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Open forest successional stages and landscape heterogeneity promote wild bee diversity in temperate forests

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Abstract

Recent studies have emphasized forests as crucial habitat for wild bees. In Europe, most forests are managed following the principles of close-to-nature silviculture, which combine timber production and nature conservation. However, open late and early successional stages within these forests are largely missing, which could be important for wild bees. This highlights that close-to-nature silviculture alone might not be sufficient to conserve bees within temperate forests. Open structures such as canopy gaps and road verges in forests could improve habitat for bees. To provide management recommendations for wild bee conservation in temperate forests, we analyzed how components of bee beta diversity varied between forest management types and tested how open structures, namely clear-cuts, canopy gaps, and forest road verges influenced bee abundance, richness, and diversity. In addition, we analyzed the abundance and percent of red-listed bee species at different scales. Bees were sampled using 90 pan traps on 45 (1 ha) plots in 2019 and 2020 in the Black Forest, Germany. Plots were selected in 15 triplets each consisting of three management types related to different successional stages: unmanaged, close-to-nature, and small clear-cut. Beta diversity was not consistently nested highlighting the importance of different management and successional stages within the landscape to support bees in forests. Abundance, species richness, and Shannon diversity of bees were highest on clear-cuts, compared to unmanaged- and close-to-nature plots. At landscape scale, wild bee abundance increased with canopy openness while wild bee diversity increased with landscape heterogeneity. Abundance- and percent of red-listed bee species increased with the length of forest road verges. We advocate creating habitats at local scales which offer flowering and nesting resources by providing canopy gaps. At landscape scale, heterogeneity created through different forest successional stages is needed to conserve the entire community of wild bees.

KEYWORDS
beta diversity, forest management, landscape heterogeneity, red listed wild bees, road verges

1 | INTRODUCTION

Many studies about the benefits of pollination for food production (IPBES, 2019; Klein et al., 2007) and about the drivers of bee diversity and decline are focused on agricultural landscapes (Bertrand et al., 2019; Hass et al., 2018). Although fewer bee species are associated with temperate forests in comparison to open landscapes (Collado et al., 2019; Winfree et al., 2007), a recent study in temperate forests highlights the importance of forest habitats for some wild bees (Smith et al., 2021). Forests offer a variety of important resources for wild bees such as flowering plants and shrubs (Bossuyt et al., 1999) and trees like willows (*Salix* sp.), oak (*Quercus* sp.) (Bertrand et al., 2019; Ulyshen et al., 2010) providing honeydew and resin (Cameron et al., 2019; Chui et al., 2021). Flowering resources present in forests are among the earliest throughout the year (Inari et al., 2012), and are important for bumblebee queens (Mola et al., 2021) and other early flying wild bees (Watson et al., 2011). Apart from forest associated bee species (Smith et al., 2021), ubiquitous species also use forests as a foraging habitat or rely on specific floral resources found in semi-open forests (Smith et al., 2019; Westrich, 2019). Therefore, forest-dominated landscapes can have a higher diversity of bees than agricultural or urban landscapes (Collado et al., 2019), and forests may play a bigger role as refugia in the conservation of red-listed wild bee species. The role of vital nesting and overwintering resources, as well as the provisioning of flower resources throughout the year in temperate forests are particularly under-investigated (Mola et al., 2021).

The specific management regime is one of the major determinants for forest composition, structure and the predominant successional stage (Braunisch et al., 2019; Schall et al., 2018) and this may strongly influence habitat suitability for wild bees. Natural disturbances like wildfire can also play a big role in forest ecosystems for wild bees (Gelles et al., 2022). However, in temperate forests, there are still knowledge gaps regarding the influence of forest management on pollinators (Rivers et al., 2018). Forest management has large, long-lasting effects on forest organisms, particularly on insects (Gossner et al., 2013; Seibold et al., 2016). Therefore, it is of crucial importance to understand the drivers of bee abundance and diversity related to forest management and to gather information about habitat structures important for threatened wild bee species that use forests for foraging or nesting (Hanula et al., 2016).

In Europe, the prevalent forest management type is "close-to-nature" silviculture, which seeks to maintain permanent forest cover, and natural regeneration while selectively logging trees (Bauhus et al., 2013). Although the goal of close-to-nature silviculture is to unite ecological aspects, like locally adapted tree species and the promotion of species with economic value in timber production (Bauhus et al., 2013), it has led to a structural homogenization at the landscape scale. Furthermore, late as well as early stages of forest succession that serve as important habitats for photophilic species (Braunisch et al., 2019; Hilmers et al., 2018) are largely missing. Therefore, forests which are managed following close-to-nature principles are mostly in the "optimum stages" of succession (optimal for harvesting) (successional stages following Drössler & Meyer, 2006; Hilmers et al., 2018). Hence, close-to-nature silviculture may not be sufficient in promoting photophilic species, which require greater light exposure observed in early and late successional forest stands.

Open patches within forests are known to be of high conservation value as they support light demanding species (Franc & Götmark, 2008; Svenning, 2002). Therefore, measures that promote open patches within closed canopy forests are suggested within forests that display a closed canopy (Eggers et al., 2010). For wild bees, forest stands with a high number of gaps and semi-open structures could provide better conditions than forests with a low canopy openness through an increase of understory cover, vascular plant richness, and warmer conditions (Dormann et al., 2020; Radmacher & Strohm, 2011). In contrast to managed forests, ~1% of forested area is protected and not used for timber production (unmanaged), allowing the forest to reach its climax stages and develop the associated canopy gaps, deadwood and structural complexity of late successional forests (Bauhus et al., 2009; Sabatini et al., 2018). Therefore, unmanaged forests could be crucial for wild bees as they offer nesting resources such as deadwood (Eckerter et al., 2021). Similarly, forest management actions such as clear-cuts, which create early successional habitats, promote flowering plants via increased sunlight exposure and could therefore also enhance habitat suitability for wild bees (Taki et al., 2018; Taki, Makihara, et al., 2013). Therefore, late successional stages and open patches following natural disturbance seem to be important for bees in forests and they could represent key habitat types to promote red-listed wild bee species. However, whether wild bees are influenced by the variation in habitat components among management types, or their respective successional stages within a landscape context is not well studied.

Knowledge about the compositional change of species communities between two or more sites (β—diversity), or management types, can give us crucial insights into which conservation strategies are useful in the given habitat (Socolar et al., 2016). This is because β—diversity can

be partitioned into two components: nestedness and turnover (Baselga, 2010). Nestedness occurs, when sites with a smaller species pool are a subset of the species pool of richer sites (Ulrich et al., 2009), while turnover occurs when species are replaced by other species (Qian et al., 2004). Often both occur simultaneously as only some species are nested or replaced (Baselga, 2010). If a change of species between sites would consist of only the nestedness component, this would imply that for the conservation of a species rich community, it is important to protect only the species rich management type, while a high turnover rate would imply the conservation of all management types and their successional stages within a landscape (Baselga, 2010).

Other open anthropogenic structures within forests could also be important for wild bees. Forests are intersected with roads, paths and trails, which create a network of road verges and forest edges throughout the forest matrix. Road verges are known to support pollinators as they offer a variety of feeding and nesting opportunities like flowers and bare ground (IPBES, 2019; Phillips et al., 2020). Greater floral diversity (Avon et al., 2010) and warmer microclimatic conditions observed on forest road verges compared to the forest interior, and the extensiveness of forest roads in managed areas (Coghlan & Sowa, 1998), highlight their potential for wild bee conservation (Hanula et al., 2016).

To study the effect of different management types, which relate to different forest successional stages and open structures at local and landscape scale on the abundance, richness and diversity of wild bees and the abundance of red-listed wild bees, we used a total of 90 pan traps in 2019 and 2020 in the low mountain range of the Black Forest (Germany) spanning an area of approximately 7000 km^2. We sampled bees on 45 plots, organized in 15 triplets of different management types: Unmanaged, close-to-nature silviculture, and small clear-cuts. In the present study, we tested the following hypotheses:

1. Within temperate forests, the abundance and diversity of wild bees benefit from a heterogeneous landscape with a mosaic of different successional stages created through different management types.
2. The abundance and diversity of bees in temperate forest ecosystems increases with the amount of open structures like clear-cuts, forest road verges, and canopy gaps at local and landscape scale.
3. The abundance and percent of red-listed wild bee species within temperate forests increase with an increasing amount of open structures within the surrounding landscape.

Our goal was to fill knowledge gaps and develop management recommendations for wild bee conservation in managed temperate forests.

2 | METHODS

Our study plots were spread throughout the Black Forest (Baden-Württemberg, Figure 1), a mixed coniferous forest dominated by Norway spruce (*Picea abies*), European silver fir (*Abies alba*), and Beech (*Fagus sylvatica*) as the most common broad leaf tree (BWI 3).

To study the effect of forest management types and their related successional stages on bees, 45 1 ha plots with different forest management types were established in 2018. From these 45 plots, 15 triplets, each consisting of one unmanaged forest-, one close-to-nature silviculture- and one plot with a small (0.5–1 ha) clear-cut logged in 2018 were selected (mean distance of 47 ± 31 km, with min 889 m and 108 km max distance). Plots within one triplet were near each other (mean distance of 2377 ± 1244 m, with min 500 m and max 5 km distance) and had similar exposition, forest type and site conditions. With this design, we wanted to reduce spillover between sites while maintaining the same bee community at the landscape scale (Figure 1). Close-to-nature plots were continuously managed throughout the study following the principles of close-to-nature silviculture, meaning single tree removal and a focus on the stability of the forest ecosystem. This leads to an even-aged high forest, which is why close-to-nature plots in our study are related to the optimum phase of the natural succession (Bauhus et al., 2009). The small clear-cuts of 0.5–1 ha were established in 2018 1 year prior to the sampling of the bees and involved the clearing of all trees and debris on the sites to increase the solar irradiance on the ground, allowing the natural regeneration of light depended, flowering plants. Small clear-cuts are therefore related to early successional stages of the forest. Cessation of management on unmanaged plots varied between 15 and 105 years, which lead to the natural accumulation of deadwood. Therefore, unmanaged plots resemble rather late successional stages of the forest in comparison to the other two management types.

2.1 | Bee sampling

We exposed 90 pan traps for 2 months from end of May to end of July in 2019 and 2020. On each plot, we deployed two pan-traps consisting of 3, 350 ml plastic bowls that were fixed at a pole at the two outer vegetation sample plots of our study (Figure 1). For each trap, we
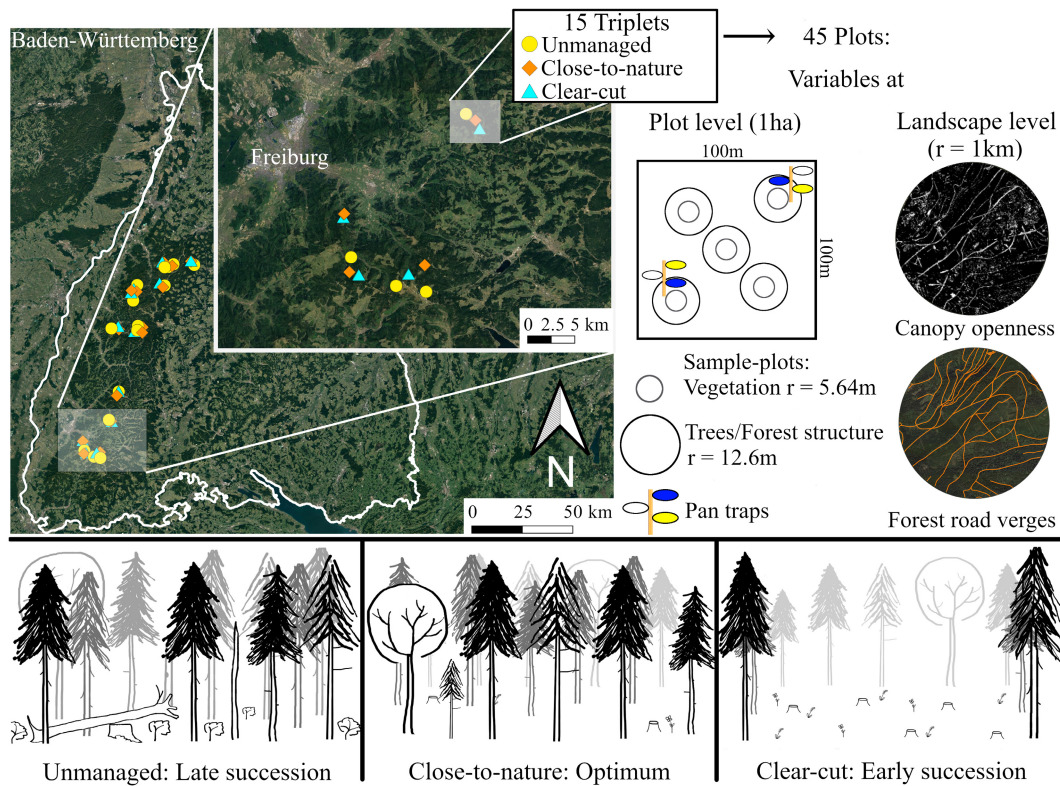
FIGURE 1   Study area in the Black Forest, Southwestern Germany, with 45 1 ha plots underlying different management types (unmanaged forests, close-to-nature silviculture, small (0.5–1 ha) clear-cuts. Three plots, one of each management type, are arranged in "triplets" with similar forest type and site conditions and with a distance to each other of 500–5000 m. On the right-hand side, the sampling design for collecting vegetation data (open circles, small radius), forest structure (open circles, large radius), the location of the pan-traps in each plot and two landscape level variables (gaps and forest roads) are depicted. Below: a depiction of the different management types and their related successional stages examined in this study. Map data: Google

used one white, one blue, and one yellow bowl. Bowls were fixed randomly at 30, 60, and 90 cm height of the poles and filled each 150 ml water and propylene glycol solution to slow down the decay of specimens (Rubene et al., 2015). One drop of odorless detergent was added to break the surface tension. Traps were emptied every 2 weeks and specimens were stored in 70% ethanol. In the laboratory, bees were washed, dried, pinned, and identified using a microscope (Bresser, Science ETD-201) and identification keys (Amiet, 1996; Amiet et al., 1999, 2001, 2004, 2007, 2010). Several species were grouped to a species complex as they were not clearly distinguishable with the proposed method: *Bombus terrestris*, *-lucorum*, *-cryptarum*, and *-magnus* to *Bombus terrestris* complex; *Halictus simplex*, *-eurygnathus* and *-langobardicus* to *Halictus simplex* complex. Approximately 50% of German bee species are red-listed and hence are important for basic and applied research when found in any sampling (Neumüller et al., 2020; von Königslöw et al., 2022; Westrich et al., 2011). Honeybees were excluded from the analysis, as we wanted to focus on wild bees. Voucher specimens were deposited at the University of Freiburg.

Bees were associated with a certain habitat type (e.g., forest associated) if the bee species are found in mainly the given habitat according Westrich (2019). Bees which could not be associated with forest habitat were classified as ubiquitous.

2.2 | Environmental variables

To characterize environmental conditions, we measured several variables at plot- and landscape scale ($r = 1$ km).

2.2.1 | Plot scale

Variables at plot scale were recorded on five permanent sample plots with two radii ($r = 5.56$ m; $r = 12.6$ m) established at every plot (Figure 1). On the smaller sample plots, all vascular plants were identified to species level and the associated cover was estimated. On the larger sample plots, deadwood was recorded as the volume of standing and lying dead trees >7 cm diameter at

breast height. As bees rely on flowering resources, we calculated the average cover of flowering plants (%) that are pollinated by insects for every plot. We further used richness of flowering plants to gauge whether species rich plots would harbor a richer bee community. Ground cover (%) was assessed to see whether a low ground cover could result in a higher availability of nesting sites for ground nesting species. To characterize management types, we used tree cover (%), shrub cover (%), light coefficient (%), and deadwood volume (m^3) (Eckerter et al., 2022). Furthermore, we tested whether the flower cover (%) was higher for a specific management type. Variables at the plot scale were averaged from the five sample plots for both years creating one value per plot.

2.2.2 | Landscape scale

To incorporate variables within the maximum flight distances of most bees, we measured data at the landscape within a 1 km buffer around the plots (Zurbuchen & Mueller, 2012). As bees are influenced by landscape composition and heterogeneity (Hass et al., 2018), we used land cover data from the official topographic-cartographic information system ATKIS (Digitales Basis-Landschaftsmodell (Basis-DLM), n.d.) and calculated the area (ha) covered by forest, grassland, seminatural habitats of woody plants, seminatural heathland and the length of forest roads around every plot using QGIS (QGIS.org, 2021). Based on these land cover classes, we calculated landscape heterogeneity with LecoS (Jung, 2016). Road length, including paths and trails was used as a proxy for road verges to test their importance for forest pollinators. Additionally, we calculated the proportion of gaps and semi-open forest in the forest structure. Gaps and semi-open forest were automatically detected based on canopy height models derived from stereo aerial imagery and a LiDAR-based Digital Elevation Model (Zielewska-Büttner et al., 2016). Gaps were defined as canopy openings of at least 10 m^2 with a vegetation height of <1 m while semi-open forests were defined as areas of at least 0.5 ha, vegetation height of >1 m and canopy cover of <60%. From these two variables, we calculated canopy openness, defined as the percentage of canopy gaps and semi-open forest within 1 km radius around each plot. Before model building, we checked for multicollinearity with the "cor" function from R. Only variables with moderate or low correlation (Pearson's; $r < |.7|$) were used in subsequent models. As we were interested in the influence of landscape heterogeneity, we did not use the land-cover data for forest, grassland and seminatural woody habitats, as they were highly correlated with heterogeneity ($r > .7$; Appendix S1). Also,

we used flower instead of ground cover as floral resources play a more important role in bee ecology (Roulston & Goodell, 2010) ($r = .7$; Appendix S1).

2.3 | Statistical analyses

2.3.1 | Management characteristics

To test the influence of management types on bee abundance and diversity, we used generalized linear mixed models (glmms; glmmTMB; Brooks et al., 2020) with management as a fixed effect and triplet as a random effect. Variables were pooled to plot scale prior to analysis. Response variables were light coefficient (%), cover of trees, shrubs (%), and deadwood volume (m^3) (Appendix S2). For light coefficient, tree, shrub, and flower cover, we used a beta distribution, while deadwood volume was modeled with a Gaussian distribution. All analyses were conducted in R (R Development Core Team, 2021).

2.3.2 | Wild bee community

To assess the compositional change of species between different management types, we looked at nestedness and turnover rates of beta diversity for every triplet. We used the "beta.multi" function with the Sørensen family of the betapart-package (Baselga & Orme, 2012), which calculates the value of overall beta diversity, measured as Sørensen dissimilarity and the associated turnover and nestedness components for multiple sites (Baselga, 2010). With this, we were able to see whether all management types would be important to foster all bee species or whether species rich sites would be sufficient. To check for spatial autocorrelation of the plots as well as triplet centroids, we conducted Moran's I tests (ape-package; Paradis & Schliep, 2019). The data were randomly disbursed (Appendix S3). We used ANOVA to test whether turnover or nestedness components differ between triplets.

As richness and diversity analyses are dependent on sample size, we calculated the sample coverage using the iNext-Package (Hsieh et al., 2020). For every management type, a high sample coverage of at least 98% was reached (Appendix S4). To test the influence of plot- and landscape-level variables on the abundance, richness, (Shannon) diversity of wild bees, as well as the abundance- and proportion of red-listed species we used glmms. For the abundance models, we used a Benjamini-Hochberg correction (Verhoeven et al., 2005). All variables and bee data of both years were pooled to plot level

prior to analysis. For plot level, we used management, cover, and richness of insect pollinated plants and at landscape level landscape heterogeneity, length of forest road verges and canopy openness as fixed effects (Appendix S2). For abundance and richness responses, we used a Poisson distribution, while diversity was modeled with a Gaussian- and percent of red-listed bee species with a beta distribution. To account for zeroinflation within the beta models we used ziformula = ~1. To incorporate the hierarchical structure of the sampling design (1|Triplet) was used as a random effect. For Poisson models, Plot_ID was used as an observation level random effect to account for overdispersion. Model residuals were inspected using the DHARMa-Package (Hartig, 2021). To test for spatial autocorrelation, we used Moran's I tests on all model residuals using the DHARMa-Package. The data were randomly disbursed for four models (Appendix S3). For the abundance model of the red-listed species, we added latitude and longitude as predictors to account for a potentially spatial signal. Following initial modeling of management effects, estimated marginal means of models were analyzed with post hoc tests (emmeans-Package; Lenth, 2020).

Wild bee community composition and the influence of management, plot- and landscape-level variables were analyzed with a nonmetric multidimensional scaling using the Bray–Curtis distance (vegan-Package; Oksanen et al., 2021). Additionally, we applied a PERMANOVA using the same variables as in the glmms (Appendix S2).

3 | RESULTS

3.1 | Management types

Clear-cuts were characterized by a high light coefficient and low cover of trees, while unmanaged plots had a high deadwood volume and a higher shrub cover in comparison to the other management types. Flower cover did not differ significantly between management types but was slightly higher on clear-cut and unmanaged plots (Appendix S5).

3.2 | Wild bee community

In 2019 and 2020, we collected 12,333 wild bee individuals from 20 genera and 141 species. The most common wild bee species with 2943 individuals (24% of catches) was *Bombus terrestris* comp. followed by *Bombus pratorum* with 2761 individuals (22% of catches). Of the 141 species collected, 26 were forest associated species. Of those 26 forest species, 21 are found in predominantly

semi-open forests or forest edges. Then, 61 species were ubiquitous and found in semi-open forests, 38 were cuckoo bees, and 16 were associated with open landscapes (Westrich, 2019). Thirty-seven (26%) species were on the red list (Westrich et al., 2011) and of those, twenty (52%) are found in forest edges and semi-open forests (Appendix S6).

3.3 | Beta diversity and composition

Beta diversity for the triplets ranged from 0.43 to 0.65 (Figure 2a) and were comprised of a higher, but not significant (ANOVA, $F_{1,28} = 2.47$, $p = .106$) proportion of the nestedness- (0.30 ± 0.11) in comparison to the turnover component (0.24 ± 0.07) (Figure 2b). Clear-cut plots harbored 47 exclusive species, while unmanaged plots harbored 11—and close-to-nature plots 7 exclusive species.
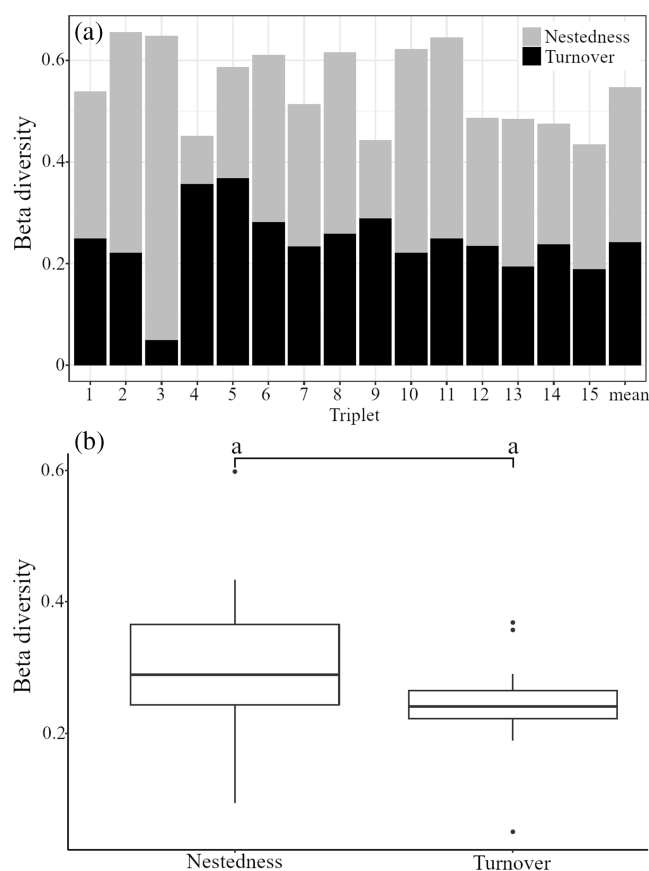

FIGURE 2 (a) Beta diversity (Sorensen dissimilarity) of the 15 triplets partitioned into nestedness and turnover components with the beta part package. (b) Boxplots for beta diversity components. Boxes represent the interquartile range, while bold line represents the median. Whiskers show the 25th and 75th quartiles, respectively. Different letters above the boxes indicate a significant difference between the means. Tested with ANOVA

TABLE 1 Final generalized linear mixed models showing the relationship of plot (1 ha) and landscape level ($r = 1$ km) predictor variables and the wild bee community. Abundance models are still significant after Benjamini–Hochberg correction

| Model and tested variables	Estimate ± SE	Z-value	*p*-Value
Bee abundance			
Management: close-to-nature	−1.2940 ± 0.2180	−5.934	<.0001
Management: unmanaged	−1.5911 ± 0.2533	−6.280	<.0001
Canopy openness	7.5729 ± 3.3630	2.252	.0243
Flower cover	0.0112 ± 0.0049	2.259	.0239
Forest paths	−0.0116 ± 0.0148	−0.787	.4315
Landscape heterogeneity	−0.6786 ± 0.5660	−1.199	.2305
Flower richness	−0.0026 ± 0.0113	−0.235	.8139
Bee richness			
Management: close-to-nature	−0.6990 ± 0.1143	−6.113	<.0001
Management: unmanaged	−0.8935 ± 0.1344	−6.648	<.0001
Canopy openness	2.6337 ± 1.8607	1.415	.1569
Flower cover	0.0044 ± 0.0027	1.656	.0977
Forest paths	0.0055 ± 0.0082	0.672	.5019
Landscape heterogeneity	0.2930 ± 0.3164	0.926	.3543
Flower richness	−0.0049 ± 0.0059	−0.832	.4052
Bee diversity			
Management: close-to-nature	−0.18631 ± 0.11056	−1.685	.0920
Management: unmanaged	−0.50110 ± 0.12862	−3.896	<.0001
Canopy openness	−1.07372 ± 1.79812	−0.597	.5504
Flower cover	0.00425 ± 0.00260	1.635	.1021
Forest paths	0.01560 ± 0.00803	1.942	.0521
Landscape heterogeneity	0.71859 ± 0.31206	2.303	.0213
Flower richness	0.00027 ± 0.00589	0.046	.9634
Abundance of red listed species			
Management: close-to-nature	−0.7314 ± 0.2078	−3.519	.00043
Management: unmanaged	−1.6511 ± 0.2567	−6.430	<.0001
Canopy openness	−9.4583 ± 4.5868	−2.062	.03920
Flower cover	0.0030 ± 0.0055	0.550	.58238
Forest paths	0.0459 ± 0.0184	2.493	.01267
Landscape heterogeneity	1.5085 ± 0.7186	2.099	.03579
Flower richness	−0.0094 ± 0.0110	−0.855	.39270
Latitude	−1.8767 ± 0.3105	−6.044	<.0001
Longitude	2.0752 ± 0.3492	5.941	<.0001
Percent of red listed species			
Management: close-to-nature	−0.24778 ± 0.13477	−1.839	.06598
Management: unmanaged	−0.19599 ± 0.15681	−1.250	.21134
Canopy openness	3.0029 ± 1.9127	1.570	.11642
Flower cover	−0.00059 ± 0.00286	−0.209	.83461
Forest paths	0.03196 ± 0.00873	3.657	.00025
Landscape heterogeneity	0.47462 ± 0.33616	1.412	.15797
Flower richness	0.00549 ± 0.00675	0.814	.41581
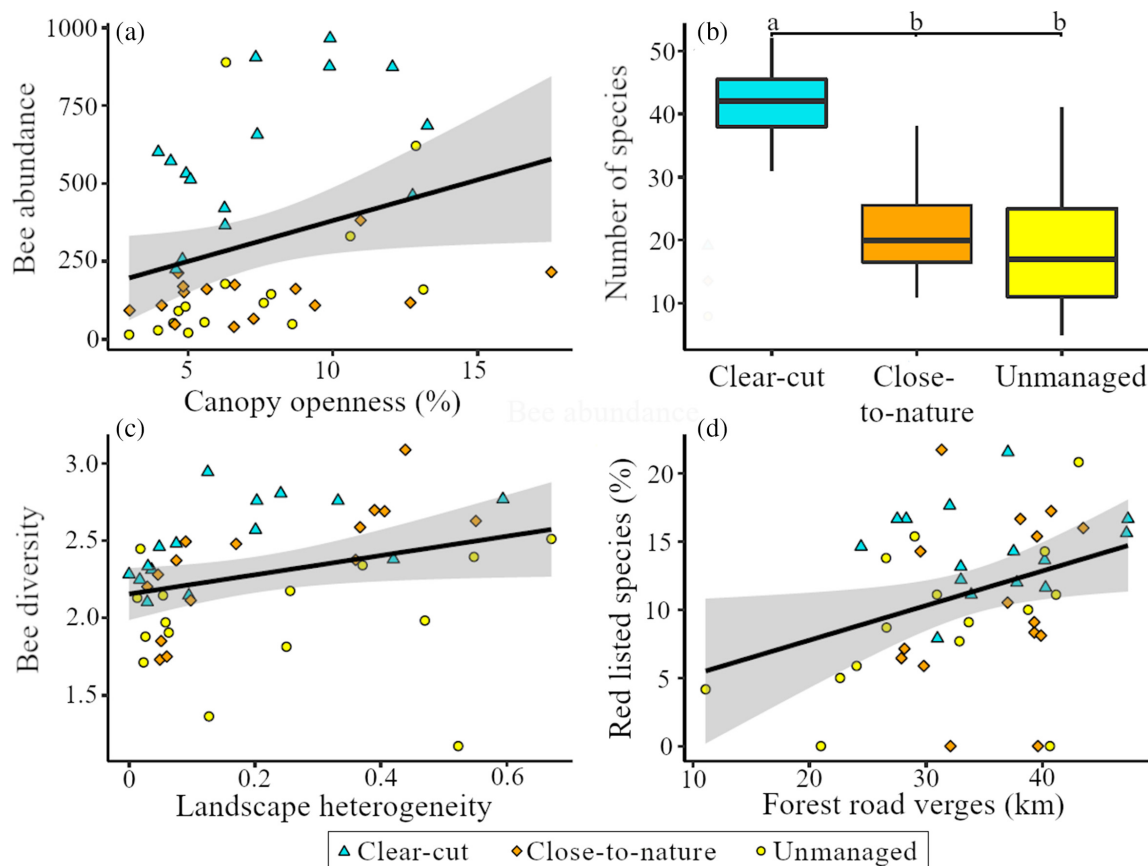
FIGURE 3 (a) Relationship between wild bee abundance and canopy openness within 1 km around the plots. The black line shows a linear regression. The gray area represents the 95% confidence interval. (b) Boxplots for the number of species per management type. Boxes represent the interquartile range, while bold line represents the median. Whiskers show the 25th and 75th quartiles, respectively. Different letters above the boxes indicate a significant difference between the means. Tested with a glmm and afterward with a post hoc Tukey test with the emmeans-package. (c) Relationship between wild bee diversity and landscape heterogeneity within 1 km around the plots. (d) Relationship between the percent of red listed wild bee species and the length of forest road verges within 1 km radius around the plot

3.4 | Effects of local and landscape variables

Wild bee abundance was highest on clear-cut (post hoc both; $p < .001$) ($n = 7851$; mean $= 523.2 \pm 228.82$) in comparison to close-to-nature (2067; 137.8 ± 77.51) and unmanaged forest plots (2418; 161.2 ± 175.34). Close-to-nature and unmanaged forest plots did not differ significantly. Abundance increased with increasing flower cover and was higher on plots that were situated in forests with a higher canopy openness (Table 1) (Figure 3a).

Wild bee richness was related to management exclusively. It was highest on clear-cut (post hoc both; $p < .001$) (124; 40.90 ± 6.37) in comparison to close-to-nature (72; 20.86 ± 7.32) and unmanaged forest plots (68; 18.06 ± 9.81), which did not differ significantly (Figure 3b).

Wild bee diversity was highest on clear-cut (2.49 ± 0.29) and close-to-nature (2.32 ± 0.36) plots, and lowest on unmanaged plots (1.97 ± 0.42) (post hoc both; clear-cut–unmanaged $p < .001$; close-to-nature–unmanaged $p = .006$). Wild bee diversity increased with increasing landscape heterogeneity (Table 1).

3.4.1 | Red-listed species and measures of openness

Abundance of red-listed wild bees was highest on clear-cut (271; 18.06 ± 15.05), followed by close-to-nature (168; 11.2 ± 12.53) and unmanaged plots (62; 4.13 ± 7.55) (post hoc; clear-cut–unmanaged $p < .001$; close-to-nature–unmanaged $p = .003$; clear-cut –close-to-nature $p = .01$). Abundance and proportion of red-listed wild bees increased with the length of forest road verges in the landscape (Table 1) (Figure 3d). The abundance of red-listed species increased with landscape heterogeneity as well as canopy openness (Table 1).

FIGURE 4 Results of the nonmetric multidimensional scaling (NMDS) based on the Bray–Curtis distance, calculated with the vegan package. Stress factor: 0.168. Arrows show the direction of the analyzed variables of the PERMANOVA
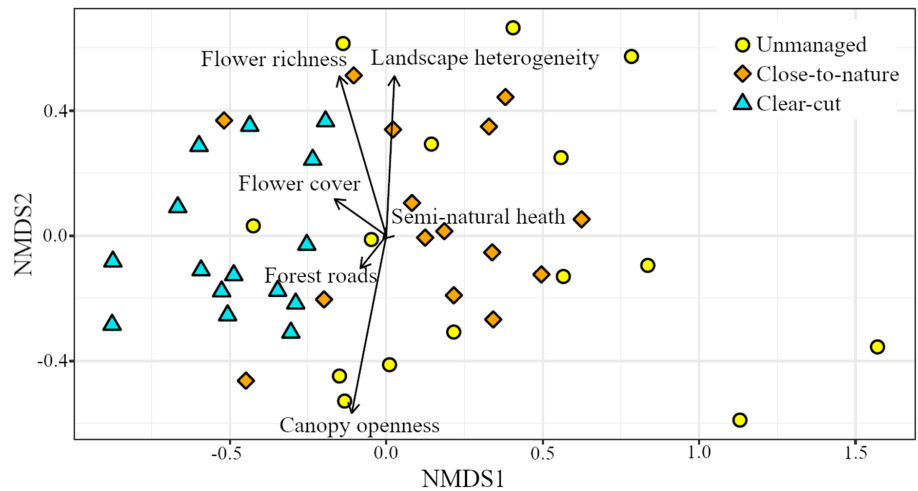
3.4.2 | Wild bee community composition

Wild bee community composition was structured by primarily management type (Figure 4). PERMANOVA revealed significant influences of management ($p = .001$, $R^2 = .250$), flower cover ($p = .035$, $R^2 = .035$), canopy openness ($p = .001$, $R^2 = .112$) and landscape heterogeneity ($p = .02$, $R^2 = .040$) for the community composition of wild bees (Appendix S7).

4 | DISCUSSION

We show that close-to-nature forestry alone is not sufficient to support the entire community of wild bees in forests. Instead, both early and late successional stages created by small clear-cuts as well as unmanaged sites which exhibit characteristics of old growth forests are important for conservation. Wild bee abundance was positively related to canopy openness while their diversity increased with landscape heterogeneity. Furthermore, we show the relevance of forest road verges for threatened wild bee species in managed forests.

4.1 | Beta partitioning and conservation implications

We hypothesized that to support all wild bee species within the landscape, all management types and successional stages would be important. Our analysis revealed that one triplet (Triplet 3; Figure 3a) had a higher proportion of the nestedness component. A proposed explanation for a high nestedness is habitat heterogeneity, where resource poor habitats with a low heterogeneity favor generalist species (Hylander et al., 2005). Consequently, high species turnover is related to high environmental

heterogeneity, as it promotes specialization and niche differentiation of species, and thus species that thrive under different conditions (Stein et al., 2014). Our results show three triplets (Figure 3a; Triplets 4, 5, and 9), which consisted of a higher turnover than nestedness component. A further inspection of these revealed that the unmanaged plots of these triplet's exhibited characteristic features of old growth forests, namely canopy gaps and standing deadwood. On average nestedness and turnover components did not differ significantly, which means on average all management types and therefore successional stages were important to promote wild bees. As early successional habitats harbored the most species-rich wild bee communities, we deduct that unmanaged and close-to-nature plots probably have some structures like deadwood or resources like resin (Chui et al., 2021) which are important for some wild bee genera like, for example, *Megachile or Hylaeus* (Eckerter et al., 2021). Therefore, while early successional forests can be considered important for wild bee conservation in forests (Roberts et al., 2017), unmanaged forests which exhibit old-growth characteristics such as large standing deadwood structures are also important. These results support recent literature, showing that while clear-cuts in forests support high number of species, they exhibit communities with lower trait diversity (Fortuin & Gandhi, 2021). Hence, conservation measures should consider the landscape context and ensure the presence of both early and late-successional forests within the foraging range of wild bees.

4.2 | Wild bees, management types, and their related successional stage

Clear-cut plots supported the highest abundance, while unmanaged and close-to-nature plots had similar low

abundances. Clear-cuts had a richer and more diverse wild bee community compared to unmanaged and close-to-nature forests. Furthermore, the abundance of red-listed bee species was highest on clear-cut plots. The importance of early successional habitats for bees in forests, created by natural disturbances or forest management, is well known (Galbraith et al., 2019; Roberts et al., 2017). Contrary to our expectations, unmanaged forest plots contained lower abundance and species richness of bees. Studies found conflicting results when comparing bee communities of old growth- (late successional) to managed forests. While there is a report of a higher diversity of bees in an old growth forest in Japan (Taki, Okochi, et al., 2013) another recent study from the United States suggests there is no significant difference in abundance, diversity, and evenness (Ulyshen et al., 2020). Interestingly, managed forests in the tropics have been shown to contain a higher diversity of wild bees (Hoehn et al., 2010). These results point to the conclusion that habitat suitability for bees in forests is related to a complex reality of structural, environmental and successional differences in these systems rather than the mere status of the forest. In our case, only few unmanaged plots showed old-growth forest characteristics such as high canopy openness and complex heterogeneous structural composition. Most unmanaged plots exhibited high canopy closure which is less suitable for photophilic wild bees (Hilmers et al., 2018). Unmanaged plots used in our study have been so for 15–107 years. Canopy cover of forest reserves in mixed-mountain forests have been shown to increase approximately five decades after management cessation before decreasing again (Braunisch et al., 2019), due to natural disturbances as well as the natural dieback of trees. The time it takes to reach late successional stages is nonlinear and dependent on specific site conditions such as exposition, weather and disturbance events, which can accelerate or dampen the succession (Bartsch & Röhrig, 2016). Accordingly, to derive exact values after which time an unmanaged site will reach the maximum conservation value for bees is not trivial; however, the majority of our unmanaged forests are not yet in the age in which the initial increase in stand density cannot yet be expected to be overruled by the development of open structures.

4.3 | Wild bees and landscape variables

We hypothesized an increasing openness within the landscape would result in a higher abundance and diversity of wild bees. Indeed, plots surrounded by forests with a high canopy openness supported more bee individuals, but diversity was not affected. While Rodríguez and

Kouki (2015) found the proportion of early successional habitats within the landscape was positively related to the abundance and diversity of bees, Rubene et al. (2015) looked at the proportion of early successional habitats and found no influence on wild bee abundance but on species richness of ground nesting bees. As we included gaps of 10 m^2 or greater in our definition of canopy openness our results emphasize the role of small gaps in addition to larger open sites.

Wild bee diversity was related to landscape heterogeneity, implying with a higher proportion of grassland and seminatural habitats within 1 km a more diverse species community was present at the forest plots. This was already shown in agricultural land, as with a more heterogeneous landscape, a higher variety of food and nesting resources is available at the landscape scale, which in turn can support more wild bees with different niche requirements (Hass et al., 2018). This emphasizes the role forests play for ubiquitous species of wild bees, which made up a large proportion (42%) of species we found. The abundance of red-listed species showed a small spatial pattern, which might point to a limitation in their spreading ability or other historic effects.

The abundance and proportion of red-listed bee species increased significantly with increasing length of forest road verges around the plots. In tropical forests, roads that intersect the forest matrix can have a negative impact on forest specialists, which tend to avoid forest edges created by roads (Laurance et al., 2009). In boreal forests, bees use anthropogenic linear corridors created for energy exploration as corridors of movement, and show increased abundance and richness on these corridors as a result (Nelson et al., 2021). This is in accordance with other studies which show that forest roads and logging legacies might be crucial components for wild bees in managed forests (Jackson et al., 2014; Twerd et al., 2021). Recent studies suggest that canopies have a higher diversity of wild bees and for some wild bees, resources offered from trees are a crucial part of their diet (Bertrand et al., 2019; Urban-Mead et al., 2021). Apart from flowering herbs (Avon et al., 2010), the increased light availability on forest edges also favors the occurrence of photophilic trees like *Crataegus* sp., *Malus sylvestris*, *Prunus avium*, several *Salix* sp. and shrubs like *Rosa canina* (Bartsch & Röhrig, 2016). As most, and especially threatened species of our study rely on forest edges (Appendix S6), verges and inner edges created by forest roads could be crucial for wild bees as dispersal and foraging corridors. The flowering resources of the forest road verges could be especially important in resource depleted managed forests where early and late successional sites are not present throughout the forest matrix.

In general, temperate forest ecosystems might also play a substantial role for some wild bee species with an early or late phenology. Especially within deciduous forests, where flowering resources available prior to leaf flushing might support wild bees with an early phenology, (e.g. bumblebee queens, Mola et al., 2021). However, a study within a mixed high conifer forest suggests that there also can be considerable variability between early-season and midsummer wild bee communities (Rhoades et al., 2018). In our study, we assessed only species which are present from end of May to July and therefore might have missed some interactions of wild bees and forest ecosystems that are based on seasonal effects. Therefore, a more rigid study about important structures and features for wild bees, like open soil nesting sites along forest road verges or flowering herbs throughout the year (Proesmans et al., 2019), is needed.

4.4 | Wild bee community composition

Community composition was structured by local factors, namely management and flower cover, as well as landscape factors such as canopy openness and landscape heterogeneity. While floral cover has been shown to impact bee communities (Neumüller et al., 2020), the effect of management is in contrast to a study where forest openings did not have an effect on the community composition between openings and mature forest (Roberts et al., 2017). However, in our study, early successional habitats were sampled 1–2 years after the measure, while the above-mentioned study sampled after 4–8 years. Therefore, communities may be especially reactive in the early years after the measure, before vegetation height and the regeneration of woody plants increases, altering resource availability on the sites (Mathis et al., 2021; Rivers & Betts, 2021). For landscape variables, a higher canopy openness and landscape heterogeneity changed the species composition. This could mean that under these conditions, the suitability of forest habitats for wild bee species which rely on semi-open forests and forest edges, could improve.

5 | IMPLICATIONS FOR WILD BEE CONSERVATION IN MANAGED FORESTS

We found convincing evidence that bees rely on early and late successional stages within the landscape and that open structures like clear-cuts, canopy gaps, semi-open forest sites as well as forest road verges within forest-dominated landscapes promote the abundance and diversity of wild bees. This is particularly true for threatened wild bee species. Open patches within the forest matrix can manifest following natural disturbances like wildfire or windthrow, which can be beneficial for wild bee abundance and diversity (Galbraith et al., 2019; Wermelinger et al., 2017). However, as preventing disturbances is a major objective in managed forests, they typically show a lower abundance of naturally open structures than their unmanaged counterparts. Active measures at local and landscape scale might therefore be needed to aid pollinator conservation in these forests.

At local scale, the establishment of small clear-cuts, or partial cutting (up to 30% of the standing biomass) can be easily integrated into regular forest management as it requires only minor adaptation of the harvesting regime. In addition, specific measures such as prescribed burning can be useful depending on the type of forest (Eckerter et al., 2022; Franc & Götmark, 2008; Rodríguez & Kouki, 2015). In addition, we showed that road verges provide open habitat for wild bees in managed forests. Management of road verges can be improved by shifting mulching measures toward the end of the growing season or by mulching every 2 years. This will help to reduce insect mortality. Moreover, increasing the share of dead-wood, for example, by retention forestry or by active girdling of trees in dense stands, will enhance nesting sites for cavity-nesting bees (Eckerter et al., 2021).

At the landscape scale a heterogeneous forest landscape, which offers both early and late successional stages in addition to close-to-nature sites in the optimum phase could help to foster bees and many other groups of organisms (Fischer et al., 2010; Seibold et al., 2016). However, this requires large areas where natural disturbances (flooding, wind-throw, wildfire, large grazers) are allowed to modulate habitat heterogeneity (Odanaka & Rehan, 2020). National parks and wilderness areas may provide such conditions. In largely human-modified landscapes, which are typical for Europe, integrating the proposed measures into landscape-scale concepts, that ideally become part of the regular forest planning in state-owned forests, and of contractual conservation programs in communal and private forests, will be key to ensure their implementation at sufficiently large scales. Workshops for foresters and landowners, demonstrating how to promote or conserve important habitat features for wild bees within the real-world constraints of their work, could raise awareness and the acceptance of such programs (Rivers et al., 2018).

DATA AVAILABILITY STATEMENT

The data has been uploaded to the Dryad server and is currently under review. The link below is the preview link for the dataset. https://datadryad.org/stash/share/NHHgyT5vWDDRXVEtMuwS6gIqYo5XwRpOSwiHEVPx1Zs.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.