, these historical uses have been largely abandoned since the 1950s (Poschlod, 2017; Moelder et al., 2019).

In addition to land use alterations, the aerial deposition of nitrogen has caused major changes to ecosystems, including forests, especially in recent decades (Dise et al., 2011; Sutton et al., 2011). The nitrogen depositions increased the growth of trees and other nitrophilic plants in the understory (Hättenschwiler et al., 1996; Thomas et al., 2010; Verheyen et al., 2012; Roth et al. 2022). Whereas, the industrial use of wood leads to a reversed process with large-scale deforestation (Keenan and Kimmins, 1993; Whitmer, 2019). Prolonged periods of drought caused by climate change can also cause large forest openings due to the death of individual trees (Seidl et al., 2017; Spathelf et al., 2022). The abandonment of historical and extensive land use, along with anthropogenic nitrogen depositions and modern forestry practices can have different effects on forests and forest gaps. There are only a few regions, where historical data of vegetation and bees are available. Therefore, there are few studies linking parallel changes, especially in a forest landscape with decreasing forest gaps.

In this study, we compared the historical proportion of forest gaps to the current allocation in the study region. We examined aerial photographs from 1945 to 2020 for landscape structures, particularly forest gaps. In addition, we repeated vegetation and bee surveys from the 1970s and 1990s in 2010 and 2020, resulting in data spanning from 1975 to 2020. Results from such long-term data is likely to yield important insights for recommendations for nature conservation.

Therefore, using the historical data we investigate the following:

- Is there a decline in forest gaps in the study area in recent decades?
- If so, can we identify changes in the vegetation using Ellenberg indicator values and indicator values developed by us and the Red List?
- If the extent of forest gaps has decreased and the vegetation has changed, this should have had an impact on the bee community. By assigning characteristics to the bees, e.g. pollen foraging behaviour or temperature preferences, can we detect parallel changes in the traits of the wild bee community?

- What are the characteristic species of vegetation and wild bee community in the habitats in 1975, 1990, 2010, and 2020?

We can derive recommendations for nature conservation from the results.

2. Methods

2.1. Study area

The study area (Jochenstein) is the easternmost section of the ‘Donauleiten von Passau bis Jochenstein’ nature reserve. The nature reserve is located in the Danube valley in south-eastern Germany, directly bordering Austria. Settlements and agricultural land that lie on the southern boundary and extend marginally into the nature reserve are excluded from the study area. The study, therefore, focussed on forest habitats and not on the intensification of agriculture or the conversion of land into settlements (see also Fig. 1). A vegetation sampling plot by Linhard and Stückl (1972) was used to delimit the study area in the west. The Danube valley has a depth of approximately 300 m in the paragneiss rock within the protected area. The slopes of the nature reserve have an average inclination of 30° and are mainly oriented south-southwest (LDBV 2012). The study area received 17–19 kg of nitrogen per hectare in 2018 (Schaap et al., 2018). The precipitation in the valley is relatively high compared to other parts of Central Europe, at approximately 950 mm/m² in 2019 and 1150 mm/m² in 2020 (wetterkontor.com 2022).

The vegetation along the slope consists of a mosaic of different forest communities. Forests of *Fagus sylvatica* (Luzulo-Fagetum) grow in mesophilic sites in one third of the study area and *Carpinus betulus* and *Quercus petraea* (Galio-Carpinetum) forests are found on the dry and warm sites in another third of the forested area. The last third of the nature reserve is covered by various forest communities, such as ravine forests (Tilio-Acerion) and others. The openness of the forest near Jochenstein reached a maximum in the Middle Ages (Braun-Reichert and Poschlod, 2018). Until approximately 1950, the forest was managed using a coppice-like system with forest pastures, and branch wood and forest litter were periodically removed. These historical land uses reduced the soil nutrient content and thus promoted the formation of open forests with small gaps until approximately 1950, when these forest uses were abandoned (Poschlod, 2017; Braun-Reichert and Poschlod, 2018). Large forest gaps discernible in the aerial photos were

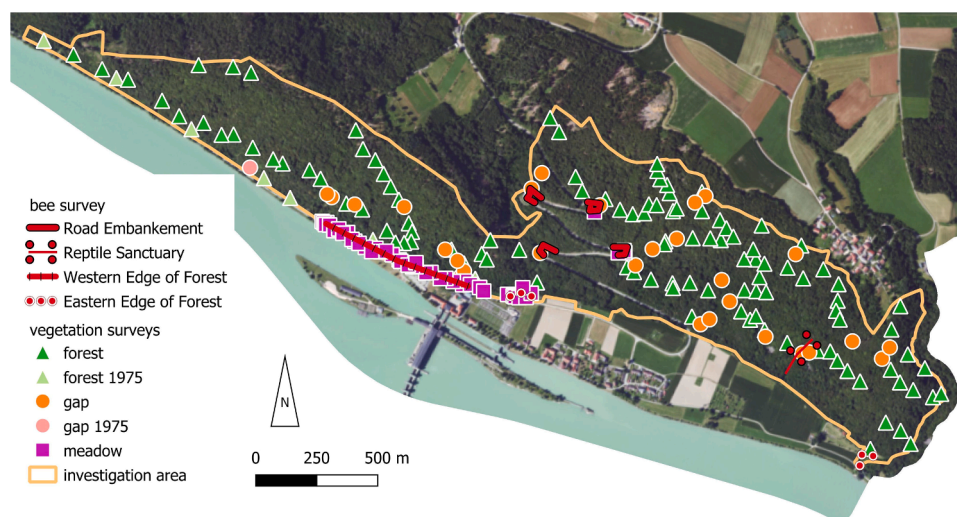


Fig. 1. Aerial photograph showing the study area (yellow line), with the location of the vegetation sampling plots (triangles, dots, and rhombuses) and the transect walks for the bee surveys (red lines, see also Table 3). Sample plots of forest, gap, and meadow were done 2010 and 2020, sample plots of forest and gap 1975 were done 1975, 2010, 2020. Austria borders to the south of the Danube River and to the east (LDBV 2021).

mainly caused by logging. Timber felling in the steep terrain has been steadily reduced since 1950, because of the high level of labour involved. Since 2010, logging in the study area has only taken place in areas accessible from the road. Nowadays, small gaps in the study area represent the character of an open forest in this region because of the typical site factors of the slope, namely a southern exposure, shallow soils, scree slopes and exposed rocks. Extreme weather events and diseases of particular tree species have promoted the formation of new small gaps in recent years. The wild bee fauna of the area has been described in detail by Braun-Reichert et al. (2021b). The region shows a considerable number of xerophilic, thermophilic and rare species.

2.2. Aerial photo analysis

Using aerial photographs, we assigned landscape features based on the following land use categories: closed forest, forest gap, meadow, field and road. Land use maps were created from aerial photos from time points in 1945, 1978, 1990, 2010 and 2020 (LDBV 2021; Table 1). The aerial photographs, vegetation and bee surveys were not available at the same years; still, the time points containing one aerial photograph, one vegetation survey and one bee survey were named according to a specific year (Table 1). The aerial photos were digitised using Q-Gis 3.6. Noosa Version and Arc-Gis 10.8 Version (QGIS.org, 2018; ESRI, 2011). The resolution of the older aerial photographs was lower than that of the more recent samples. We used the smallest discernible forest gap in the 1945 aerial photograph with 134 m² as a benchmark for comparison with forest gaps in more recent aerial photographs, where we were able to detect gaps of 1 m². Smaller forest gaps than 134 m² in the more recent aerial photographs were attributed to closed forest.

2.3. Vegetation analysis

The first eight known vegetation sampling plots in the study area were examined in 1970 and 1971 (Linhard and Stückl, 1972, see Table 1 and Table 2). Linhard provided us with personal notes for precise localisation of the sampling plots in the steep slopes above the road. In 1989 and 1990, Herrmann (Aßmann et al., 1990) reported 96 sampling plots distributed throughout the study area recorded between May and July without indicating the precise location. We examined 198 sampling plots in 2011, 2012, 2013 and again in 2021 between 29th of April and 4th of August including the locations of 1970 and 1971. We increased the number of sampling plots to cover the area better and thus improve the quality of the survey. We repeated the surveys in the same way to make a comparison possible and meaningful. The number of the first vegetation sampling plots were relatively low, particularly in relation to forest gaps, with one sampling plot in time point 1975 and six sampling plots in 1990. The total number of sampling plots is shown in Table 2 and the locations are presented in Fig. 1.

The vegetation was surveyed in the habitats of closed forest, forest gaps and adjacent narrow meadows sharing edges with the forest. These meadows had long edges to the forest due to their long, narrow shape. Environmental conditions such as light, soil moisture and wind protection were like those in forest gaps. But the species composition was clearly that of meadows. In 1990, some of the bee transect walks took place there, so that the vegetation of meadows was also surveyed. By repeating most of the recordings on the same date and for 1975, 2010 and 2020 at the same locations, we can compare the recordings. The

Table 1

Time points at which the single surveys are combined, year of aerial photographs (aer. photo; LDBV 2021), of vegetation surveys and bee surveys.

| time point | 1945 | 1975 | 1990 | 2010 | 2020 |
|--------------------|------|---------|---------|-----------|---------|
| aerial photographs | 1945 | 1978 | 1990 | 2010 | 2020 |
| vegetation | | 1970/71 | 1989/90 | 2011–2013 | 2021 |
| bees | | 1980 | 1988/89 | 2010–2012 | 2019/20 |

Table 2

Number of sampling plots of vegetation surveys in closed forest, forest gap, and adjacent meadow and number of transect walks of wild bee surveys.

| Time point | 1975 | 1990 | 2010 | 2020 |
|----------------------------|------|------|------|------|
| vegetation closed forest | 7 | 57 | 126 | 126 |
| vegetation forest gap | 1 | 6 | 26 | 26 |
| vegetation adjacent meadow | | 33 | 47 | 47 |
| bees | 1 | 14 | 24 | 24 |

vegetation in closed forests and forest gaps was recorded in 10 m × 10 m plots and in 2 m × 2 m plots for meadows by all surveyors. Woody plants were distinguished in the growth habits herbaceous, bush or tree. Linhard estimated plant species cover according to Braun-Blanquet (1964), Herrmann used the finer scale of Reichelt and Wilmanns (1973), and Braun-Reichert used the even finer scale of Schmidt (1974).

To obtain references to site conditions from the vegetation, we calculated the Ellenberg Indicator Values (EIV) for light, temperature, soil moisture and soil nutrients for each vegetation sampling plot. For this purpose, the indicator values of the plants are multiplied by their mean degree of cover and the mean value for the sample plot is calculated (Ellenberg et al. 1991). The number of Red List of Bavaria species (LFU, 2003) was used as a measure of plant species endangerment. Thus, the surveyed plant species were assigned to the categories ‘with Red List status’ and ‘without Red List status’. Neophytes were assigned to the category ‘without Red List status’. Additionally, we developed two indicator values for the value of plant species as food to bees. The first indicator distinguished the quality of a plant as a food. Based on our observations over years, we estimated the food value of a plant for all wild bees (e.g., Frankl et al. 2005; Braun-Reichert 2010; Braun-Reichert et al. 2021a). To calibrate our estimation of food value, we considered information from the literature, such as that of Westrich (1989), and our personal observations in the study area. We did not distinguish between pollen and nectar as a reward for bees. The values approximated the ratio of bee numbers at the flowers on a simplified scale: 0 = no bee visits = no food value, 1 = sporadic bee visits = low food value, 5 = mean number of bee visits = medium food value and 10 = many bee visits = high food value. Coniferous trees were given a score of 0, as the collection of honeydew could not be observed on the respective trees (Westrich, 2022). Grasses or woody plants in the herb layer or trees in the shrub layer were assigned a value of 0. The second plant value indicator relates to Westrich (2022), who listed plants as well as bee species that use these plants as pollen sources. From the numerical number of bee species found on the respective plant species, we created the indicator ‘number of pollen collecting bee species. We excluded plants for which no information was included by Westrich (2022). And Westrich did not count any bumblebee species, so that plants valuable to bumblebees were given a relatively lower indicator value.

2.4. Analysis of wild bee communities

The development of the bee community was compared on a landscape level at the sites with the best suitability for bees and the opportunities to catch them there. The most important basis for determining the transect walks was the availability of older data for a more far-reaching comparison. Warncke recorded wild bees on one transect walk in the “reptile sanctuary” in the study area in 1980, while Voith reported wild bees on 14 transect walks in 1988 and 1989 (ABSP, 2004), both by sweep netting. Voith communicated length and location of the transect walks (pers. comm.). In the time points 2010 and 2020 we repeated all transect walks of a location at a similar date supplemented by nine additional transect walks, for a total of 23 (see Table 3). The transect walks took place between 8th of April and 20th of September, in the forest gaps and meadows sharing edges with the forest, but not in the closed forest (see Fig. 1), under conditions absent of rain or strong winds and with temperatures between 20 and 28°C. Along the transects we

Table 3
Dates of bee transect walks and their localisation in the time points.

| no | localisation | 1975 | 1990 | 2010 | 2020 |
|----|---------------------|------------|------------|------------|------------|
| 1 | reptile sanctuary | 08.08.1980 | | 10.09.2011 | 13.09.2019 |
| 2 | road embankments | | 23.05.1988 | 23.05.2010 | 17.05.2019 |
| 3 | road embankments | | 31.05.1988 | 20.05.2012 | 01.06.2019 |
| 4 | road embankments | | 21.06.1988 | 24.06.2012 | 04.06.2019 |
| 5 | road embankments | | 01.07.1988 | 06.07.2011 | 17.07.2019 |
| 6 | road embankments | | 30.07.1988 | 05.08.2011 | 31.07.2019 |
| 7 | western forest edge | | 28.08.1988 | 22.08.2011 | 08.08.2019 |
| 8 | road embankments | | 28.08.1988 | 25.08.2011 | 23.08.2019 |
| 9 | road embankments | | 05.05.1989 | 29.04.2012 | 08.05.2020 |
| 10 | road embankments | | 16.06.1989 | 20.06.2012 | 02.06.2019 |
| 11 | road embankments | | 17.07.1989 | 16.07.2010 | 27.06.2019 |
| 12 | western forest edge | | 17.07.1989 | 07.07.2010 | 05.07.2019 |
| 13 | western forest edge | | 05.08.1989 | 11.08.2010 | 08.08.2019 |
| 14 | road embankments | | 07.09.1989 | 10.09.2011 | 13.09.2019 |
| 15 | road embankments | | | 08.06.2012 | 24.05.2019 |
| 16 | eastern forest edge | | | 11.05.2010 | 24.05.2019 |
| 17 | eastern forest edge | | | 28.06.2010 | 02.06.2019 |
| 18 | eastern forest edge | | | 28.06.2010 | 27.06.2019 |
| 19 | western forest edge | | | 07.07.2010 | 18.07.2019 |
| 20 | road embankments | | | 16.09.2011 | 14.09.2019 |
| 21 | road embankments | | | 17.09.2011 | 20.09.2019 |
| 22 | road embankments | | | 08.04.2010 | 09.04.2020 |
| 23 | eastern forest edge | | | 08.04.2010 | 09.04.2020 |

caught bees by sweep netting for about 45 minutes. Bees were killed for identification. Few species could be identified alive visually (e.g. some *Bombus* spec.). Warncke identified the Hymenoptera caught in 1975, Voith in 1990, Schmid-Egger in 2010 and Doczkal in 2020. The studies of Amiet (1996), Amiet et al. (1999, 2001, 2004, 2007), Scheuchl (1995, 2006) and Schmid-Egger and Scheuchl (1997) were used for identification and nomenclature.

The abundances of the bees captured differed strongly among certain walks. To minimise methodological differences (e.g., different surveyors or weather conditions), we analysed presence or absence and not the abundance of the species in a transect walk (Packer and Darla-West, 2021).

We examined the following traits. Species that could be assigned to several categories within a trait were counted separately for each category, for example, bees nesting in both stems and wood.

- Diet: oligolectic or polylectic (Scheuchl and Willner, 2016).
- Flower visit (Westrich, 1989): open access (e.g. *Rubus*, *Ranunculus*, *Apiaceae*), intermediary flower access (e.g. *Taraxacum*, *Centaurea*, *Cirsium*, *Jasione*, *Lotus*), long tubed flowers (e.g. *Trifolium pratense*, most Lamiaceae and Scrophulariaceae)
- Pollen collection system: goitre, ventral scopa, other parts of body and hindlegs, no pollen collection (Scheuchl and Willner, 2016).

- The body size of females of bee species has certain ranges. We took the mean values from the literature (Amiet, 1996; Amiet et al., 1999, Amiet et al., 2001; Amiet et al., 2004; Amiet et al., 2007; Scheuchl, 1995, 2006, Schmid-Egger and Scheuchl, 1997)
- Phenology: Westrich (1989) described the first and the last observation of the year of every species. We involved voltinism (uni-, bivoltine), beginning, end, length of phenology, mean date. For statistical analyses we calculated the data as the respective day during a year, irrespective of lap years (1st of January = 1; 31st of December = 365).
- Humidity and temperature preference: according to Pittioni and Schmidt (1942) in Mandery (2001) and Pachinger and Hölzler (2006), supplemented by information from Scheuchl and Willner (2016) and Westrich (2018): eremophilic species are instructed or prefer warmth and drought environments; hypereuryoecious -intermediate species do not have discernible warmth or humidity preferences, can be considered distinctly euryoec; hylophilic species require a certain degree of humidity and moderately cool conditions.
- Nesting site: endogeic locations, stems, wood, resin or clay buildings, other cavities (*Bombus*). Parasites were counted in the nesting habits of their hosts (Westrich, 2018). *Hylaeus difformis*, *Megachile centuncularis*, *M. rotundata*, *M. versicolor*, *M. willughbiella*, *Osmia bicornis*, *O. caerulescens* were counted in more than one nesting site category.
- Social status (Westrich, 2018): solitary, parasitic, social nesting or unknown.
- Red List of Bavaria (Lfu, 2021): the surveyed bee species were assigned to the categories 'with Red List status' and 'without Red List status'.

Mean values of specific traits and categories were calculated as a proportion for each transect walk and included in the analysis. Only the Red List species were included in absolute numbers.

2.5. Statistical analyses

Data were analysed using R version 3.6.3 (R-core team 2021). To determine changes in the landscape structure, specifically closed forest, forest gaps and adjacent meadows, we analysed the total area of these landscapes across the available five time points in the study area using linear regression. To analyse the vegetation and its traits we used the degree of species cover. In the case of bees, species occurrence in a transect walk was included in the analysis as presence/absence, while trait categories were proportionally to number of transect walks included. We analysed vegetation traits and bee traits across time points using Kruskal-Wallis tests, since our data could not be transformed for normality and homogeneity of group variances. Detailed information on the sample size can be found in the supplementary material. Post hoc pairwise comparison was conducted using a Dunn's test with Bonferroni adjustments (Rice, 1989; Tölgyesi et al., 2014; Kassambara 2020). Similarities and differences in the species composition of the vegetation in closed forest, forest gaps, adjacent meadows and in the bee community between the time points were analysed separately using non-metric multidimensional scaling (NMDS). We used Bray-Curtis dissimilarity for vegetation data and Jaccard exponent for binary dissimilarities of wild bee communities (Oksanen et al. 2019). Trait data such as EIVs could not always be obtained from a sample plot because dominant species, such as *Fagus sylvatica* without EIV for soil nutrient were present. For detailed information about sample sizes see supplementary material. Species and traits correlating with species composition were plotted as vectors with a cutoff for vegetation species as $r^2 > 0.3$, vegetation traits $r^2 > 0.2$, bee species $r^2 > 0.3$, and bee traits $r^2 > 0.35$. One symbol represents the species composition of one sample plot or transect walk. Samples from 1975 and 1990 are highlighted in grey.

The use of older data resulted in legitimate limitations in the

analyses. Detailed code and data of the analysis is provided in the Electronic [Supplementary Material](#) (ESM).

3. Results

3.1. Shift of landscape features in aerial photos

The study area covered a total of 129 ha. We observed a significant decline in the extent of forest gaps with more than 134 m² ($p < 0.005$; $R^2 = 2345.5 \pm 124.5$) from 19.8 ha (15.4% of the study area) in 1945, to 2.3 ha (1.8% of the study area) in 2020. This corresponds to a difference of 13.6% of the study area. In 1975, forest gaps accounted for 8.2% of the study area, 6.4% in 1990, and 2.2% in 2010. Taking the area of forest gaps in 1945 as reference, we revealed a loss of 88% of the gaps between 1945 and 2020. From 1975–2020, the gaps decreased by 74%, while a decrease of 68% was recorded from 1990 and still a decrease of 12% from 2010 ([Table 4](#)). Closed forest covered the largest extent of the study area and significantly increased with time ($p < 0.005$, $R^2 = -2400.6 \pm 158.9$), with 105.9 ha (82%) in 1945, 113.6 ha (88%) in 1975 and 122.3 ha (95%) in 2020. Meadows maintained a 2% share of the area from 2.3 ha in 1945–2.0 ha in 2020 ($p = 0.043$; $R^2 = -25 \pm 27.31$). The use as arable land of 0.7 ha (1%) was abandoned after 1975. Prior to 1975, a street was constructed through the forest, covering 1.5 ha (1%) ([Table 4](#)).

3.2. Changes in vegetation

In total 333 plant species were recorded, 216 in closed forest, 194 in forest gaps and 208 in adjacent meadows (see [supplementary table vegetation](#)). The results of the Kruskal-Wallis test of vegetation traits are presented in [Table 5](#), while full statistical analyses can be found in the [supplementary material](#). In closed forest, EIVs for light (L), as well as Red List species (RL) significantly decreased, while EIVs for temperature (T) showed a decreasing trend. Significant increases were found in EIVs for moisture (F) and the indicator value for the potential number of bees collecting pollen (P), while EIVs for nutrients (N) showed a positive trend. The Dunn's post hoc test among time points showed five significant changes between 1990 and later time points, two significant changes between 1975 and later time points, and one significant change between 2010 and 2020. The EIVs for light (L) in forest gaps significantly decreased over time. The EIV for moisture (F) and soil nutrients (N), and the indicator values for food plants for bees (B) and for the potential number of bees collecting pollen (P) increased significantly. The Dunn's test with Bonferroni adjustments showed ten significant changes between 1990 and later time points. In adjacent meadows the EIVs for temperature (T), for humidity (F) and for soil nutrients (N) increased significantly. The indicator values of foot plant for bees (B), and the number of Red List species (RL) significantly decreased over time. The potential number of bees collecting pollen (P) significantly decreased from 1990 to 2010 and increased significantly from 2010 to 2020. The EIV for light (L) showed increasing trends. The Dunn's test

Table 4

Total area of identified features in aerial photographs available for each time point in ha., and percentage loss of the total extent of forest gaps more than 134 m² in 2020 compared to the respective time points. Identified features were fields, streets, adjacent meadows, closed forest, forest gaps more than 134 m².

| Time point | 1945 | 1975 | 1990 | 2010 | 2020 |
|--|-------|-------|-------|-------|-------|
| area of arable land in ha | 0.6 | 0.7 | 0.0 | 0.0 | 0.0 |
| area of street in ha | 0.0 | 1.5 | 1.5 | 1.4 | 1.4 |
| area of all adjacent meadows in ha | 2.3 | 2.1 | 2.4 | 2.2 | 2.0 |
| area of closed forest in ha | 105.9 | 113.8 | 116.5 | 122.2 | 122.8 |
| area of all forest gaps in ha | 19.8 | 10.6 | 8.3 | 2.8 | 2.3 |
| Loss of forest gaps area in 2020 compared to time step | 88% | 74% | 68% | 12% | |

with Bonferroni adjustments showed eleven significant changes between 1990 and later time points and one significant change between 2010 and 2020.

3.3. Changes in the wild bee community

In total, 140 species were recorded (see [supplementary table bees](#)).

The Kruskal Wallis test of bee traits showed significant decreases in species that visit flowers with long tubes and in hylophilic species that prefer cooler and more humid habitats ([Table 6](#)). Species with a longer phenology, eremophilic species that prefer warmer and dry habitats, social nesting species and parasitic species increased significantly. The number of Red List species showed a decreasing trend from 1990 to 2010 and a significant increase from 2010 to 2020. Oligolectic species, the body length of the females of species showed a decreasing trend and the onset of the phenology of the species showed a trend towards an earlier begin. Seven significant changes took place between 1990 and later time points and four significant changes between 2010 and 2020.

3.4. Species composition of vegetation and wild bee communities

In closed forest, no clear patterns can be recognised in the non-metric multidimensional scaling (NMDS, [Fig. 2a](#)). Sample plots of all time points were characterised by high abundances of *Fraxinus excelsior*, *Galeobdolon montanum* and a community with high EIV for nutrients. Sample plots of 1990, 2010, and 2020 are characterised by high abundances of *Fagus sylvatica*. Apart from one sample plot, those of 1975 were characterised by high abundances of *Carpinus betulus*, and generally, by a thermophilic plant community. In the other time points, plots were more variable in vegetation. Plots with extremely high abundances of *Picea abies* were only recorded in 2010 and 2020, with one exception in 1990. A striking number of sample plots from 1990 are characterised by the tree *Carpinus betulus* and the EIV for temperature on the one hand and *Avenella flexuosa* on the other. In forest gaps ([Fig. 2b](#)), *Hylotelephium maximum* and *Campanula rotundifolia*, as well as Red List species and the Ellenberg Indicator Values for temperature and light, characterised mainly sample plots from 1990 and one from 1975. *Rubus fruticosus* agg. and the Ellenberg Indicator Values for soil nutrients and moisture characterised exclusively sample plots from 2010 and 2020, as do *Fagus sylvatica* trees, *Betula pendula* tree, *Vaccinium myrtillus*, *Calluna vulgaris*, *Quercus petraea* herbaceous. In adjacent meadows ([Fig. 2c](#)), *Teucrium scorodonia* and Red List species characterised only sample plots from 1990. *Poa pratensis* and EIV N for soil nutrients and F for moisture characterised only records from 2010 and 2020. *Rubus fruticosus* agg. and *Taraxacum officinalis* characterised mainly records from 2010 and 2020.

The wild bee communities of earlier times of more recent transect walks in [Fig. 2d](#) were characterised by *Lasioglossum morio*, *L. politum*, *Halictus subauratus*, *H. tumulorum*, and *Hylaeus communis*. Species communities of the highlighted and more historical transect walks could not be characterised by single bee species. Flower access long tube characterised most historical transect walks. Likewise, species that feed oligolectic characterised some historical transect walks, while polylectic species characterised the more recent transect walks. Social status solitary characterised especially some historical transect walks, social the more recent ones. Nest site stem and endogecic were opposite, but both still characterised the highlighted range of historical transect walks. Hylophilic species characterised the historical transect walks, eremophilic bees characterised the recent ones. Large body lengths of females characterised communities of recent transect walks. Species whose phenology begins increasingly later in the year characterised mostly some historical transect walks, species whose phenology mean occurs later in the year characterised mostly communities of recent transect walks. Species whose phenology ends later in the year and lasts longer in the year characterised especially recent transect walks.

Table 5

Results of the Kruskal Wallis tests and the Dunn's post-hoc tests with Bonferroni adjustments for differences among the time points. We analysed vegetation traits of closed forest, forests gaps and adjacent meadows (veg unit). Traits: L = EIV light, T = EIV temperature, F = EIV moisture, N = EIV soil nutrients, B = food value of plants for wild bees, P = number of pollen collecting bee species, RL = number of Red List species. Kruskal Wallis test: H = test statistic; degree of freedom in closed forest = 3, in forest gaps and adjacent meadows = 2; p = probability of error; sig. = significance levels: * p < 0.05, ** p < 0.01, *** p < 0.001. m = mean scale in the time points, different letters show differences in Dunn's post-hoc tests with Bonferroni adjustments of pairwise comparisons between time points.

| veg unit | trait | H | p | sig | 1975 | 1990 | 2010 | 2020 |
|-----------------|-------|----|---------|-----|------|-------|-------|-------|
| closed forest | L | 16 | 0.0013 | ** | med | 3.96 | 4.14 | 4.03 |
| | T | 7 | 0.0732 | | 5.75 | 5.45 | 5.38 | 5.42 |
| | F | 9 | 0.0297 | * | 5.03 | 5.00 | 5.02 | 5.04 |
| | N | 7 | 0.0711 | | 5.25 | 4.75 | 5.46 | 5.27 |
| | B | 1 | 0.768 | | 1.10 | 1.70 | 1.75 | 1.75 |
| | P | 12 | 0.0073 | ** | 6.62 | 20.00 | 25.60 | 24.20 |
| forest gap | RL | 46 | < 0.001 | *** | 3 | 3 | 1 | 1 |
| | L | 11 | 0.0044 | ** | | 8.25 | 4.56 | 4.40 |
| | T | 3 | 0.233 | | | 6.42 | 5.50 | 5.54 |
| | F | 16 | < 0.001 | *** | | 2.42 | 5.18 | 5.10 |
| | N | 15 | < 0.001 | *** | | 1.58 | 5.27 | 5.37 |
| | B | 7 | 0.0327 | * | | 1.05 | 2.64 | 2.63 |
| adjacent meadow | P | 9 | 0.0117 | * | | 6.82 | 26.20 | 26.30 |
| | RL | 2 | 0.466 | | | 4.5 | 3 | 3 |
| | L | 6 | 0.0615 | | | 6.40 | 6.83 | 6.81 |
| | T | 12 | 0.0024 | ** | | 5.31 | 5.74 | 5.63 |
| | F | 50 | < 0.001 | *** | | 4.19 | 4.98 | 5.07 |
| | N | 58 | < 0.001 | *** | | 2.84 | 5.59 | 5.66 |
| | B | 20 | < 0.001 | *** | | 3.03 | 1.28 | 1.58 |
| | P | 20 | < 0.001 | *** | | 29.70 | 11.20 | 19.40 |
| | RL | 26 | < 0.001 | *** | | 4 | 2 | 2 |

Table 6

Results of the Kruskal Wallis tests and the Dunn's post-hoc tests with Bonferroni adjustments for differences among the time points. We analysed the traits and categories of the wild bee communities. Traits and categories: oligolectic diet, flower access long tube, body length of females, length of phenology, hylophilic species, eremophilic species, social nesting species, parasitic species, number of Red List species. Kruskal Wallis test: H = test statistic; degree of freedom is 2; p = probability of error; sig = significance levels: * p < 0.05, ** p < 0.01, *** p < 0.001. m = mean scale in the time points, different letters show differences in Dunn's post-hoc tests with Bonferroni adjustments.

| trait | category | H | p | sig | 1990 | 2010 | 2020 |
|------------------------------------|------------------------|----|---------|-----|-------|-------|-------|
| diet | oligolectic | 6 | 0.0624 | | med | med | med |
| flower access | long calyx | 6 | 0.0421 | * | 0.25 | 0.08 | 0.08 |
| pollen transport | intermediary | 2 | 0.374 | | 0.67 | 0.77 | 0.75 |
| | open | 2 | 0.321 | | 0.09 | 0.17 | 0.17 |
| body length | crop | 2 | 0.336 | | 0.13 | 0.04 | 0.10 |
| | ventralscopa | 1 | 0.652 | | 0,0 | 0.09 | 0.07 |
| | hind legs & body parts | 2 | 0.43 | | 0.67 | 0.73 | 0.71 |
| phenology | no pollen transport | 4 | 0.141 | | 0.13 | 0,0 | 0.09 |
| | female | 5 | 0.0748 | | 0.64 | 0.61 | 0.75 |
| | bivoltine | 4 | 0.144 | | 0.17 | 0.17 | 0.11 |
| | begin | 5 | 0.0714 | | 109,0 | 101,0 | 100,0 |
| humidity & temperature preferences | end | 3 | 0.193 | | 259,0 | 268,0 | 265,0 |
| | length | 8 | 0.0219 | * | 142,0 | 158,0 | 160,0 |
| | mean day | 0 | 0.789 | | 221 | 219,0 | 218,0 |
| | hylophilic | 19 | < 0.001 | *** | 0.27 | 0.17 | 0.08 |
| nest site | hyperuoyocious | 2 | 0.326 | | 0.43 | 0.42 | 0.41 |
| | eremophilic | 27 | < 0.001 | *** | 0.25 | 0.38 | 0.50 |
| social status | endogeic | 1 | 0.754 | | 0.71 | 0.77 | 0.78 |
| | wood | 0 | 0.947 | | 0,0 | 0,0 | 0,0 |
| | stem | 0 | 0.933 | | 0.14 | 0.15 | 0.14 |
| Red List | cavities | 1 | 0.514 | | 0.14 | 0.11 | 0.09 |
| | solitary | 4 | 0.111 | | 0.56 | 0.47 | 0.47 |
| | social | 12 | 0.0024 | ** | 0.36 | 0.50 | 0.45 |
| | parasitic | 7 | 0.0331 | * | 0 | 0,0 | 0,09 |
| | number species | 9 | 0.0094 | ** | 0.17 | 0,0 | 0.17 |

4. Discussion

4.1. The loss of forest gaps as small landscape features

This study was able to quantify an 88% loss of forest gaps between 1945 and 2020. The changes between 2010 and 2020 were not very pronounced but between 1945 and 1975 and between 1990 and 2010. Until 1950, almost the entire study area was regularly thinned out by

regular strip cutting with coppice-like utilisation. Forest litter removal and other historical forms of forest use also took place until 1950 and were then abandoned (Braun-Reichert and Poschlod, 2018). These historical land uses reduced the soil nutrient content and thus promoted the formation of open forests with small gaps until approximately 1950. These historical forms of forest utilisation took place very frequently in the vicinity of settlements in Central Europe and were abandoned after 1950 (Poschlod, 2017). Forests that were light due to historical forms of

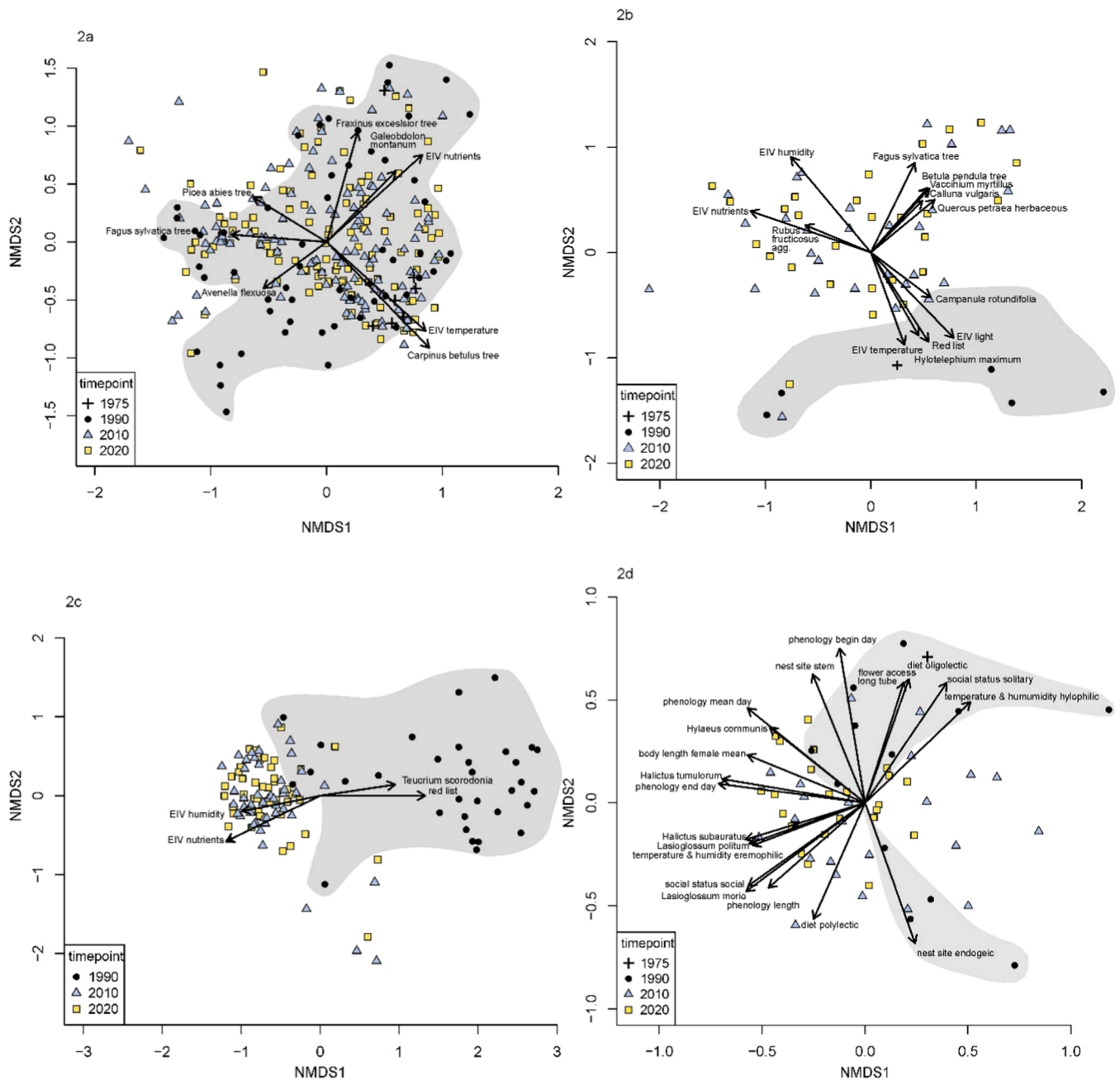


Fig. 2. depicts non-metric multidimensional scaling (NMDS) ordinations of the species communities of the different sample plots and transect walks. The ranges highlighted in grey include all surveys from 1975 and 1990. Surveys from 2010 and 2020 may be included in the highlighted ranges. Unmarked ranges are 2010 and 2020 surveys only. Sample plots of vegetation a) in closed forest (stress = 0.16), b) in forest gaps (stress = 0.12), and c) in adjacent meadows (stress = 0.14), as well as d) transect walks of bee community (stress = 0.18) are shown. Plant species and plant traits (a-c), and bee species and bee traits (d) most correlating with the axes are also given. Sample sizes were N (forest)= 293, N (gap) = 60, N (meadow)= 125, N(bees)= 57.

use have almost completely disappeared (Rupp, 2013; Regierung von Mittelfranken, 2016; Kamp, 2022). Michelis (2015) noted that reliable historical data of open forests and forest gaps were difficult to obtain. Based on the forest biotope mapping in Baden-Württemberg, he stated an area share of 0.2% of the forest area that were permanently open due to edaphic traits. Today, as in our study, the proportion of gaps in forest areas, mostly due to felling, in Germany is 2% (Ammer et al., 2009; Schmalfuß and Aldinger, 2012; Hampicke, 2018).

The loss of forest gaps applies to the conditions in Central Europe, while in northern and eastern Europe, logging is taking place on an unnaturally large scale. In southern Europe, mediterranean forests are struggling with the effects of climate change, which is also leading to

more open forests (Cozma and Achim, 2023; Palmero-Iñiesta et al., 2021).

4.2. Changes of vegetation over time

The increase in EIVs soil nutrients observed over the studied time points reflects the increased trophic level due to atmospheric nitrogen deposition in habitats (Sutton et al., 2011; Stevens et al., 2018). Nitrogen depositions lead to increased plant growth and dense vegetation (Verheyen et al., 2012). In forest ecosystems, anthropogenic nitrogen depositions cause large increases in tree growth which results in denser canopies (Wallace et al., 2007; Thomas et al., 2010). This results in

reduced radiation penetrating to the forest floor. And if light reached the floor it is used by nitrogen-demanding and strong-growing plants such as *Rubus fruticosus* agg. and others, which completely covered the ground of forest gaps in the study area (Verheyen et al., 2012; Roth et al., 2022). These processes are taking place all over Europe and are also reflected in our data by the drop in EIVs for light in closed forests and forest gaps as well as EIVs for temperature in closed forests (Dise et al., 2011; Sutton et al., 2011; Perring et al., 2017). Any autotrophic seed plant of forests and of forest gaps require light to persist, to develop flowers, and to ripe seeds (Decocq et al., 2004; Braun-Reichert et al., 2021a). The increase in EIVs for light and temperature in the meadow, on the other hand, could be an adaptation to increasing temperatures and thus a consequence of climate change because some plants with a higher EIV for temperature also have higher EIV for light (Tardella et al., 2016; Skalova et al., 2022). Thanks to the improved availability of soil nutrients as nitrogen, plants can compensate for a lack of water and thrive better in dry conditions. (Saud et al., 2017; Kumari et al., 2022). Therefore, plants with higher EIV for moisture increased in our observations. In the investigation area we were able to observe this even in dry sites such as rocky outcrops.

The developed food values of plants for bees did not meet our experiences and expectations: they increased in closed forest and forest gaps. Braun-Reichert et al. (2021a) counted the cover of flowers and the number of flowering species and found significantly lower numbers in closed forest than in forest gaps. In adjacent meadows, however, this value fluctuated up and down, but the food value of the meadow for bees decreased. Obviously, the presence of a plant species, as considered in the study, does not automatically mean the appearance of its flower. Other factors may need to be considered to adequately characterise the nutritional value of vegetation units (Frankl et al., 2005).

As a result of the described changes, especially the decline in open forest areas, many typical plants of this habitat are on the Red List (LfU, 2003; Rupp, 2013; Regierung von Mittelfranken, 2016; Hurskainena et al., 2017). As expected, the number of Red List species was also decreasing in line with the decline in forest gaps. However, the decline of Red List species in forest gaps was not statistically significant. The loss of Red List species in grassland is confirmed in many other studies (Schreiber et al., 2009; Hilpold et al., 2018).

Parallel to the large losses of forest gaps, most of the significant changes in vegetation also took place in the twenty years between 1990 and 2010. In the ten years between 2010 and 2020 we found only a low number of significant changes in vegetation (see post hoc analyses Tables 5 and 6).

4.3. Changes in the wild bee community over time

In general, specialised species endure greater negative effects from environmental changes than those of generalist species (Roberts et al., 2011; Bogusch et al., 2020; LfU, 2021). Examples of this can be observed in our study: species that visited flowers with long tubes declined and oligolectic bees, i.e. bees that only collect pollen from one plant species or family, characterised the bee communities of 1975 and 1990 (LfU, 2021). In contrast, common, ubiquitous species characterise the transect walks of 2010 and 2020 in the NMDS, while those of 1975 and 1990 are not characterised by any species. The increase in eremophilic species and the decrease in hylophilic species are very likely related to changes in the temperature and humidity preferences of wild bee communities in the study area. The increase in the EIV of moisture, and the decrease in EIV of light in closed forest and forest gaps, and the marking of the forest gaps from 1990 by the temperature indicated conditions that have become too poor even for hylophilic bee species. Dormann et al. (2020) found that wild bee species diversity increased with the availability of light in the forest. The loss of forest gaps meant direct habitat loss for wild bee species. Temperatures and light conditions in the closed forest were too low for most wild bee species and their food plants, as they require warm and bright habitats such as forest gaps (Corbet et al., 1993; Braun-Reichert et al., 2021a). As sunny ground patches in the forest

were no longer available as potential nesting sites and the extent of gaps decreased, the observed changes in vegetation correspond to a deterioration in habitat quality. On the other hand, we observed a longer duration of the phenology of the wild bee community. A late start of phenology characterises the wild bee community from 1975 and 1990, a late end from 2010 and 2020. We see this as an indication of the effects of climate change (Bässler et al., 2013).

The negative influences of direct habitat loss and habitat quality deterioration, as well as the sensitivity of specialised species to environmental changes, suggest decreasing population trends for endangered species. However, a statistically not significant decreasing trend was only observed between 1990 and 2010. In the period from 2010 to 2020, the endangered species included on the Bavarian Red List (2021) slightly increased, presumably as a result of climate change (LfU, 2021). Hymenoptera react more positively to global warming than certain other insect groups (Bässler et al., 2013). As the steep slopes face south and are particularly exposed to solar radiation, increased temperatures have a particularly strong effect in the study area (Braun-Reichert et al., 2021b). Furthermore, rivers such as the Danube act as migration corridors for wild bees (Schmid-Egger, 2020; Braun-Reichert et al., 2021b). The study area borders directly on Austria, and this location favours the immigration of, in Germany rare, thermophilic species into the study area from the south-east through the warmer Danube valley (LfU, 2021).

The great importance of forest gaps is supported by the results of different studies. Roberts et al. (2017) found a positive relationship among light, early successional stages of forest clearings in the landscape and abundance and diversity of wild bees. The general importance of forest gaps, their related vegetation and their potential nesting structures has been confirmed by Hanula et al. (2016), Proctor et al. (2012) and Eckerter et al. (2021, 2022). Franzen et al. (2009) showed that solitary bees may establish local populations even in relatively small habitats of approximately 1.25 ha. Exceptionally small landscape fragments can harbour unique plant-pollinator interactions, which Librán-Embid et al. (2021) did not observe in larger fragments. Odonaka and Rehan (2020) demonstrated that maximising successional patches across forested landscapes increases the diversity of bees. The results of these studies revealed that wild bees benefit from forest gaps in many ways.

4.4. Consequences for nature conservation

Forest gaps are not only important habitats for typical and endangered plants and wild bees, but also for many other rare and threatened organisms (Gatter, 2004; Benes et al., 2006; Barbier et al., 2008; Spitzer et al., 2008; Fartmann et al., 2013; Bußler, 2016; Dietz et al., 2016; Hurskainena et al., 2017; Vogel et al., 2020; Braun-Reichert et al. 2021a; Braun-Reichert et al. 2021b). Forest gaps form ecotones in which organisms find suitable environmental conditions of light, temperature, moisture and nutrient availability along many environmental gradients (Swanson et al., 2011; Hilmers et al., 2018; Vogel et al., 2020).

We suspect that anthropogenic nitrogen deposition is one of the main drivers of the observed changes in forest gaps, in vegetation and in wild bee communities (Verheyen et al., 2012; Stevens et al., 2018). Therefore, anthropogenic nitrogen depositions must be significantly reduced (Sutton et al., 2011; Fartmann et al., 2021; Kammer et al., 2022).

Diverse food resources and landscape features have positive effects on pollinator diversity and networks (Rodríguez et al., 2019; Gómez-Martínez et al., 2022). Therefore, nature conservation methods should include possibilities for colonisation of food plants when establishing new forest gaps and optimising existing forest gaps (Rivers and Betts, 2021; Korbacher et al., 2023). In addition, a mosaic of uses gives rise to different structures which are valuable to pollinator communities (Zurbuchen and Müller, 2012; Weiss et al., 2020).

Open forests in Central Europe and the organisms residing within them are often a product of historical human uses and form part of the cultural landscape (Bradshaw et al. 2015, Poschlod, 2017). Nature

conservation should develop an increased awareness of the importance of cultural landscapes such as forest gaps to forest ecosystems (Poschlod and Braun 2017; Fartmann et al. 2021). The development of pristine forests is an important goal of nature conservation, e.g., in the studied nature reserve by the authorities. However, the preservation of ecologically valuable forest gaps should be considered equally important in historical cultural landscapes (Poschlod and Braun 2017). In a mosaic of retained forest and open areas, both concepts could be implemented to form habitat complexes (Spitzer et al., 2008). Nature conservation is often understood as the prevention of all direct human intervention in ecosystems, especially in relation to forest ecosystems. The truth is, human intervention in ecosystems occurs globally through anthropogenic nitrogen depositions and the regulation of carnivore and herbivore populations (Verheyen et al., 2012; Pereira and Navarro, 2015). In the study area, red deer still try to get from the mountains of the Bavarian Forest to the Danube in winter. But, as their presence is only permitted in the “red deer district” of the Bavarian Forest, they are driven back to where they are fed in winter. However, red deer can cause similar effects to coppice utilisation and create small gaps in the forest through frequent peeling of the trees. Conservation of forest ecosystems should include the protection of processes, e.g. herbivory (Cromsight et al., 2018). These relationships should be included in conservation communications and education, as they are often unfamiliar to non-experts. Furthermore, in Central Europe gaps are reforested quickly according to modern forestry practices (Rock et al. 2019). Nature conservation organisations have criticised these guidelines for reforestation, with the argument that they often lead to further losses of the natural structural elements provided by forest gaps (BUND 2021).

Nature conservation methods should include the creation, maintenance, and development of forest gaps. These recommendations particularly apply to forest gaps and open forests which currently accommodate a typical and valuable range of species. Historically open forests should be preserved as part of the European cultural landscape and as important habitats for flora and fauna, and pollinators in particular (Muscolo et al., 2014; Poschlod, 2017; Fartmann et al., 2021).

CRediT authorship contribution statement

Julia Sattler: Formal analysis. **Peter Poschlod:** Writing – review & editing, Validation, Supervision, Software, Project administration, Methodology, Conceptualization. **Ralf Braun-Reichert:** Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alexandra Koch:** Writing – review & editing, Software, Methodology, Formal analysis.

Declaration of Competing Interest

All authors disclose any financial or personal relationships that may be perceived as influencing our work.

Data availability

Data will be made available on request.

Acknowledgements

We thank Dr Helmut Linhard (†) and Thomas Herrmann for providing us with their vegetation data and Johannes Voith from the Bavarian State Office for the Environment for permission to use his bee data from the ABSP. We also thank Christian Schmid-Egger and Dieter Doczkal for the identification/verification of bees, and Verbund AG - Donaukraftwerk Jochenstein AG for allowing us to publish bee data from expert reports. The government of Lower Bavaria has gratefully granted permits for entering protected areas and trapping hymenoptera. We would like to thank Sabine Fischer for her support with the

Land Survey Office for providing aerial pictures, Dr. Matthias Lohr, Andre Kuklik, Markus Pabst for providing useful comments on earlier drafts, and Prof. Dr. Florian Hartig for his assistance with statistical questions.

Authors contributions

Ralf Braun-Reichert and Peter Poschlod conceived the research and designed the methodology, Ralf Braun-Reichert collected and analysed the data. Julia Sattler performed the statistical analyses by NMDS, Alexandra Koch the Kruskal-Wallis Test. Ralf Braun-Reichert led the writing of the manuscript. Peter Poschlod, Julia Sattler and Alexandra Koch reviewed the writing and supported the editing. All authors contributed critically to the drafts and gave their final approvals for publication.

Data accessibility

None

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121968](https://doi.org/10.1016/j.foreco.2024.121968).

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