

RESEARCH ARTICLE

Landscape diversity, habitat connectivity, age and size determine the conservation value of limestone quarries for diverse wild bee communities

Felix Kirsch^{1,2}  | Annika Hass¹  | Thomas Alfert³ | Catrin Westphal^{1,4} 

¹Functional Agrobiodiversity & Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

²Thünen Institute of Biodiversity, Braunschweig, Germany

³Nature and Biodiversity Conservation Union (NABU), Rhede, Germany

⁴Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Germany

Correspondence

Felix Kirsch
Email: kirsch.felix.ecology@gmail.com

Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: 405945293 and 493487387

Handling Editor: Yi Zou

Abstract

1. Abandoned and even active limestone quarries (excavation sites) can represent important secondary habitats for many species, including wild bees, associated with dry grasslands, which are threatened biodiversity hotspots in Europe. However, is not well understood how interactions between local habitat and landscape characteristics influence the value of limestone quarries for wild bees and how this could guide conservation schemes.
2. We studied how wild bee communities in limestone quarries are affected by landscape variables (connectivity to neighbouring dry grasslands, landscape diversity), local quarry characteristics (area, age, woody vegetation cover, flowering plant species) and their interactions. We surveyed bee communities during 208 transects in 19 quarries in southern Lower Saxony, Germany.
3. In total, we recorded 114 bee species (2360 individuals), including 35 endangered species. High flowering plant species richness positively affected bee abundance and richness. Large quarry area was important for determining the presence of endangered bee species. High levels of woody vegetation cover had a negative effect on bee abundance and richness. Bee abundance and richness can increase with quarry age, but only at sites with moderate woody vegetation cover.
4. We found potentially positive interactions between quarry age and landscape diversity and/or habitat connectivity to neighbouring dry grasslands. In particular, high habitat connectivity ensured stable richness of endangered species in old quarries.
5. *Synthesis and applications.* Observed negative effects of high woody vegetation cover on bee communities highlight the importance of local management to reduce shrub encroachment and reset successional processes in limestone quarries. Local management is particularly important in old quarries of great ecological value, where the adverse impact of high woody vegetation cover on wild bees appears to be most severe. Large and old quarries with high connectivity to neighbouring dry grasslands are especially valuable for endangered bee species.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

Therefore, landscape-scale restoration and conservation of dry grasslands is the most promising approach to promote endangered bee species through enhanced habitat connectivity.

KEYWORDS

calcareous grassland, landscape heterogeneity, mining, pollinator, red list of threatened species, restoration, semi-natural habitat, succession

1 | INTRODUCTION

Grasslands are crucial for maintaining biodiversity worldwide, but are under severe threat due to land use change causing habitat degradation, fragmentation and loss (Fartmann, 2024). In Central Europe, the centuries-old practices of traditional grazing and hay-making have led to the development of extensive grasslands, which are crucial habitats for numerous plant and animal species (Dengler et al., 2014). In particular, dry semi-natural grasslands with low productivity are among the most plant species rich habitats worldwide (Wilson et al., 2012) and represent valuable habitats for insects (Fartmann, 2024). Besides land use intensification, these grasslands are threatened by the abandonment of traditional land use practices (Janssen et al., 2016; Poschlod & Wallis De Vries, 2002). Considering these multiple threats, conservation strategies are needed to promote the local and landscape-scale restoration and conservation of dry grasslands (Fartmann, 2024).

In the context of dry grassland conservation, secondary habitats created by non-agricultural land use, such as mining, may be important (Twerd & Banaszak-Cibicka, 2019). Excavation sites in limestone (i.e. limestone quarries) have the potential to serve as substitute habitats for insects usually inhabiting dry grasslands (e.g. Beneš et al., 2003; Münsch & Fartmann, 2021), an important function given the value of dry grasslands as insect habitats (Fartmann, 2024) and alarming reports of ongoing insect decline (Wagner et al., 2021). The reason why limestone quarries can serve as dry grassland substitutes are shared environmental characteristics (Ellenberg, 1996) that lead to the establishment of similar plant communities when site conditions, management and connectivity to source habitats are suitable (e.g. Novák & Konvička, 2006; Pitz et al., 2018).

The conservation value of limestone quarries as substitute habitats for dry grassland inhabiting insects likely depends on local site characteristics. According to species–area relationships (Rosenzweig, 1995), large quarries can sustain more species-rich insect communities (e.g. Krauss et al., 2009). Moreover, quarry age could be an important factor, as insect communities in quarries may diversify over time due to the immigration of new species (Twerd et al., 2021). However, site age does not necessarily have a positive influence on insect diversity in quarries (Krauss et al., 2009), maybe because potential benefits are negated by progressive succession and the associated loss of vital open habitat patches (Gardein et al., 2022; Kettermann et al., 2022). For instance, structures with little shrub cover, favourable micro-climate, flower-rich pioneer

vegetation and/or bare ground could disappear from old quarries, resulting in the loss of nesting opportunities and important food and host plants for bees and butterflies associated with dry grasslands (Kettermann et al., 2022; Münsch & Fartmann, 2021). Thus, it is crucial to understand interactive effects between habitat age and successional processes in quarries.

Besides local site characteristics, the surrounding landscape may determine the conservation value of limestone quarries as replacement habitats for dry grasslands. Insects are unlikely to colonize and establish stable populations in quarries isolated from suitable dry grasslands serving as source habitats (Klaus et al., 2021). Thus, insect populations in quarries could benefit from heterogeneous landscapes with many dry grasslands and other semi-natural structures and high habitat connectivity between habitat patches (Beyer et al., 2021; Brückmann et al., 2010). Additionally, it is likely that landscape parameters and local quarry characteristics interact with each other (George & Zack, 2001). For example, low local habitat quality of a quarry could be compensated by high landscape heterogeneity and vice versa (Krimmer et al., 2019). Despite these potentially crucial mechanisms, the landscape context is rarely considered in biodiversity studies in quarries (e.g. Tropek et al., 2012; Twerd et al., 2021). To our knowledge, only a few studies consider landscape parameters (e.g. Beneš et al., 2003; Kettermann et al., 2022; Münsch & Fartmann, 2021), but not their interactions with local site characteristics.

Considering the need to restore dry semi-natural grasslands as one of the most species-rich habitats in Europe and other regions, we studied the role of limestone quarries as secondary habitats for dry grassland insect communities. In our study, we focused on wild bees since both dry grasslands and limestone quarries represent suitable habitats for many bee species, offering important forage and nesting resources for common, but also for many threatened and specialized species (e.g. Kettermann et al., 2022; Theunert, 2002; Westrich, 2018). Extending the scope of a previous study (Krauss et al., 2009), we investigated interactive effects of local site characteristics, landscape diversity and connectivity to neighbouring calcareous grasslands on bee communities in limestone quarries with special emphasis on endangered species. Our aim was to gain a better understanding of how landscape-scale conservation management of limestone quarries could contribute to the reversal of bee decline and conservation of endangered species.

We hypothesize (I) that the abundance and species richness of wild bees in general, and richness of endangered bee species

in particular, increase with quarry area and flower resources. We expect (II) that quarry age has a positive effect on bee abundance and richness, but only if quarries still have sufficient open patches in early successional stages not dominated by shrubs and trees. We hypothesize (III) that bee abundance and richness increase with increasing landscape diversity and connectivity between quarries and dry grasslands and that (IV) low landscape quality (homogeneous landscapes, low connectivity) is compensated by high local habitat quality determined by quarry area and age and vice versa.

2 | MATERIALS AND METHODS

2.1 | Study sites and local site characteristics

We surveyed wild bees in 19 abandoned limestone quarries near Göttingen (Lower Saxony, Germany; [Figure S1](#)). The sites represented a subset of quarries studied by [Krauss et al. \(2009\)](#) and [Alfert \(2000, unpublished data\)](#). We calculated quarry ages in years ([Table S1](#)) using information provided by [Krauss et al. \(2009\)](#) and [Alfert \(2000, unpublished data\)](#) who estimated quarry ages based on historical maps and information of landowners. Using aerial images taken with an unmanned aerial vehicle, we calculated area (m²) and woody vegetation cover (%; i.e. trees and shrubs) of each quarry in QGIS (QGIS Development Team, [2022; Table S1](#)). For details, see [Section 1.1](#) in Supporting Information.

2.2 | Study landscapes and landscape metrics

Four buffer zones were established, extending 250, 500, 750 and 1000m, respectively, from the edges of the quarries into the surrounding landscape (QGIS Development Team, [2022](#)). Landscape elements within each buffer were classified into 14 different land use types ([Table S2](#)). Landscape parameters were calculated in R (R Core Team, [2022](#)). We calculated the landscape diversity for each of the four buffers with the Vegan package ([Oksanen et al., 2022](#)) using the Shannon–Wiener diversity index ([Beyer et al., 2021; Table S3](#)). Landscape diversity can be beneficial for bees by providing complementary habitat types ([Beyer et al., 2021](#)). However, bees in quarries might depend more on specific habitat types of high ecological value in the surrounding landscape that provide similar conditions ([Brückmann et al., 2010](#)). For that reason, we additionally calculated for each of our study sites the habitat connectivity to neighbouring dry grasslands and other quarries. For this, we used a modified version of Hanski's Connectivity Index $S_i = \sum e^{-d_{ij}} \times A_j$, where S_i is the connectivity of a study site i , d_{ij} is the edge-to-edge distance between the study site i and adjacent dry grasslands and quarries j (in km) and A_j is the area of adjacent dry grasslands and quarries (m²; [Loos et al., 2021; see Table S1](#)). As quarry and/or dry grassland patches were found in all study landscapes within a radius of 3000m around the centroid of each study area, a radius of 3000m

was considered for the connectivity calculations. For details, see [Section 1.2](#) in Supporting Information.

2.3 | Bee surveys

Bee sampling was conducted during four runs between 16 April and 18 September 2020. Quarries were visited in random order. Transects of 2m width were conducted on days with warm weather in the most flower-rich areas of each quarry to achieve a complete assessment of the bee communities. Transects varied in length (mean 105.14m ± 41.19 (SD)) and did not have fixed, linear walkways to account for difficult terrain in quarries (e.g. cliffs, slopes). Therefore, transects were standardized over time instead of area (i.e. timed surveys of 15 min pure observation, cf. [Kadlec et al., 2012; Krauss et al., 2009; Wurz et al., 2022](#)). The number of transects per quarry ranged from 1 to 5, depending on the quarry area ([Alfert, 2000, unpublished data; Krauss et al., 2009; Table S1](#)). Transect locations occasionally changed between runs to adapt to changes in flower phenology. During each run, we aimed to maximize the surveyed area by arranging transects evenly over the quarry, but we avoided surveying the same area twice ([Figure S2](#)). In two very small quarries (<0.1 ha), the sampling procedure had to be modified by repeatedly sampling the same area during one transect walk. During transects, we recorded present wild bee individuals. Bees were identified to species in the field or, if not possible, captured, killed and sent to wild bee experts for identification (Dr. Reiner Theunert, Umwelt & Planung Dr. Theunert, 31249, Hohenhameln, Germany; Fionn Pape, Biologische Schutzgemeinschaft Göttingen, 37073, Göttingen, Germany). Wild bee abundance and species richness were averaged over all transects per study site and run to correct for differences in transect numbers between study sites. We used the Red List of Wild Bees of Germany ([Westrich et al., 2011](#)) and the Red List of Invertebrates of the Federal State of Lower Saxony (Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz, [2015](#)), which is based on [Theunert \(2008\)](#), to classify bees according to their conservation status. As for wild bee abundance and richness, the richness of endangered wild bees was averaged over all transects per study site and run. During fieldwork, we followed the regulations of the responsible environmental authority, the Lower Saxon State Department for Waterway, Coastal and Nature Conservation (NLWKN), which granted us a permit for legal bee sampling (permit number: H72.22202/2019-Kirsch). No ethical approval was required for this study. For details, see [Section 1.3](#) in Supporting Information.

2.4 | Vegetation surveys

Parallel to bee surveys, we recorded flowering plants (except grasses) within each 15 min transect. Plants were identified to the lowest taxonomic level possible using literature ([Spohn et al., 2015](#)), applications ([Mäder et al., 2021](#)) and/or expert knowledge (Fionn

Pape, Biologische Schutzgemeinschaft Göttingen, pers. comm.). In total, we recorded 290 plant taxa. Moreover, we visually estimated percentage flower cover per transect. Plant species richness and percentage flower cover were averaged over all transects per study site and run to correct for differences in sampling effort between study sites. We found seasonal correlations between the average flower cover and plant species richness and woody vegetation cover. These seasonal correlations were particularly consistent for the average plant species richness: With the exception of the first study run in spring (16 April 2020 to 25 May 2020), there was a significant negative correlation between plant species richness and woody vegetation cover throughout the year. For details, see Section 1.4 in Supporting Information.

2.5 | Statistical analyses

Statistical analyses were conducted with R (R Core Team, 2022). Using the 'glmmTMB' package (Brooks et al., 2017), we fitted global generalized linear mixed-effects models either with Gaussian or zero inflated Gamma distribution (see below; Table 1; Tables S4–S6). Response variables were (1) wild bee abundance, averaged over all transects per run (2) wild bee richness, averaged over all transects per run and (3) richness of endangered wild bees, averaged over all transects per run (for simplicity hereafter referred to as average wild bee abundance, average wild bee richness and average richness of endangered wild bees). We included the local quarry characteristics—(1) quarry age, (2) quarry area (m²), (3) plant species richness, averaged over all transects per run (hereafter referred to as average plant species richness) and (4) woody vegetation cover (%) as explanatory variables. Quarry area (m²) was log-transformed to assure a linear relationship. As average plant species richness and average flower cover (%) were correlated ($p < 0.012$, $R^2 = 0.28$), only average plant species richness was included as explanatory variable in the models. Furthermore, we added the landscape characteristics (1) landscape diversity and (2) habitat connectivity as explanatory variables. Landscape diversity calculated for the 1000-m buffer around each site was selected, as the strongest correlation between landscape diversity and the three response variables was found on this scale (Table S7). We added ecologically meaningful two-way interactions between (1) woody vegetation cover (%) and quarry age, (2) habitat connectivity and quarry age, (3) habitat connectivity and quarry area (m²), (4) landscape diversity and quarry age and (5) landscape diversity and quarry area (m²) to the global models. Study site was included as a random factor. Run could not be added as a random factor because it did not have enough levels (Bolker, 2015) and was therefore included as a co-variable. Continuous variables were z-transformed to improve model performance.

Using a multi-model inference approach (Burnham & Anderson, 2002), we created a set of candidate models for each global model. For this, we used the dredge() function (R package 'MuMIn'; Barton, 2018), which aims to select the most parsimonious model among all possible combinations of explanatory

variables included in the global model (Logan, 2011). Dredging was performed with the setting that candidate models were evaluated and ranked according to their AICc value (Barton, 2018; Burnham & Anderson, 2002; Table 1). Since we have 76 data points in our data set, we limited the number of explanatory variables in created candidate models to seven to avoid overfitting. According to Burnham and Anderson (2002), candidate models ranked within a delta AICc range <2 in comparison to the candidate model with the lowest AICc value have substantial empirical support. Thus, we considered all candidate models in this AICc range as best-fitting (Table 1). For interpretation, we calculated Akaike weights (w_i) and sums of Akaike weights ($\sum w_i$) as measures of the relative likelihood of each candidate model and of the relative importance of explanatory variables over the entire set of candidate models, respectively. We only report and discuss effects of explanatory variables included in the best-fitting models with $\sum w_i$ of 0.25 and higher. We tested global models and best-fitting candidate models for over- and underdispersion and checked their residuals and VIFs using the R packages 'DHARMA' (Hartig, 2022) and 'performance' (Lüdecke et al., 2021). Furthermore, global models and best-fitting candidate models were compared with their corresponding null models with the AICctab() function of the 'bbmle' package (Bolker, 2022). The response variable average wild bee abundance was subjected to a square root transformation to achieve a normal distribution, as the residuals of the global model and the best-fitting candidate models were not well-fitting when calculated with the response variable untransformed. The global model and candidate models for the average richness of endangered wild bees were found to be zero inflated as shown with 'DHARMA' (Hartig, 2022) as this response variable included many zeros (46.7% of all observations). For that reason, we fitted the global model for this response variable with zero-inflated Gamma distribution (link='log'). Different versions of the global model with varying zero-inflation factors (~1, all explanatory variables alone and together) were run and compared with the AICctab function() (Bolker, 2022). We selected the global model including quarry area (m²) as zero-inflation factor as it had the lowest AICc value of all compared global models (AICc 7.7 lower than of 2nd best-fitting model). To ensure that the zero-inflation factor was included in all created candidate models, it was defined as a fixed term during model dredging.

We used the R packages 'ggplot2' (Wickham, 2016) and 'ggeffects' (Lüdecke, 2018) to create graphs. Graphs were based on the candidate models with the lowest AICc values that contained the explanatory variables to be visualized. We calculated the estimated wild bee richness and sample-based rarefaction using the 'INEXT' package (Hsieh et al., 2022) to assess sample completeness (Figure S3). For details, see Section 1.5 in Supporting Information.

3 | RESULTS

We recorded 2360 wild bee individuals during the study of which 1065 individuals belonged to the genus *Bombus*. Moreover, we

TABLE 1 Overview over calculated null models, global models and best-fitting candidate models, including their response and explanatory variables, random factors, distribution families and zero-inflation factors.

Response variable	Model category	Number	AICc	dAICc	Model weight	Explanatory variables	Random factor	Family	Zero-inflation factor
Average wild bee abundance	Best-fitting candidate models	Model 1.1	196.9	0.0	0.128	Average plant species richness + run + woody vegetation cover (%) + quarry age + landscape diversity + landscape diversity: quarry age	(1 Study site)	Gaussian	
		Model 1.2	197.1	0.2	0.114	Average plant species richness + run + woody vegetation cover (%) + quarry age + quarry area (m ²) + woody vegetation cover (%): quarry age			
		Model 1.3	197.1	0.2	0.114	Average plant species richness + run + woody vegetation cover (%) + quarry age + landscape diversity + quarry area (m ²) + woody vegetation cover (%): quarry age			
	Model 1.4	197.5	0.6	0.095	Average plant species richness + run + woody vegetation cover (%) + quarry age + landscape diversity + woody vegetation cover (%): quarry age + landscape diversity: quarry age				
	Model 1.5	197.8	0.9	0.083	Average plant species richness + run + woody vegetation cover (%) + quarry age + quarry area (m ²) + woody vegetation cover (%): quarry age + habitat connectivity				
	Model 1.6	198.7	1.8	0.051	Average plant species richness + run + woody vegetation cover (%) + quarry age + landscape diversity + landscape diversity: quarry age				
Average wild bee abundance	Global model	Model 1.7	201.8	4.9	Average plant species richness + habitat connectivity + landscape diversity + quarry age + quarry area (m ²) + run + woody vegetation cover (%) + habitat connectivity: quarry age + habitat connectivity: quarry area (m ²) + landscape diversity: quarry age + landscape diversity: quarry area (m ²) + woody vegetation cover (%): quarry age	(1 Study site)	Gaussian		
	Null model	Model 1.8	245.9	49.0	1	(1 Study site)	Gaussian		

(Continues)

TABLE 1 (Continued)

Response variable	Model category	Number	AICc	dAICc	Model weight	Explanatory variables	Random factor	Family	Zero-inflation factor
Average wild bee richness	Best-fitting candidate models	Model 2.1	304.2	0.0	0.127	Average plant species richness + run + woody vegetation cover (%) + habitat connectivity + quarry age + woody vegetation cover (%): quarry area + quarry area (m ²)	(1 Study site)	Gaussian	
		Model 2.2	304.3	0.2	0.108	Average plant species richness + run + woody vegetation cover (%) + habitat connectivity + quarry age + woody vegetation cover (%): quarry age			
		Model 2.3	304.5	0.3	0.099	Average plant species richness + run + woody vegetation cover (%) + habitat connectivity			
		Model 2.4	305.5	1.3	0.062	Average plant species richness + run + woody vegetation cover (%) + habitat connectivity + landscape diversity			
		Model 2.5	305.5	1.3	0.0611	Average plant species richness + run + woody vegetation cover (%) + quarry age + woody vegetation cover (%): quarry age + landscape diversity			
		Model 2.6	305.7	1.5	0.056	Average plant species richness + run + woody vegetation cover (%) + habitat connectivity + quarry age + woody vegetation cover (%): quarry age + landscape diversity			
		Model 2.7	306.0	1.8	0.048	Average plant species richness + run + woody vegetation cover (%) + quarry age + woody vegetation cover (%): quarry age			
		Model 2.8	306.1	1.9	0.046	Average plant species richness + run + woody vegetation cover (%) + landscape diversity			
Average wild bee richness	Global model	Model 2.9	314.9	10.7	Average plant species richness + habitat connectivity + landscape diversity + quarry age + quarry area (m ²) + run + woody vegetation cover (%) + habitat connectivity: quarry age + habitat connectivity: quarry area (m ²) + landscape diversity: quarry age + landscape diversity: quarry area (m ²) + woody vegetation cover (%): quarry age	(1 Study site)	Gaussian		
		Model 2.10	351.3	47.1	1			Gaussian	

TABLE 1 (Continued)

Response variable	Model category	Number	AICc	dAICc	Model weight	Explanatory variables	Random factor	Family	Zero-inflation factor
Average richness of endangered wild bees	Best-fitting candidate models	Model 3.1	129.5	0.0	0.105	Habitat connectivity + quarry age + run + quarry age: habitat connectivity	(1 Study site)	ziGamma (link = 'log')	Quarry area (m ²)
		Model 3.2	130.1	0.6	0.077	Average plant species richness + habitat connectivity + run + quarry age + quarry age: habitat connectivity			
	Model 3.3	130.8	1.3	0.055	Average plant species richness + habitat connectivity + quarry age + quarry age: habitat connectivity				
	Model 3.4	131.4	1.9	0.042	Average plant species richness + habitat connectivity + landscape diversity + quarry age + quarry age: habitat connectivity + quarry age: landscape diversity				
Average richness of endangered wild bees	Null model	Model 3.5	141.7	12.2	1		(1 Study site)	ziGamma (link = 'log')	Quarry area (m ²)
Average richness of endangered wild bees	Global model	Model 3.6	146.5	17.0	Average plant species richness + habitat connectivity + landscape diversity + quarry age + quarry area (m ²) + run + woody vegetation cover (%) + habitat connectivity: quarry age + habitat connectivity: quarry area (m ²) + landscape diversity: quarry area (m ²) + woody vegetation cover (%): quarry age	(1 Study site)	ziGamma (link = 'log')	Quarry area (m ²)	

Note: Candidate models and their corresponding global models and null models were ranked based on their AICc values (Bolker, 2022). Candidate models within a delta AICc range between 0 and 2 in comparison to the candidate model with the lowest AICc values were considered as best fitting (Burnham & Anderson, 2002). Model weights of candidate models are shown (Barton, 2018). Each candidate model has an individual number for identification.

identified 114 bee species. The observed wild bee species richness corresponded to 81.1% of the estimated species richness (Figure S3). The most common species were *Bombus pascuorum* ($n=405$), *B. lapidarius* ($n=316$) and *Lasioglossum pauxillum* ($n=138$). Furthermore, we recorded 175 individuals of 35 endangered bee species, with *Halictus simplex* (endangered; $n=24$), *Megachile pilidens* (critically endangered; $n=23$) and *Anthidium punctatum* (endangered; $n=22$) being the most frequently encountered species. In total, we observed 1430 flower visits of wild bees, of which the vast majority was conducted on herbaceous plants and only slightly more than 10% on woody vegetation (trees, shrubs and subshrubs; for details, see Section 1.6 in Supporting Information).

3.1 | Average wild bee abundance

Six models with a relative likelihood between 13% ($\omega_i=0.13$) and 5% ($\omega_i=0.05$) were selected as best-fitting models from a total of 372 candidate models, as they fell within a delta AICc range between 0 and 2 in comparison to the candidate model with the lowest AICc value (Table 1; Tables S8–S13). Following explanatory variables with a $\Sigma\omega_i$ of 0.25 and higher were found within these models: Average plant species richness ($\Sigma\omega_i=1.00$), run ($\Sigma\omega_i=1.00$), woody vegetation cover (%) ($\Sigma\omega_i=0.97$) and quarry age ($\Sigma\omega_i=0.78$) were included in all six models and were of high relative importance. Of moderate/lower importance were landscape diversity ($\Sigma\omega_i=0.68$), quarry area (m^2 ; $\Sigma\omega_i=0.58$), habitat connectivity ($\Sigma\omega_i=0.26$) and the interactions between woody vegetation cover (%) and quarry age ($\Sigma\omega_i=0.44$) and landscape diversity and quarry age ($\Sigma\omega_i=0.33$). These variables were found in a subset of the best-fitting models (Table 1). See Table S14 for a complete list of $\Sigma\omega_i$ values.

Average richness of flowering plants (Figure 1a; Model 1.1, Table 1) and quarry area (m^2 ; Figure 1b; Model 1.2, Table 1) had a positive effect on average wild bee abundance. Furthermore, there was a decrease in average wild bee abundance with woody vegetation cover (Figure S4; Model 1.1, Table 1). An influence of quarry age was observed when considered in form of an interaction with woody vegetation cover (Model 1.2, Table 1): Average abundance increased with quarry age in quarries with moderate woody vegetation cover, while a decline with quarry age was observed in quarries with high woody vegetation cover (Figure 1c). Landscape diversity had a slightly positive influence on the wild bee abundance (Figure S5; Model 1.3, Table 1) and appeared to moderate the effect of quarry age (Model 1.1, Table 1), when considered with this variable in a two-way interaction: Quarry age had a positive effect on average wild bee abundance, but only if sites were located in less diverse landscapes (Figure 1d). Old quarries did not differ in terms of abundance between simple and complex landscapes (Figure 1d). Additionally, habitat connectivity had a positive but weak influence on average wild bee abundance (Figure S6; Model 1.5, Table 1). After remaining relatively stable during the first three runs of the study, the average wild bee abundance dropped in late summer during the last run (16 August 2020 to 18 September 2020; Figure S7; Model 1.1, Table 1).

3.2 | Average wild bee richness

For the response variable average wild bee richness, eight best-fitting models were identified from a total of 372 candidate models ($\omega_i=0.12$ – 0.05 ; Table 1; Tables S15–S22). Following explanatory variables with a $\Sigma\omega_i$ of 0.25 and above were found within these models: Average flowering plant species richness ($\Sigma\omega_i=1.00$), run ($\Sigma\omega_i=0.98$) and woody vegetation cover (%) ($\Sigma\omega_i=0.97$) were included in all; and habitat connectivity ($\Sigma\omega_i=0.66$), quarry age ($\Sigma\omega_i=0.65$), landscape diversity ($\Sigma\omega_i=0.41$), quarry area (m^2 ; $\Sigma\omega_i=0.32$) and the interactions between woody vegetation cover (%) and quarry age ($\Sigma\omega_i=0.50$) in a subset of the best-fitting models. See Table S23 for a complete list of $\Sigma\omega_i$ values.

Average flowering plant species richness (Figure S8; Model 2.1, Table 1) and quarry area (Figure S9; Model 2.1, Table 1) had a positive influence on average wild bee richness. High woody vegetation cover in quarries resulted in a lower wild bee richness (Figure S10; Model 2.1, Table 1). Furthermore, there was an effect of quarry age if considered in a two-way interaction with woody vegetation cover (Model 2.1, Table 1): Higher average richness could be found in older quarries given that the woody vegetation cover was moderate, whereas there was a decline in average bee richness when the woody vegetation cover was high (Figure S11). Furthermore, habitat connectivity (Figure 2a; Model 2.1, Table 1) and landscape diversity (Figure 2b; Model 2.4, Table 1) had a positive effect on the average wild bee richness. After a slight increase between the first (16 April 2020 to 25 May 2020) and the second run of the study, the average wild bee richness remained almost constant in the second and third run (27 May 2020 to 12 August 2020). A significant decline in average wild bee richness was observed during the last run in late summer (16 August 2020 to 18 September 2020; Figure S12; Model 2.1, Table 1).

3.3 | Average richness of endangered wild bees

In case of average richness of endangered wild bees, we selected four best-fitting candidate models from a total of 291 candidate models ($\omega_i=0.11$ – 0.04 ; Table 1; Tables S24–S27). These models contained the following explanatory variables with a $\Sigma\omega_i$ of 0.25 and more: Habitat connectivity ($\Sigma\omega_i=0.83$), quarry age ($\Sigma\omega_i=0.81$) and the interaction between quarry age and habitat connectivity ($\Sigma\omega_i=0.60$) were included in all, while run ($\Sigma\omega_i=0.70$) and average plant species richness ($\Sigma\omega_i=0.50$) could only be found in a subset of three and two of the best-fitting models, respectively. Landscape diversity ($\Sigma\omega_i=0.34$) was included in a single model. As a fixed term, the zero-inflation factor quarry area (m^2) was included in all four models and was of high importance ($\Sigma\omega_i=1.0$). See Table S28 for a complete list of $\Sigma\omega_i$ values.

As explained by the zero-inflation factor quarry area, the smaller a quarry was, the higher was the probability to observe no endangered wild bees within a quarry (Figure 3a; see Section 1.5 in Supporting Information). The average richness of endangered wild

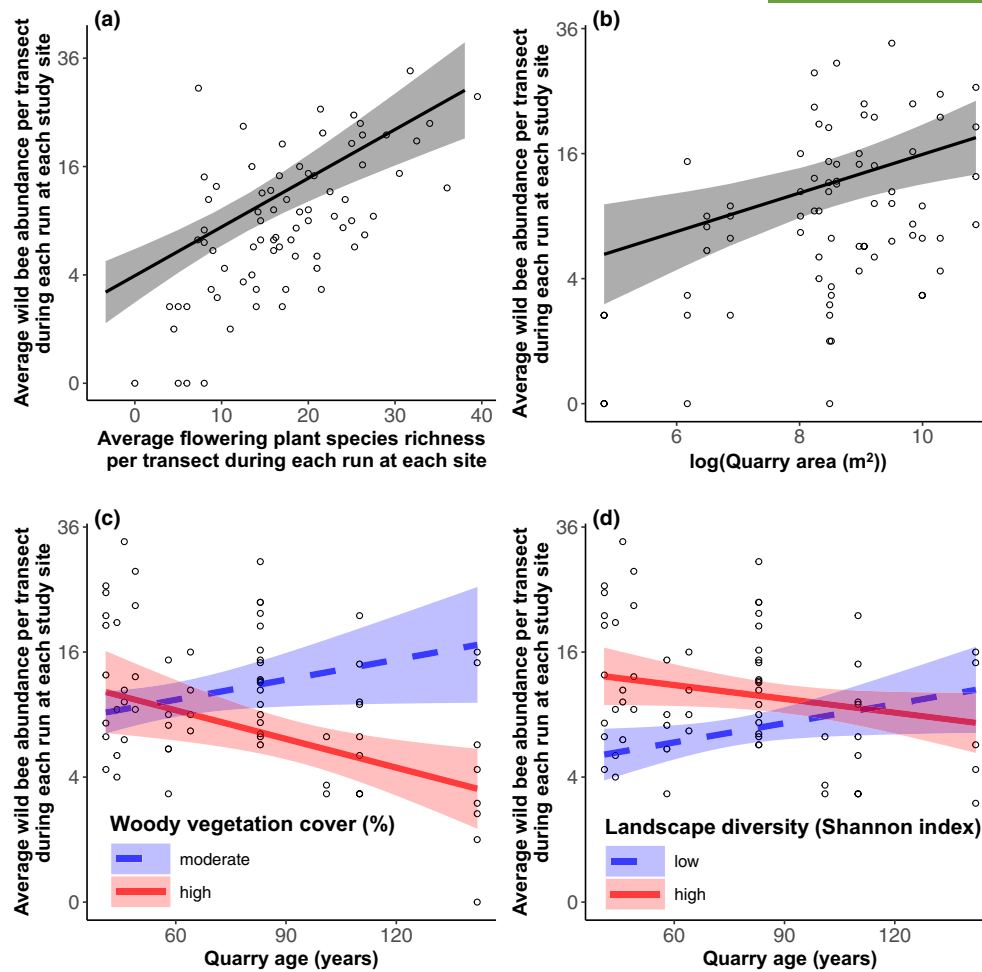


FIGURE 1 (a) Effect of the average flowering plant species richness per transect during each run at each study site on the average wild bee abundance per transect during each run at each study site. The figure is based on the predictions of model 1.1 (Table 1). (b) Effect of quarry area (m²) in logarithmic form on the average wild bee abundance per transect during each run at each study site. The figure is based on the predictions of model 1.2 (Table 1). (c) Effect of quarry age and woody vegetation cover (%) on the average wild bee abundance per transect during each run at each study site. The effect differs for quarries with moderate (equals 53.41% \pm 25th percentile; dashed line, blue shaded confidence interval) and high woody vegetation cover (equals 96.84% \pm 75th percentile; solid line, red shaded confidence interval). The figure is based on the predictions of model 1.1 (Table 1). (d) Effect of quarry age and landscape diversity (Shannon–Wiener diversity index) on the average wild bee abundance per transect during each run at each study site. The effect differs for landscapes with low (Shannon–Wiener diversity index equals 1.15 \pm 25th percentile; dashed line, blue shaded confidence interval) and high landscape diversity (Shannon–Wiener diversity index equals 1.55 \pm 75th percentile; solid line, red shaded confidence interval). The figure is based on the predictions of model 1.1 (Table 1).

bees declined with quarry age in quarries with low connectivity to neighbouring dry grasslands/other quarries, while in quarries with high connectivity, increasing quarry age resulted in a slight increase in their richness (Figure 3b; see Section 1.5 in Supporting Information). Furthermore, average richness of flowering plant species had a positive effect on average richness of endangered wild bees (Figure S13; Model 3.2, Table 1). Even though landscape diversity appeared as an explanatory variable in a single best-fitting model, it was of low relative importance and had no influence on the average richness of endangered wild bees (Figure S14; Model 3.4, Table 1). The average richness of endangered wild bees was lowest in spring during the first run of the study (16 April 2020 to 25 May 2020), after which it increased and peaked during the third and

fourth run in early and late summer (07 July 2020 to 18 September 2020; Figure S15; Model 3.1, Table 1).

4 | DISCUSSION

Our results show that wild bee abundance and richness in limestone quarries are promoted by increasing floral resources availability. Moreover, high woody vegetation cover in quarries had a negative effect on wild bee communities. An interaction between quarry age and woody vegetation cover indicates that individual-rich, diverse bee communities thrive in old quarries with limited woody vegetation. Importantly, not only local site characteristics seem to be

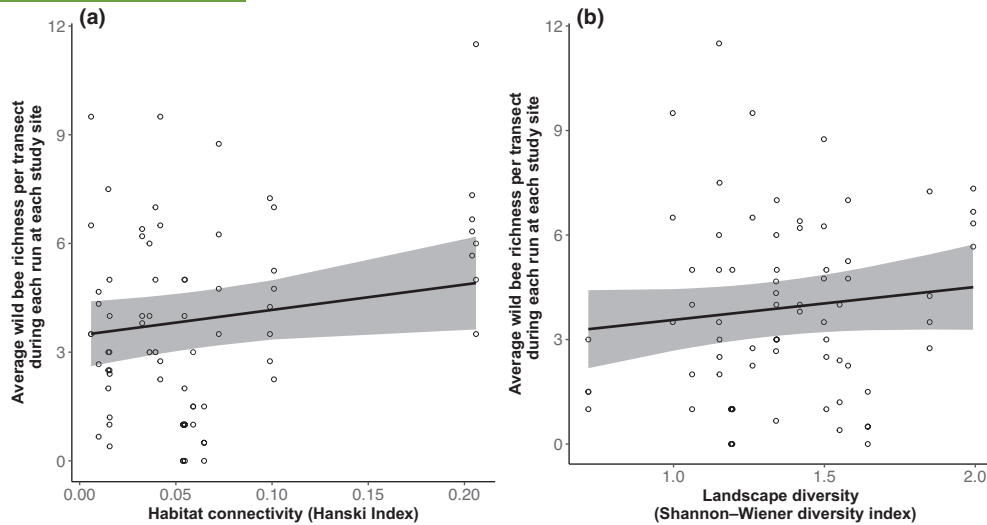


FIGURE 2 (a) Effect of habitat connectivity and (b) landscape diversity on the average wild bee richness per transect during each run at each study site. Figures are based on the predictions of model 2.1 and model 2.4 (Table 1), respectively.

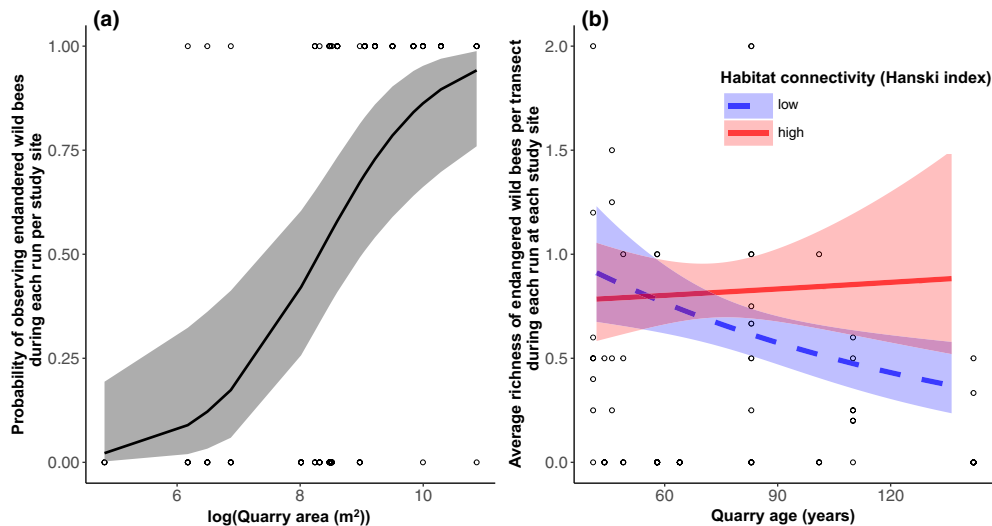


FIGURE 3 (a) Probability to observe endangered wild bees per study site and run explained by quarry area (m^2) in logarithmic form (zero-inflation factor). (b) Effect of quarry age and habitat connectivity on the average richness of endangered wild bees per transect during each run at each study site. The effect differs with connectivity between study sites and neighbouring dry grasslands and quarries (low = Hanski index equals 0.0363 ± 25 th percentile; dashed line, blue shaded confidence interval; high = Hanski index equals 0.0989 ± 75 th percentile; solid line, red shaded confidence interval). The package `ggeffects` (Lüdtke, 2018) was used throughout the manuscript to visualize regression lines. However, no way was found to represent effects of zero-inflation factors and two-way interactions between two continuous variables with this package for models based on family = 'ziGamma'. Thus, figures were instead based on a binomial model for the zero-inflation factor and a model fitted with Gamma distribution for two-way interaction (excluding zeros). For details, see Section 1.5 in Supporting Information.

important factors for maintaining species-rich bee communities in quarries, but also high landscape diversity and connectivity to neighbouring dry grasslands and other quarries. Like woody vegetation cover, these landscape variables possibly moderated the effect of quarry age on bees. Our results show that quarries are valuable habitats for diverse bee communities, including endangered species, and that management of these habitats is needed both at the local and landscape level.

Using a multi-model inference approach, we were unable to identify single, best-fitting models for the response variables. Our results are therefore based on a set of best-fitting candidate models that differ in included variable combinations. Consequently, they must be considered as alternative and sometimes contradictory explanations for the explained variance in our models. Therefore, some of our results should be interpreted with caution, which we have indicated when discussing individual effects below.

4.1 | Local site characteristics

In accordance with our first hypothesis, we demonstrated that wild bee abundance and species richness are positively affected by increasing richness of flowering plant species in quarries. This positive relationship was also reported in other studies in quarries (Kettermann et al., 2022; Krauss et al., 2009) and other semi-natural habitats within agricultural landscapes (e.g. Beyer et al., 2021). Our finding underlines the importance of high flowering plant richness, which serves as diverse forage resource for wild bees (Kuppler et al., 2023). It is very likely that a high richness of pollen- and nectar-providing plants is also beneficial for endangered wild bees (Kuppler et al., 2023). However, based on our model selection, this cannot be confirmed with absolute certainty, as the variable average richness of flowering plant species was included only in three and not in all four best-fitting models for the average richness of endangered wild bees (not included in Model 3.1, Table 1).

We further expected a positive effect of habitat area on wild bees. Candidate models that included this explanatory variable showed that average wild bee abundance and, to a lesser extent, richness increased with increasing habitat area. This is in line with Krauss et al. (2009), who found a similar positive effect of quarry area, as predicted by the species–area relationship (e.g. Rosenzweig, 1995). The reason for this finding could be that larger quarries are characterized by greater habitat heterogeneity (Ricklefs & Lovette, 1999), which promotes wild bees through a higher diversity of microhabitats and ecological niches (cf. Willis et al., 2005). However, quarry area only appears in a subset of the best-fitting models for average wild bee abundance and species richness (Table 1). Although previously positive effects of quarry area have been shown (Krauss et al., 2009), other combinations of local and landscape characteristics can probably have similar effects on both response variables, indicating complex interactions across multiple local and landscape characteristics. Moreover, quarry area played an important role in explaining the probability of observing endangered wild bee species, with smaller quarries tending to have no endangered species in contrast to larger ones. A positive relationship between habitat size and population persistence is assumed (Fahrig & Merriam, 1994). Due to lower dispersal capacity or a higher degree of specialization in terms of foraging resources and/or habitats (Bogusch et al., 2020; Bommarco et al., 2010), endangered bee species are likely especially dependent on a sufficient amount of high-quality habitat to be able to survive, explaining their absence from small quarries.

As it was consistently included across best-fitting candidate models (Table 1), we could clearly show that the woody vegetation cover was relevant for the average wild bee abundance and richness in quarries. It was mostly included in form of two-way interactions with other habitat and landscape characteristics, but it also appeared alone as a main effect in several, alternative candidate models for average wild bee abundance and richness (e.g. Model 1.1, Model 2.3, Table 1). The dominance of late

successional stages, such as shrubby vegetation, could result in fewer forage resources and nesting sites with favourable microclimate (Kettermann et al., 2022), probably leading to the observed decline in wild bee abundance and richness. This does not mean that woody plants are generally not exploited by wild bees. They can serve as sources of pollen and nectar, and as nesting habitats (Westrich, 2019). However, during our survey, herbaceous plants appeared to be more attractive than woody plants, as the majority of observed flower visits occurred on them. With the exception of the first study run (16 April 2020 to 25 May 2020), which was probably due to the presence of spring ephemerals (Lapointe, 2001), there was also a negative correlation between flowering plant species richness and woody vegetation cover. Both factors are likely related to the observed negative effect of high woody vegetation cover on wild bees.

In contrast to woody vegetation cover, quarry age was never included only as a main effect in the best-fitting candidate models for wild bee abundance and wild bee richness, but consistently appeared in form of interactions with other habitat or landscape variables. As predicted in our second hypothesis, several models included an interaction between quarry age and woody vegetation cover (Table 1): Average wild bee abundance and richness increased with quarry age at sites with moderate woody vegetation cover, whereas both variables were declining at sites with high woody vegetation cover. This suggests that an increase in quarry age could be beneficial, for example, due to the arrival and successful establishment of individuals/species and an increase in habitat heterogeneity over time (Brown & Southwood, 1983; Twerd et al., 2021), but only if quarries are well-managed and not completely dominated by woody vegetation (Kettermann et al., 2022). Similar to calcareous grasslands, keeping limestone quarries open through appropriate management measures (e.g. extensive grazing and mowing, shrub removal) could maintain a high habitat quality for bees (e.g. Fartmann, 2024). Furthermore, small-scale removal of vegetation and top soil by scraping or extensive mining could create open soil patches with flower-rich pioneer vegetation and nesting opportunities for soil-nesting bee species (Gardein et al., 2022; Kettermann et al., 2022). The interaction between quarry age and woody vegetation cover was included in most of the best-fitting candidate models for average wild bee abundance, but in one model it was accompanied (Model 1.4; Table 1) and in two models (Model 1.1, Model 1.6, Table 1) replaced by a different interaction between quarry age and landscape diversity (see Section 4.2). This shows that alternative combinations of local and landscape variables may result in similar outcomes of average wild bee abundance. In case of average wild bee richness, quarry age was completely absent from a minority of candidate models (Model 2.3, Model 2.4, Model 2.8, Table 1). The lack of an age effect would be consistent with Krauss et al. (2009), who found no influence of habitat age on wild bee communities in quarries and attributed this to their ability to colonize new quarries within short periods of time. Due to these alternative models with their contradictory variable combinations, age effects on the overall average wild bee abundance and richness should be considered with caution.

4.2 | Landscape characteristics

In accordance with our third hypothesis, bee communities in limestone quarries were influenced by the surrounding landscape. In case of average wild bee abundance and richness, landscape diversity and habitat connectivity to adjacent dry grassland and quarries were included in the best-fitting models. However, both variables were rarely included together in the same candidate models (e.g. Model 2.4, Model 2.6, Table 1); they were usually found in different models and appeared to be interchangeable to a certain extent (Table 1). As these models are not substantially different in their empirical support ($\Delta AIC_c < 2$; Burnham & Anderson, 2002), they must be considered as alternative and equivalent scenarios. Nevertheless, all alternative models predict a slight to moderate increase in average wild bee abundance and richness with increasing habitat connectivity and/or landscape diversity. The positive effect of habitat connectivity could be due to a facilitation of dispersal and related benefits. Considering that wild bees are often limited in their mobility (Gathmann & Tscharntke, 2002), high connectivity probably makes it easier for them to reach and successfully colonize quarries (Steffan-Dewenter, 2003). Consequently, high connectivity could be beneficial for wild bee communities in quarries due to improved genetic exchange (Stacey & Taper, 1992), reduced dispersal costs (Bonte et al., 2012) and the possibility to exploit resources in neighbouring dry grasslands (Westrich, 1996). Thus, connectivity represents a form of spatial insurance (Thompson et al., 2017) that facilitates the survival of bee species and individuals. Furthermore, the positive influence of landscape diversity on average wild bee abundance and richness is in line with previous studies (Beyer et al., 2021; Schweiger et al., 2022). The effects could be related to a permanent provision of floral resources throughout the year due to complementary habitats (Mallinger et al., 2016) and a high availability and diversity of nesting opportunities (Potts et al., 2005). Again, there were alternative ways to explain the variance in wild bee abundance, as landscape diversity was included in the best-fitting models for this response variable as main effect (Model 1.3), but also as a two-way interaction with quarry age (see below; Model 1.1, 1.4, 1.6, Table 1).

In contrast, the average richness of endangered wild bees was not related to landscape diversity, as it was mostly absent from the best-fitting models and, when included, had no influence on this response variable (Model 3.4, Table 1). Wild bees often have strong preferences for local habitat quality, nesting sites and materials and foraging resources (Bommarco et al., 2010; Theunert, 2002; Westrich, 1996). Consequently, these local requirements seem to be more important in the case of endangered species than high landscape diversity (e.g. Bogusch et al., 2020), which in our study was also based on land use types not necessarily favourable for specialized bee species (e.g. arable land, settlements, closed-canopy forests; Carré et al., 2009; Mullally et al., 2019).

As hypothesized in our fourth hypothesis, we found interactions between landscape variables and local habitat characteristics. A subset of best-fitting models for the average wild bee abundance

included an interaction between landscape diversity and habitat age (Table 1). This interaction appears to be to a certain degree interchangeable with the interaction between woody vegetation cover and quarry age (see Section 4.1; i.e. Model 1.1 and Model 1.6. versus Model 1.2, Table 1) and can therefore be viewed as an alternative explanation for the variance in wild bee abundance. As predicted by the models including this interaction, younger quarries (ca. 40–90 years old) located in diverse landscapes were characterized by a higher average wild bee abundance than similarly aged quarries in simple landscapes. However, no such difference between both landscape types could be found for older quarries (>90 years old). High landscape diversity leads to higher bee abundance at landscape scale (e.g. Mallinger et al., 2016). This increased bee abundance could result in greater spillover of bee individuals to younger quarries in diverse landscapes compared to simple landscapes. However, higher quarry age might compensate for lower landscape diversity, for example, due to increasing population size caused by the arrival and establishment of generalist bee species (e.g. bumblebees; Twerd et al., 2021; Westphal et al., 2006) and/or increasing local habitat complexity over time (Brown & Southwood, 1983), explaining why bee abundance in old quarries did not differ between landscape types.

Consistently across all best-fitting models for the response variable average richness of endangered wild bees, there was an interaction between habitat age and habitat connectivity. Their richness stayed stable with increasing habitat age in well-connected quarries, while there was a decline with age in the case of isolated quarries. At isolated sites, recolonization from neighbouring dry grassland and quarries is probably not sufficiently functioning and therefore unable to compensate local species extinctions (Fahrig & Merriam, 1994). Furthermore, populations of endangered species are likely small and smaller populations have a higher probability to get extinct over time (cf. Berger, 1990). Thus, it is possible that particularly endangered wild bees disappear from quarries with increasing habitat age. In well-connected quarries, this mechanism could be compensated by the exchange of bee species and individuals between neighbouring habitat patches, keeping the richness of endangered species stable with increasing quarry age (Thompson et al., 2017). These results underline that it is not only important to maintain quarries in good ecological conditions through efficient local management, but also to preserve nearby dry grasslands to ensure high habitat connectivity.

5 | CONCLUSIONS

Here, we demonstrate that local and landscape-scale characteristics are important for the conservation of wild bees associated with species-rich and threatened dry grasslands. In line with Krauss et al. (2009), our findings emphasize the importance of preserving large limestone quarries to benefit local wild bee communities that harbour many endangered wild bee species. However, in contrast to Krauss et al. (2009), we found that also quarry age

is an important factor determining habitat quality in interaction with other local and landscape characteristics. Older quarries appear to be more valuable for wild bees than younger ones, but only if overgrowth with woody vegetation remained at a moderate level. This interaction was not always included in our candidate models, which we selected using a multi-model inference approach (Burnham & Anderson, 2002), and must therefore be considered with caution. Nevertheless, we found that high woody vegetation cover as a main effect has a clear negative impact on wild bee communities. Similar to semi-natural dry grassland, limestone quarries must therefore be kept open through local management (e.g. extensive grazing, mowing or manual scrub clearance; Fartmann, 2024). Finally, we consistently found an interaction between habitat age and connectivity to neighbouring semi-natural dry grasslands, showing that high connectivity has a stabilizing effect on populations of endangered bee species in old quarries. In addition to the local control of woody vegetation, maintaining high levels of habitat connectivity through the conservation and restoration of dry grasslands across the landscape is therefore a priority approach for the conservation of diverse bee communities, including many endangered species.

AUTHOR CONTRIBUTIONS

Catrin Westphal conceived the study; Felix Kirsch and Catrin Westphal designed methodology with advice of Thomas Alfert; Felix Kirsch implemented study sites with advice of Thomas Alfert; Felix Kirsch collected the data; Felix Kirsch and Annika Hass analysed the data with advice of Catrin Westphal; Felix Kirsch wrote the manuscript with advice of Annika Hass, Thomas Alfert and Catrin Westphal. All authors contributed critically to the draft and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Susanne Jahn for support during fieldwork preparation and laboratory work, and Heike Francoli for project administration. We thank our student assistants Aiza Fernanda Cantillo Rodriguez, Fabian Osten, Friederike Grau, Klara Küpers, Margaux Tréguy, Noah Janotta and Taalke Lengert. We thank Thomas Möckel (née Astor) and the Department of Grassland Sciences and Renewable Resources at the University of Kassel for lending us a drone and instructing us in its use. We thank Felix Klaus for UAV-related advice. We thank Felipe Librán-Embid and Jochen Krauss for providing information on the location of semi-natural dry grasslands. We thank Annemarie Wurz and Mike Kuschereitz for supporting UAV mapping. We thank the Section for Agricultural Engineering of the University of Göttingen for lending us a differential GPS. We thank Nicole Beyer for providing statistical knowledge and R scripts. We thank Triini Reitalu for providing an R script to calculate Hanski connectivity of our study sites. We thank Reiner Theunert and Laura Marrero Palma for bee identification. We thank Fionn Pape for sharing information on study site management and for helping with plant and bee identification. We thank Thomas Fechtler and Christoph Bleidorn for advice on bee taxonomy. We thank

the NLWKN, the authorities of the county of Northeim, the city and county of Göttingen, especially Bertram Preuschhof, the municipality of Dransfeld and the forestry offices of Hann. Münden and Reinhausen for providing information and granting necessary permits. We thank the Graf Metternich Adelebsen Foundation, the mining companies August Oppermann Kiesgewinnungs- und Vertriebs-GmbH and the Unternehmensgruppe Wegener, Hermann Wegener GmbH & Co. KG, private landowners and the (real) municipalities, hunting and road cooperatives and hunting tenants of Adelebsen, Diemarden, Friedland, Gladebeck, Güntersen, Klein Lengden, Meensen, Ossensfeld, Sattenhausen, Scheden and Sudheim for allowing us to research on their properties and use their forest and field roads. We thank Jochen Krauss and Ingolf Steffan-Dewenter for inspiring this study. We thank Annemarie Wurz for providing pictures for the graphical abstract. Moreover, we thank Romina Rader, Martin Nuñez, Yi Zou, Lydia Groves and the three anonymous reviewers for their comments and for the administration of the review process. Catrin Westphal is grateful for funding by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)—Project number 405945293 and 493487387. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data available via the Gro.data Repository <https://doi.org/10.25625/FV59S0> (Kirsch et al., 2024).

ORCID

Felix Kirsch  <https://orcid.org/0000-0002-5645-2490>

Annika Hass  <https://orcid.org/0000-0002-3377-4622>

Catrin Westphal  <https://orcid.org/0000-0002-2615-1339>

REFERENCES

- Alfert, T. (2000). Die Besiedlung von Kalksteinbrüchen durch Bienen und Wespen (Hymenoptera, Aculeata): Der Einfluss von Flächengröße und Flächenalter (unpublished Thesis). University of Göttingen, Göttingen.
- Barton, K. (2018). *MuMIn: Multi-model inference*. R package version 1.42.1. <https://CRAN.R-project.org/package=MUMIN>
- Beneš, J., Kepka, P., & Konvička, M. (2003). Limestone quarries as refuges for European xerophilous butterflies. *Conservation Biology*, 17, 1058–1069. <https://doi.org/10.1046/j.1523-1739.2003.02092.x>
- Berger, J. (1990). Persistence of different-sized populations: An empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology*, 4, 91–98. <https://doi.org/10.1111/j.1523-1739.1990.tb00271.x>
- Beyer, N., Kirsch, F., Gabriel, D., & Westphal, C. (2021). Identity of mass-flowering crops moderates functional trait composition of pollinator communities. *Landscape Ecology*, 36, 2657–2671. <https://doi.org/10.1007/s10980-021-01261-3>
- Bogusch, P., Bláhová, E., & Horák, J. (2020). Pollen specialists are more endangered than non-specialised bees even though they collect pollen on flowers of non-endangered plants. *Arthropod-Plant Interactions*, 14, 759–769. <https://doi.org/10.1007/s11829-020-09789-y>

- Bolker, B. M. (2015). Linear and generalized linear mixed models. In G. A. Fox, S. Negrete-Yankelevich, & V. J. Sosa (Eds.), *Ecological statistics* (pp. 309–333). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199672547.003.0014>
- Bolker, B. M. (2022). *bbmle: Tools for general maximum likelihood estimation*. R package version 1.0.25. <https://CRAN.R-project.org/package=bbmle>
- Bommarco, R., Biesmeijer, J. C., Meyer, B., Potts, S. G., Pöyry, J., Roberts, S. P. M., Steffan-Dewenter, I., & Öckinger, E. (2010). Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B*, *277*, 2075–2082. <https://doi.org/10.1098/rspb.2009.2221>
- Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., ... Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, *87*, 290–312. <https://doi.org/10.1111/j.1469-185X.2011.00201.x>
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*, 378–400. <https://CRAN.R-project.org/package=glmmTMB>, <https://doi.org/10.32614/RJ-2017-066>
- Brown, V. K., & Southwood, T. R. E. (1983). Trophic diversity, niche breadth and generation times of exopterygote insects in a secondary succession. *Oecologia*, *56*, 220–225.
- Brückmann, S. V., Krauss, J., & Steffan-Dewenter, I. (2010). Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes: Connectivity effects on species richness. *Journal of Applied Ecology*, *47*, 799–809. <https://doi.org/10.1111/j.1365-2664.2010.01828.x>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd ed.). Springer.
- Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S. G., Roberts, S. P. M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyörgyi, H., Tschulin, T., Westphal, C., Woyciechowski, M., & Vaissière, B. E. (2009). Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture, Ecosystems & Environment*, *133*, 40–47. <https://doi.org/10.1016/j.agee.2009.05.001>
- Dengler, J., Janišová, M., Török, P., & Wellstein, C. (2014). Biodiversity of palaeartic grasslands: A synthesis. *Agriculture, Ecosystems & Environment*, *182*, 1–14. <https://doi.org/10.1016/j.agee.2013.12.015>
- Ellenberg, H. (1996). *Vegetation Mitteleuropas mit den Alpen* (5th ed.). UTB. Ulmer.
- Fahrig, L., & Merriam, G. (1994). Conservation of fragmented populations. *Conservation Biology*, *8*, 50–59.
- Fartmann, T. (2024). Insect Conservation in Grasslands. In J. S. Pryke, M. J. Samways, T. R. New, P. Cardoso, & R. Gaigher (Eds.), *Routledge Handbook of Insect Conservation, Routledge Environment and Sustainability Handbooks* (pp. 263–274). London, New York: Routledge, Taylor & Francis Group. <https://doi.org/10.4324/978103285793>
- Gardein, H., Fabian, Y., Westphal, C., Tscharnkte, T., & Hass, A. (2022). Ground-nesting bees prefer bare ground areas on calcareous grasslands. *Global Ecology and Conservation*, *39*, e02289. <https://doi.org/10.1016/j.gecco.2022.e02289>
- Gathmann, A., & Tscharnkte, T. (2002). Foraging ranges of solitary bees. *The Journal of Animal Ecology*, *71*, 757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>
- George, T. L., & Zack, S. (2001). Spatial and temporal considerations in restoring habitat for wildlife. *Restoration Ecology*, *9*, 272–279. <https://doi.org/10.1046/j.1526-100x.2001.009003272.x>
- Hartig, F. (2022). *DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package version 0.4.6. <http://florianhartig.github.io/DHARMA/>
- Hsieh, T. C., Ma, K. H., & Chao, A. (2022). *iNEXT: iNterpolation and EXTrapolation for species diversity*. R package version 3.0.0. http://chao.stat.nthu.edu.tw/wordpress/software_download/
- Janssen, J. A. M., Rodwell, J. S., García Criado, M., Gubbay, S., Haynes, T., Nieto, A., Sanders, N., Landucci, F., Loidi, J., Ssymank, A., Tahvanainen, T., Valderrabano, M., Acosta, A., Aronsson, M., Arts, G., Attorre, F., Bergmeier, E., Bijlsma, R.-J., Bioret, F., ... European Commission (Directorate General for the Environment). (2016). *European red list of habitats. Part 2, Terrestrial and freshwater habitats*. Publication Office of the European Union.
- Kadlec, T., Tropek, R., & Konvicka, M. (2012). Timed surveys and transect walks as comparable methods for monitoring butterflies in small plots. *Journal of Insect Conservation*, *16*, 275–280. <https://doi.org/10.1007/s10841-011-9414-7>
- Kettermann, M., Poniatowski, D., & Fartmann, T. (2022). Active management fosters species richness of wild bees in limestone quarries. *Ecological Engineering*, *182*, 106733. <https://doi.org/10.1016/j.ecoleng.2022.106733>
- Kirsch, F., Annika, L. H., Alfert, T., & Catrin, W. (2024). *Data from: Landscape diversity, habitat connectivity, age and size determine the conservation value of limestone quarries for diverse wild bee communities*. <https://doi.org/10.25625/FV59S0>
- Klaus, F., Tscharnkte, T., Uhler, J., & Grass, I. (2021). Calcareous grassland fragments as sources of bee pollinators for the surrounding agricultural landscape. *Global Ecology and Conservation*, *26*, e01474. <https://doi.org/10.1016/j.gecco.2021.e01474>
- Krauss, J., Alfert, T., & Steffan-Dewenter, I. (2009). Habitat area but not habitat age determines wild bee richness in limestone quarries. *Journal of Applied Ecology*, *46*, 194–202. <https://doi.org/10.1111/j.1365-2664.2008.01582.x>
- Krimmer, E., Martin, E. A., Krauss, J., Holzschuh, A., & Steffan-Dewenter, I. (2019). Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. *Agriculture, Ecosystems & Environment*, *284*, 106590. <https://doi.org/10.1016/j.agee.2019.106590>
- Kuppler, J., Neumüller, U., Mayr, A. V., Hopfenmüller, S., Weiss, K., Prosi, R., Schanowski, A., Schwenninger, H.-R., Ayasse, M., & Burger, H. (2023). Favourite plants of wild bees. *Agriculture, Ecosystems & Environment*, *342*, 108266. <https://doi.org/10.1016/j.agee.2022.108266>
- Lapointe, L. (2001). How phenology influences physiology in deciduous forest spring ephemerals. *Physiologia Plantarum*, *113*, 151–157. <https://doi.org/10.1034/j.1399-3054.2001.1130201.x>
- Logan, M. (2011). *Biostatistical design and analysis using R a practical guide*. Wiley.
- Loos, J., Krauss, J., Lyons, A., Föst, S., Ohlendorf, C., Racky, S., Röder, M., Hudel, L., Herfert, V., & Tscharnkte, T. (2021). Local and landscape responses of biodiversity in calcareous grasslands. *Biodiversity and Conservation*, *30*, 2415–2432. <https://doi.org/10.1007/s10531-021-02201-y>
- Lüdecke, D. (2018). Ggeffects: Tidy data frames of marginal effects from regression models. *Joss*, *3*, 772. <https://doi.org/10.21105/joss.00772>
- Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *Joss*, *6*, 3139. <https://doi.org/10.21105/joss.03139>
- Mäder, P., Boho, D., Rzanny, M., Seeland, M., Wittich, H. C., Deggelmann, A., & Wäldchen, J. (2021). The Flora incognita app – Interactive plant species identification. *Methods in Ecology and Evolution*, *12*, 1335–1342. <https://doi.org/10.1111/2041-210X.13611>

- Mallinger, R. E., Gibbs, J., & Gratton, C. (2016). Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology*, 31, 1523–1535. <https://doi.org/10.1007/s10980-015-0332-z>
- Mullally, H. L., Buckley, D. S., Fordyce, J. A., Collins, B., & Kwit, C. (2019). Bee communities across gap, edge, and closed-canopy microsites in forest stands with group selection openings. *Forest Science*, 65, 751–757. <https://doi.org/10.1093/forsci/fxz035>
- Müsch, T., & Fartmann, T. (2021). Limestone quarries are the most important refuge for a formerly widespread grassland butterfly. *Insect Conservation and Diversity*, 15, 200–212. <https://doi.org/10.1111/ica.12544>
- Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz. (2015). *Verzeichnis der in Niedersachsen besonders oder streng geschützten Arten*. Schutz, Gefährdung, Lebensräume, Bestand, Verbreitung (Aktualisierte Fassung 1. Januar 2015). Wirbellose Tiere.
- Novák, J., & Konvička, M. (2006). Proximity of valuable habitats affects succession patterns in abandoned quarries. *Ecological Engineering*, 26, 113–122. <https://doi.org/10.1016/j.ecoleng.2005.06.008>
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., ... Weedon, J. (2022). *Vegan: Community ecology package*. R package version 2.6-4. <https://CRAN.R-project.org/package=vegan>
- Pitz, C., Piqueray, J., Monty, A., & Mahy, G. (2018). Naturally recruited herbaceous vegetation in abandoned Belgian limestone quarries: Towards habitats of conservation interest analogues? *Folia Geobotanica*, 53, 147–158. <https://doi.org/10.1007/s12224-018-9313-8>
- Poschold, P., & Wallis De Vries, M. F. (2002). The historical and socio-economic perspective of calcareous grasslands—Lessons from the distant and recent past. *Biological Conservation*, 104, 361–376. [https://doi.org/10.1016/S0006-3207\(01\)00201-4](https://doi.org/10.1016/S0006-3207(01)00201-4)
- Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., & Willmer, P. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, 30, 78–85. <https://doi.org/10.1111/j.0307-6946.2005.00662.x>
- QGIS Development Team. (2022). *QGIS geographic information system*. QGIS Association.
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Ricklefs, R. E., & Lovette, I. J. (1999). The roles of Island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *The Journal of Animal Ecology*, 68, 1142–1160. <https://doi.org/10.1046/j.1365-2656.1999.00358.x>
- Rosenzweig, M. L. (1995). *Species diversity in space and time* (1st ed.). Cambridge University Press. <https://doi.org/10.1017/CBO9780511623387>
- Schweiger, S. E., Beyer, N., Hass, A. L., & Westphal, C. (2022). Pollen and landscape diversity as well as wax moth depredation determine reproductive success of bumblebees in agricultural landscapes. *Agriculture, Ecosystems & Environment*, 326, 107788. <https://doi.org/10.1016/j.agee.2021.107788>
- Spohn, M., Golte-Bechtle, M., & Spohn, R. (Eds.). (2015). *Was blüht denn da?* 59th, updated and expanded edition, the 1st edition was published in 1934, written by Alois Koch. ed, Kosmos-Naturführer. Kosmos.
- Stacey, P. B., & Taper, M. (1992). Environmental variation and the persistence of small populations. *Ecological Applications*, 2, 18–29. <https://doi.org/10.2307/1941886>
- Steffan-Dewenter, I. (2003). Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*, 17, 1036–1044. <https://doi.org/10.1046/j.1523-1739.2003.01575.x>
- Theunert, R. (2002). *Rote Liste der in Niedersachsen und Bremen gefährdeten Wildbienen mit Gesamtartenverzeichnis*, 1. Fassung. ed. Informationsdienst Naturschutz Niedersachsen, Niedersächsisches Landesamt für Ökologie.
- Theunert, R. (2008). Verzeichnis der in Niedersachsen besonders oder streng geschützten Arten. Schutz, Gefährdung, Lebensräume, Bestand, Verbreitung. Teil B: Wirbellose Tiere. *Informationsdienst Naturschutz Niedersachsen*, 28, 153–210.
- Thompson, P. L., Rayfield, B., & Gonzalez, A. (2017). Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*, 40, 98–108. <https://doi.org/10.1111/ecog.02558>
- Tropek, R., Kadlec, T., Hejda, M., Kocarek, P., Skuhrovec, J., Malenovsky, I., Vodka, S., Spitzer, L., Banar, P., & Konvicka, M. (2012). Technical reclamations are wasting the conservation potential of post-mining sites. A case study of black coal spoil dumps. *Ecological Engineering*, 43, 13–18. <https://doi.org/10.1016/j.ecoleng.2011.10.010>
- Twerd, L., & Banaszak-Cibicka, W. (2019). Wastelands: Their attractiveness and importance for preserving the diversity of wild bees in urban areas. *Journal of Insect Conservation*, 23, 573–588. <https://doi.org/10.1007/s10841-019-00148-8>
- Twerd, L., Szefer, P., Sobieraj-Betlińska, A., & Olszewski, P. (2021). The conservation value of Aculeata communities in sand quarries changes during ecological succession. *Global Ecology and Conservation*, 28, e01693. <https://doi.org/10.1016/j.gecco.2021.e01693>
- Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2023989118. <https://doi.org/10.1073/pnas.2023989118>
- Westphal, C., Steffan-Dewenter, I., & Tschardtke, T. (2006). Bumblebees experience landscapes at different spatial scales: Possible implications for coexistence. *Oecologia*, 149, 289–300.
- Westrich, P. (1996). Habitat requirements of central European bees and problems of partial habitats. In A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, I. H. Williams, & International Bee Research Association, Linnean Society of London (Eds.), *The conservation of bees, Linnean society symposium series* (pp. 1–16). Academic Press.
- Westrich, P. (2018). *Die Wildbienen Deutschlands*. Eugen Ulmer KG.
- Westrich, P. (2019). *Die Wildbienen Deutschlands*, 2., aktualisierte Auflage. ed. Verlag Eugen Ulmer.
- Westrich, P., Frommer, U., Mandery, K., Riemann, H., Ruhnke, H., Saure, C., & Voith, J. (2011). Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. In M. Binot-Hafke, S. Balzer, N. Becker, H. Gruttke, H. Haupt, N. Hofbauer, G. Ludwig, G. Matzke-Hajek, & M. Strauch (Eds.), *Rote Liste Gefährdeter Tiere, Pflanzen Und Pilze Deutschlands. Band 3. Wirbellose Tiere (Teil 1), Naturschutz Und Biologische Vielfalt* (Vol. 70, pp. 373–416). Landwirtschaftsverlag.
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis* (2nd ed.). Springer International Publishing. <https://doi.org/10.1007/978-3-319-24277-4>
- Willis, S. C., Winemiller, K. O., & Lopez-Fernandez, H. (2005). Habitat structural complexity and morphological diversity of fish assemblages in a neotropical floodplain river. *Oecologia*, 142, 284–295. <https://doi.org/10.1007/s00442-004-1723-z>
- Wilson, J. B., Peet, R. K., Dengler, J., & Pärtel, M. (2012). Plant species richness: The world records. *Journal of Vegetation Science*, 23, 796–802. <https://doi.org/10.1111/j.1654-1103.2012.01400.x>
- Wurz, A., Grass, I., Lees, D. C., Rakotomalala, A. A. N. A., Sáfián, S., Martin, D. A., Osen, K., Loos, J., Benasoavina, E., Alexis, T., & Tschardtke,

T. (2022). Land-use change differentially affects endemic, forest and open-land butterflies in Madagascar. *Insect Conservation and Diversity*, 15, 606–620. <https://doi.org/10.1111/icad.12580>

SUPPORTING INFORMATION

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

Data S1: Supplementary information on material and methods, supporting figures and tables.

How to cite this article: Kirsch, F., Hass, A., Alfert, T., & Westphal, C. (2024). Landscape diversity, habitat connectivity, age and size determine the conservation value of limestone quarries for diverse wild bee communities. *Journal of Applied Ecology*, 00, 1–16. <https://doi.org/10.1111/1365-2664.14820>