Journal of Environmental Management 392 (2025) 126628

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Disturbance fosters vascular plant and bee species richness in sand quarries

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ARTICLE INFO

Keywords:
Conservation
Habitat quality
Mining
Neophyte
Orthoptera
Sand pit

ABSTRACT

Industrialized forms of disturbance such as quarrying may unintentionally contribute to biodiversity conservation. To determine the role of disturbance for species richness in sand quarries, we compared environmental conditions and species numbers of three indicator groups (vascular plants, bees and grasshoppers) in regularly disturbed (actively mined or grazed) and abandoned sand quarries. Sampling of environmental parameters and indicator groups was conducted in 25 randomly selected sand quarries in northwestern Germany (Central Europe). Our study revealed clear differences in habitat quality and species richness of the indicator groups between disturbed and abandoned sand quarries. Disturbed quarries were larger and characterized by a higher availability of bare ground and earthen banks/scarps but a lower proportion of areas filled with allochthonous soil in comparison to abandoned quarries. As a result, species richness of vascular plants and bees was higher in disturbed quarries. In the multivariable models, disturbance was also an important predictor. It had a positive effect on species richness of threatened plants and all bees. In conclusion, our study highlights the high value of sand quarries for the conservation of species richness in general and threatened species in particular. Overall, disturbance fostered vascular plant and bee species richness by creating and maintaining nutrient-poor, early successional stages such as patches of bare ground and earthen banks/scarps. For the conservation of species richness in abandoned sand quarries, regular disturbance that maintains nutrient-poor, early-successional stages is required. Therefore, we recommend low-intensity grazing (e.g. by cattle) after cessation of mining.

1. Introduction

Disturbance is an important driver of biodiversity (White and Jentsch, 2004; Wohlgemuth et al., 2019). In particular, many threatened species are dependent on early successional stages (Warren and Büttner, 2008; Pardini et al., 2015; Fartmann et al., 2022) and, therefore, require regular disturbance of their habitats either by man or natural dynamics. However, due to human prevention of dynamic processes (e.g. flooding and fire control) and intensive land use, early successional stages of habitats are rare in todays' landscape (Fartmann et al., 2021). Consequently, disturbance of habitats has become an important conservation strategy for promoting threatened species dependent on early successional stages. For example, in Central European semi-natural grasslands, which evolved by traditional land use and have undergone a dramatic decline in the past decades due to land-use intensification, the most important conservation measure is regular disturbance by low-intensive mowing or grazing (Halada et al., 2011; Fartmann, 2024). Under such a disturbance regime and low nutrient availability, semi-natural grasslands are amongst the most species-rich habitats in Central Europe and characterized by a high proportion of threatened species (Fumy and Fartmann, 2023; Guariento et al., 2023). On the one hand, low-intensity management of semi-natural grasslands fosters phytodiversity with cascading effects on phytophagous species such as bees of which many have specific demands in terms of pollen sources (Westrich, 2018). On the other hand, it favours an open vegetation structure with a warm microclimate, which benefits many, often thermophilous insect species that depend on early successional stages (e.g. Stuhldreher et al., 2012; Fartmann, 2024). However, for highly specialized species such as ground-nesting bees and less-competitive plant species that require patches of bare ground for nesting and germination, respectively, a higher disturbance intensity is crucial. For promoting these species, the creation of bare ground by mechanical soil disturbance (e.g. by ploughing or sod cutting) represents a suitable conservation tool (Ödman et al., 2012; Olsson et al., 2014; Streitberger et al., 2021;

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https://doi.org/10.1016/j.jenvman.2025.126628
Received 21 October 2024; Received in revised form 3 July 2025; Accepted 15 July 2025
Available online 23 July 2025

Gardein et al., 2022).

Due to heavy disturbance favoring the establishment of early successional stages, industrialized forms of land use may unintentionally contribute to biodiversity conservation. One example are quarries where early successional stages of open habitats with a high proportion of bare ground are regularly created by the depletion of rocks or sediments. For Central Europe, there are numerous studies highlighting the importance of quarries for different species groups (e.g. plants, arthropods), especially from the Czech Republic (e.g. Heneberg et al., 2013; Řehounková et al., 2020). Most studies focus on abandoned (areas of) quarries where different successional stages of spontaneous revegetation were analyzed in terms of biodiversity. Within these quarries, especially open dry habitats and their early successional stages were revealed as relevant refugia for threatened and specialized, xero- or psammophilous species (Dekoninck et al., 2010; Tropek et al., 2010; Heneberg et al., 2013, 2016; Heneberg and Řezáč, 2014; Řehounková et al., 2020).

However, studies focusing on the importance of disturbance for biodiversity in quarries, e.g. by comparing species assemblages among active quarries, where mining regularly takes place, and abandoned ones are still rare. One exception is the study of Kettermann et al. (2022), which analyzed overall bee species richness in active and abandoned limestone quarries. The study revealed that total species richness and the richness of threatened species were higher in active quarries compared to abandoned ones due to a high proportion of early successional stages and a high diversity of pollen sources in active quarries. Comparably, Řehounková et al. (2016) found a higher number of threatened species and open sand specialists of vascular plants and arthropods in areas used for recreational activities and disturbed by human trampling compared to undisturbed and forested areas in the abandoned part of a large sand quarry.

In this study, we analyze environmental conditions and species richness in 25 randomly selected sand quarries in northwestern Germany (Central Europe). We compare regularly disturbed (actively mined or grazed) and abandoned sand quarries to determine the role of disturbance for species richness and to derive management recommendations. We applied a multi-taxa approach by focusing on three indicator groups with different biological and ecological traits: vascular plants as primary producers (Grime et al., 2007), bees as pollinators directly dependent on phytodiversity (Westrich, 2018) and Orthoptera (hereinafter termed 'grasshoppers') as consumers that feed on a wide range of plants or arthropods (Fartmann and Poniatowski, 2025). In particular, we addressed the following questions.

- How do environmental factors at the habitat (quarry) and landscape (200 m buffer around quarry) level differ among disturbed and abandoned sand quarries?
- What environmental factors promote overall species richness of vascular plants, bees and grasshoppers in sand quarries? Depending on indicator group, we distinguished between native and non-native (vascular plants), all (bees, grasshoppers) and threatened species (vascular plants, bees).
- What management recommendations can be derived from the study for the conservation of species richness in sand quarries?

2. Material and methods

2.1. Study area

The research was carried out in the west of Lower Saxony (NW Germany). The study area had an overall size of 3.500 km^2 and covered parts of the districts of Emsland, Oldenburg and Vechta. The study area has an oceanic climate with a mean annual temperature of 9.8 °C and an annual precipitation of 843 mm (meteorological station: Visbek [51 m a.s.l.], period: 1991–2000; German Meteorological Service, 2024). The landscape is flat and dominated by sandy sediments of the Saale Ice Age (Schmidt and Roeschmann, 2014). Intensive agriculture with high fertilizer input is the prevalent type of land use. In addition, the study area represents one of the most important strongholds of sand excavation in Germany (Elsner, 2022). Accordingly, sand quarries are widespread.

2.2. Study plots

Within the study area, 25 sand quarries were randomly selected using the function 'create random points' in ArcGIS 10.2. In total, 14 sand quarries were abandoned and 11 were classified as disturbed ones (Fig. 1). The latter included nine actively mined sand quarries and two sand quarries where quarrying has been ceased but which have been grazed by cattle since then. Grazed quarries were structurally comparable to active sand quarries, especially due to a high proportion of early successional stages of open habitats. On average (±SE), quarrying has been ceased in the abandoned quarries for 15 ± 3.2 years. Due to a clustered distribution, the quarries were assigned to five subareas that were separated from each other by a minimum distance of 5 km to account for spatial autocorrelation in the statistical analyses (see section 2.5).

2.3. Sampling of indicator groups

In each sand quarry, vascular plant, bee and grasshopper assemblages were sampled in 2022. For sampling vascular plants, the sand quarries were visited twice. In May, early flowering species (e.g. *Montia arvensis*, *Spergula morisonii*, *Vicia lathyroides*) were surveyed by checking their presence in each terrestrial and semi-terrestrial habitat type that occurred in a quarry during a standardized time of 1 h per quarry. Similarly, all other vascular plants were sampled in June/July by noting all species in the aforementioned habitat types of a quarry during a standardized period of 4 h per quarry. Species determination was carried out by using Müller et al. (2021) and Oberdorfer (2001).

For sampling grasshoppers, each quarry was visited at the beginning of June for the detection of early species (e.g. *Tetrix* spp., *Gryllus campestris*) and in August (all other species). During both visits, the entire quarry was searched for grasshopper species in a standardized time of 1.5 h. All species that were detected by sight or stridulation were recorded. In order to detect species that produce high-frequency signals (e.g. *Conocephalus dorsalis*), additionally, a bat recorder was used during the August survey. Sampling of grasshoppers was only carried out under favourable weather conditions (sunny conditions, air temperature: >16 °C, wind: <3 Beaufort). Species were determined with the help of Fischer et al. (2020).

Bee assemblages were sampled from mid-March to the beginning of September. In this period, the quarries were visited seven times with an interval of three weeks between each survey. Per quarry and survey, we visited all potential bee resources (especially patches with high flower abundance and nesting structures) that occurred in a quarry during a standardized time of 2 h (Kettermann et al., 2022). Sampling was only carried out under favourable weather conditions (see above) from 10 a.m. to 5 p.m. Detected bees were collected by using an insect net. Species identifiable in the field were released after determination. All other individuals were killed with ethyl acetate and identified in the lab by using a binocular microscope. Bees were determined to species level according to the following identification keys: Amiet (1996); Amiet et al. (1999, 2001, 2004, 2007, 2010); Bogusch and Straka (2012); Dathe et al. (2016); Praz et al. (2022); Scheuchl (2000, 2006); Schmid-Egger and Scheuchl (1997); Straka and Bogusch (2011).

For further analysis, we differentiated between the following species groups: native, non-native and threatened vascular plant species, all and threatened bee species and all grasshopper species. Non-native vascular plant species included species that were classified as neophytes or not listed in the red data book of Lower Saxony (Garve, 2004). Furthermore, species that were not distributed or had an unstable (i.e. unnatural) distribution in the lowland of Lower Saxony according to Garve (2004)

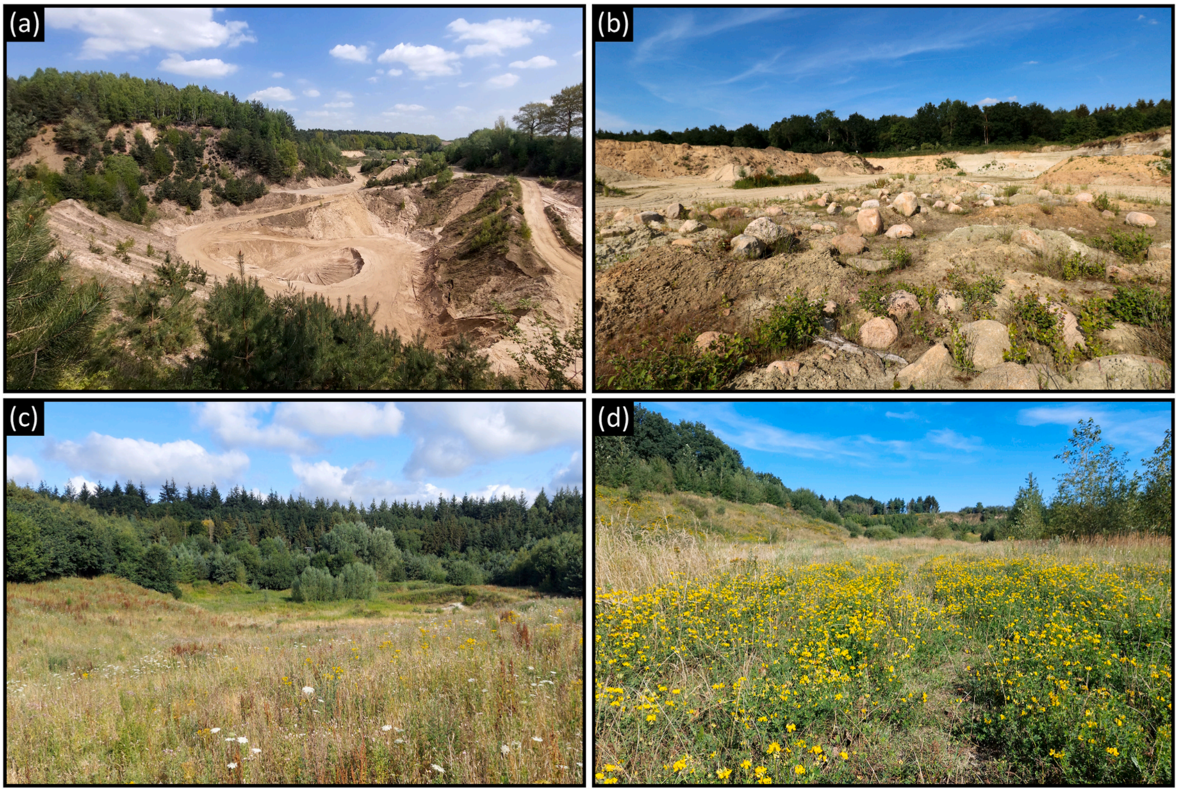

Fig. 1. Examples for disturbed (a, b) and abandoned (c, d) sand quarries in the study area (Photo credits: a, c and d – Marcel Kettermann; b – Dominik Poniatowski).

were classified as non-native. For species, that were distributed naturally in the lowland of Lower Saxony, but were characterized by local non-indigenous populations (species marked with an 'S', Garve, 2004), distribution status was checked for the study area according to distribution maps in NetPhyD, BfN (2013). Among these species, those were classified as non-native that were not distributed or had an unnatural distribution in the study area. Species that were not assigned to one of these criteria were regarded as native vascular plant species. Threatened vascular plant and bee species were classified according to Garve (2004) and Theunert (2002), respectively. All species that were listed as threatened (red-list categories: 0, 1, 2, 3, G and V) in the lowland of Lower Saxony were included in these groups. In the case of vascular plants, non-native species that were classified as threatened, were excluded from the analysis. As the number of threatened grasshopper species (according to Grein, 2005) was generally low in the quarries (seven species in total, Appendix B, Table B.4), this group was not analyzed separately.

2.4. Environmental conditions

Several environmental parameters were assessed to characterize habitat quality of the sand quarries. Information on quarry size was provided by the local nature conservation authorities. In May 2022, habitats were mapped in each sand quarry according to the habitat mapping guidelines of Lower Saxony (von Drachenfels, 2021) with the help of aerial photographs and digitized in ArcGIS 10.2. Based on the number and proportion of the habitat types, the Shannon index was determined for each quarry as a measure of habitat diversity (Kettermann et al., 2022). In addition to overall habitat diversity, the Shannon index was calculated solely for habitats that were protected (e.g. dry grassland) by law due to their special importance for biodiversity conservation (according to von Drachenfels, 2021; hereinafter referred to as 'habitat diversity$_{protected}$'). Furthermore, the age of the quarries and the proportion of area filled with allochthonous soil material were included in the analysis. Information on these parameters was supplied by the local nature conservation authorities. Additionally, the proportion of the following habitat types were included in the analysis due to their special relevance as habitats for the sampled indicator groups: bare ground, ruderal tall herb communities, psammophilous grassland/heathland (cf. Fartmann et al., 2012; Kettermann et al., 2022).

With respect to bees, all flowering plant species that are considered as potential pollen sources for oligolectic bee species according to Westrich (2018) were recorded. During each survey, all habitat types within the respective quarry were visited and the plant species were noted within 1 h. Based on this species list, the number of pollen sources relevant for the oligolectic species that were detected in at least one of the studied quarries was derived for each quarry and used as an explanatory variable. Furthermore, the total area of sunlit earthen banks/scarps (those with southern, southeastern or western aspect) were considered as suitable nesting structures for specialized bee species and mapped in each quarry (Kettermann et al., 2022). Density of earthen banks/scarps (m^2/ha) was used as an explanatory variable.

Besides the above-mentioned habitat quality parameters, the proportions of the following four broad land-use types were analyzed in a 200 m wide buffer around each quarry as measures of landscape quality: arable land, forest, grassland and urban area. For this purpose, the areas of the different land-use types in the 200 m wide buffer were digitized in ArcGIS 10.2 based on aerial photographs. Furthermore, connectivity of the quarries was determined with the help of aerial photographs by calculating the mean of the distances to the three nearest quarries in ArcGIS 10.2 (Kettermann and Fartmann, 2023). Only those sand quarries were considered where early successional stages (habitats with a high proportion of bare ground >30 %) were present with a minimum area of 1.000 m^2.

2.5. Statistical analysis

All statistical analyses were carried out with R 4.3.2 (R Core Team, 2023). Significant differences in environmental conditions among disturbed and abandoned sand quarries were detected by using (generalized) linear mixed Models (GLMM; LMM; R packages lme4, Bates et al., 2023) with subarea as a random factor. In all models, disturbance type (disturbed/abandoned) was used as a nominal explanatory variable and the environmental variables were inserted as dependent variables. Depending on the distribution of the variables, binomial GLMM (percentage data) or LMM (other variables) were applied. Observation-level random effects were added within over-dispersed binomial GLMM (Harrison, 2015). The effect of disturbance on the dependent variables was analyzed with likelihood-ratio tests (comparison of full model and model without explanatory variable, $P < 0.05$). Differences in species numbers among the two sand quarry types were analyzed accordingly. Depending on the distribution of the species variable either negative binomial GLMM (native/non-native/threatened vascular plant species, all/threatened bee species) or LMM (grasshopper species) were applied.

To detect the effect of the environmental variables on species richness of the different species groups, we applied multivariable (G)LMMs (negative binomial GLMM and LMM, see above). Due to the high number of environmental variables, we applied univariable models as a preparatory step. The univariable models were applied in a similar way as described above. Species richness was used as the dependent variable and the environmental variables served as the explanatory variables. Subarea was included as a random effect and significance was detected with likelihood-ratio tests ($P < 0.05$). Area of earthen banks/scarps and number of pollen sources were only considered as explanatory variables for bees. In the multivariable models, only those variables were included that were detected as significant in the univariable models (Table A.1, Appendix A). Furthermore, only non-intercorrelated variables were used in the models (Spearman correlation [r_s], $|r_s| > 0.6$, $P < 0.05$). As the proportions of arable land and forest were intercorrelated ($r_s = -0.86$, $P < 0.001$), the proportion of arable land was excluded from modelling species richness of threatened vascular plants (cf. Table B.1, Appendix B). All other variables were non-intercorrelated. All explanatory variables were standardized (centered and scaled) to make their effect size comparable. In order to identify the most relevant environmental parameters within our multivariable models, we applied model averaging based on an information-theoretic approach (Grueber et al., 2011). Model averaging was conducted using the ‘dredge’ function (package MuMIn; Bartoń, 2023) and only included top-ranked models within $\Delta AIC_C < 3$ (cf. Grueber et al., 2011; Schirmel et al., 2016; Scherer et al., 2025).

3. Results

3.1. Environmental conditions

Landscape quality parameters did not differ between disturbed and abandoned sand quarries. However, some habitat quality parameters varied between the two quarry types (Table 1). Disturbed quarries were larger, had a higher density of earthen banks/scarps and were characterized by a higher proportion of bare ground. By contrast, abandoned quarries exhibited a higher proportion of areas filled with allochthonous soil.

3.2. Species richness

In total, 403 native vascular plant species, including 50 (12 %) threatened ones, were recorded in the 25 studied sand quarries (Tables B.1 and B.2, Appendix B). Overall, 166 (41 %) of these species occurred in more than half of the quarries. Of the 193 detected non-native plant species, only 20 (10 %) were recorded in more than half of the quarries (Table B.1, Appendix B). Moreover, a total of 153 bee species, among them 62 (41 %) threatened ones (Table B.3, Appendix B), and 23 grasshopper species, among them 7 (30 %) threatened ones, were recorded in the quarries (Table B.4, Appendix B). Mean species richness of vascular plants (native, non-native, threatened species) and bees (all and threatened species) was higher in disturbed compared to abandoned quarries (Fig. 2). Solely, species richness of grasshoppers did not differ between quarry types.

Table 1
Mean (±SE) of landscape and habitat quality parameters in disturbed ($n = 11$) and abandoned ($n = 14$) sand quarries. Differences between the two quarry types were detected by using (generalized) linear mixed-effects models (see section 2 for details). *$P < 0.05$, **$P < 0.01$, n.s. = not significant ($P > 0.05$).

Parameter	Disturbed	Abandoned	*P*
Landscape quality			
Arable land (%)	36.9 ± 6.2	45.1 ± 5.9	n.s.
Forest (%)	46.8 ± 4.7	32.6 ± 7.3	n.s.
Grassland (%)	4.0 ± 1.8	7.1 ± 1.7	n.s.
Urban area (%)	6.1 ± 2.0	8.1 ± 2.2	n.s.
Connectivity[a] (m)	2037 ± 436	2592 ± 707	n.s.
Habitat quality			
Size (ha)	14.5 ± 2.3	6.8 ± 1.2	**
Age (a)	22.5 ± 3.2	26.7 ± 2.7	n.s.
Habitat diversity[b]	1.9 ± 0.1	1.7 ± 0.1	n.s.
Habitat diversity$_{protected}$[b]	0.7 ± 0.2	0.5 ± 0.1	n.s.
No. of pollen sources (plant species)	33.8 ± 1.9	32.0 ± 1.4	n.s.
Density of earthen banks/scarps (m^2/ha)	52.4 ± 15.0	11.5 ± 4.8	**
Bare ground (%)	12.3 ± 3.6	3.2 ± 1.6	*
Ruderal tall herb communities (%)	11.9 ± 2.7	14.1 ± 3.7	n.s.
Psammophilous grassland/heathland (%)	3.6 ± 1.5	4.1 ± 2.5	n.s.
Allochthonous soil (%)	22.1 ± 5.1	40.7 ± 5.2	*

[a] Mean of the distances to the three nearest sand quarries with early successional stages of a minimum size of 1.000 m^2.
[b] Shannon index.

3.3. Environmental drivers of species richness

Quarry size was the only predictor of species richness of native and non-native vascular plants and had a positive effect (Table 2). By contrast, species richness of threatened vascular plants was favoured by disturbance and a high forest cover in the 200 m wide buffer around the quarries. For bee species richness, the number of pollen sources was the main predictor. It fostered both the overall number of bee species and those of threatened species. Moreover, disturbance had a positive and the proportion of areas filled with allochthonous soil a negative effect on overall bee species richness. In threatened bee species, the proportion of bare ground positively affected species richness, in addition to the number of pollen sources. The number of grasshopper species only increased with the diversity of protected habitats.

4. Discussion

Our study revealed clear differences in habitat quality and species richness of the indicator groups between disturbed and abandoned sand quarries. Disturbed quarries, which were either grazed by cattle or actively used for sand mining, were larger and characterized by a higher availability of bare ground and earthen banks/scarps but a lower proportion of areas filled with allochthonous soil in comparison to abandoned quarries. As a result, species richness of vascular plants and bees was higher in disturbed quarries, and, in the multivariable models, disturbance was also an important predictor. It had a positive effect on species richness of threatened plants and all bees. Further essential predictors were the size of the quarry and the number of pollen sources. They favoured species richness of plants (native and non-native species) and bees (all and threatened species), respectively.

In the 25 sand quarries, we detected 403 native plant, 153 bee and 23 grasshopper species, which was 28 %, 49 % and 64 %, respectively, of the regional species pool of each of the indicator groups (cf. Theunert, 2002; Garve, 2004; Grein, 2005). Moreover, the share of threatened species was quite high, it varied between 30 and 41 % per indicator

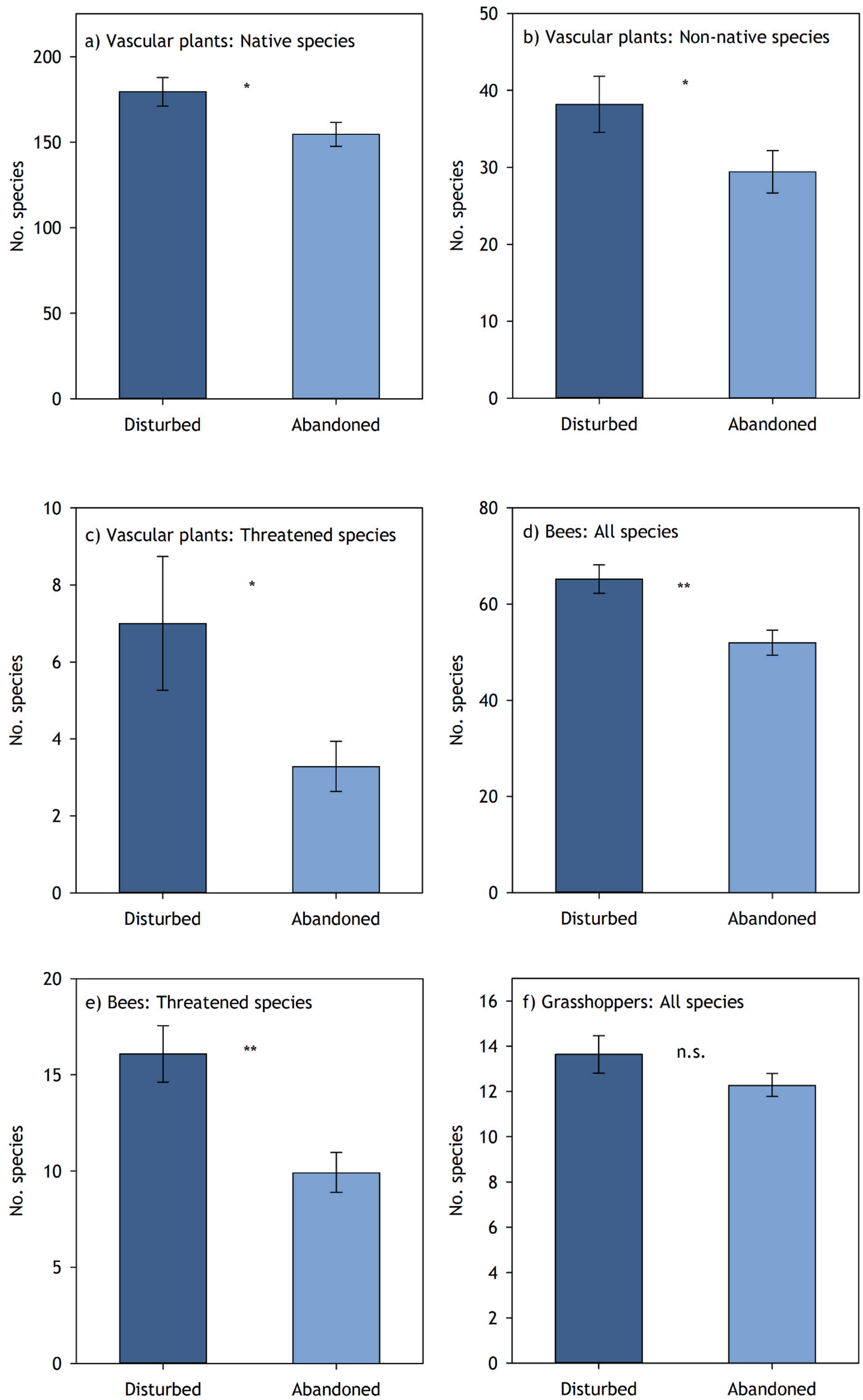

Fig. 2. Mean (±SE) species richness of vascular plants (native, non-native and threatened species), bees (all and threatened species) and grasshoppers (all species) in disturbed ($n = 11$) and abandoned ($n = 14$) sand quarries. Differences between the two quarry types were detected by using (generalized) linear mixed-effects models (see section 2 for details). $^*P < 0.05$, $^{**}P < 0.01$, n.s. = not significant ($P > 0.05$).

group. Accordingly, overall, our study generally confirms the high value of sand quarries for the conservation of species richness in general and threatened species in particular (e.g. Heneberg et al., 2013; Heneberg and Řezáč, 2014; Řehounková et al., 2020).

Disturbance (disturbed vs. abandoned quarries) was identified as the main predictor of species richness in our study. Density of earthen banks/scarps and the proportion of bare ground and areas filled with allochthonous soil were three of the four parameters that differed between the two quarry types and were related to disturbance. In disturbed quarries, due to quarrying and grazing, earthen banks/scarps and bare ground regularly emerge or are maintained (own observation). By contrast, parts of abandoned quarries were much more often back-filled with allochthonous soil after quarrying has been ceased. All three variables were not intercorrelated and alone had usually no effect on species richness in one of the multivariable models, except bare ground and allochthonous soil (one model in each case). Consequently, we

Table 2
Multivariable models: Effects of landscape and habitat quality on the species numbers of the different species groups in sand quarries ($n = 25$). Effects were analyzed with (generalized) linear mixed-effects models (see section 2 for details). Presented are the model-averaged coefficients (conditional average) that were derived from the top-ranked models ($\Delta AIC_C < 3$) (see section 2 for details). R^2_m = variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa et al., 2017). Variables that were identified as significant by univariable models (Appendix B), but are not presented were not included within the top-ranked models. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, n. s. = not significant ($P > 0.05$).

Parameter	Estimate	SE	P
(a) Native vascular plant species ($R^2_m = 0.49–0.55$, $R^2_c = 0.49–0.55$)			
(Intercept)	5.10145	0.02451	***
Size	0.10761	0.03020	***
Habitat diversity$_{protected}$	0.05310	0.02932	n.s.
(b) Non-native vascular plant species ($R^2_m = 0.35–0.38$, $R^2_c = 0.35–0.38$)			
(Intercept)	3.48418	0.05471	***
Size	0.19780	0.06133	**
Habitat diversity$_{protected}$	0.06960	0.06531	n.s
(c) Threatened vascular plant species ($R^2_m = 0.16–0.41$, $R^2_c = 0.24–0.54$)			
(Intercept)	1.6633	0.2495	***
Forest	0.3203	0.1380	*
Disturbance			
Abandoned	−0.5580	0.2493	*
Habitat diversity	0.3685	0.1965	n.s.
(d) All bee species ($R^2_m = 0.47–0.56$, $R^2_c = 0.55–0.57$)			
(Intercept)	4.09707	0.05956	***
Size	0.03542	0.03706	n.s.
Disturbance			
Abandoned	−0.15226	0.06644	*
No. of pollen sources	0.09899	0.03269	**
Allochthonous soil (%)	−0.08821	0.03609	*
(e) Threatened bee species ($R^2_m = 0.44–0.48$, $R^2_c = 0.53–0.57$)			
(Intercept)	2.50818	0.12217	***
Size	0.09390	0.07362	n.s.
Disturbance			
Abandoned	−0.27684	0.16900	n.s.
Habitat diversity	0.07761	0.07594	n.s.
No. of pollen sources	0.23539	0.07058	**
Bare ground (%)	0.22540	0.07745	**
(f) All grasshopper species ($R^2_m = 0.37–0.41$, $R^2_c = 0.41–0.47$)			
(Intercept)	12.9869	0.4433	***
Size	0.5053	0.4427	n.s.
Habitat diversity$_{protected}$	1.3846	0.4195	**

interpret disturbance as a surrogate variable that particularly combines the effects of earthen banks/scarps, bare ground and allochthonous soil. In our multivariable models, disturbance had a positive effect on species richness of threatened plants and all bees.

Bare soil is well known to be of critical importance for plant and bee species richness. Many plant species, in particular threatened ones, need bare soil for germination and successful establishment (Münzbergová and Herben, 2005; Grime et al., 2007; Streitberger et al., 2017). This is also true for the numerous threatened plant species in our study, which were often annuals and/or low-competitive species dependent on open soil (e.g. *Aira caryophyllea*, *Centaurium erythraea*, *Isolepis setacea*, *Montia arvensis* or *Vicia lathyroides*; cf. Fleischer et al., 2013; Řehounková et al., 2020). Accordingly, we observed a positive relationship between species richness of threatened plant species and disturbance.

Sunlit open soil in earthen banks/scarps but also on flat ground is of great significance as a nesting habitat for bees (Buchholz et al., 2020; Antoine and Forrest, 2021; Gardein et al., 2022; Kettermann et al., 2022; Albrecht et al., 2023). Almost 60 % of the bee species in Germany breed in the soil (Westrich, 2018). In line with this, disturbance in general and bare ground in particular (threatened species) had a positive effect on bee species richness.

Most abandoned quarries in our study were partly filled with allochthonous soil and mean cover was almost two times higher than in disturbed quarries. The vast majority of the backfilled material originated from urban areas (own observation). As a result, the soils were characterized by higher contents of clay and silt, which made them more fertile. Moreover, they already contained many diaspores and plant material, often from non-native species such as ornamental plants (e.g. *Alchemilla mollis*, *Lychnis coronaria*, *Yucca filamentosa*). Consequently, allochthonous soils were usually characterized by a higher successional speed and later successional stages compared to the originally nutrient-poor sandy soils, which were lacking any seeds directly after mining. Therefore, we argue that the deposition of allochthonous soils fostered the disappearance of crucial early successional stages and, thus, had negative effects on species richness of threatened plants as part of the disturbance variable. For overall bee species richness, we even observed a direct negative effect of allochthonous soil.

The two further essential predictors of species richness were the size of the quarry (plants) and the number of pollen sources (bees). The number of plant species usually increases with habitat area due to a higher variability of environmental conditions in larger habitats (Brose, 2001; Krauss et al., 2004; Kallimanis et al., 2008; Holtmann et al., 2019). Indeed, in our study, disturbed quarries were larger and had a higher species richness of vascular plants (all three species groups) than abandoned ones. Additionally, quarry size was the only predictor of species richness of native and non-native plants. However, habitat diversity in general and those of protected habitat types in particular did not differ between disturbed and abandoned quarries. Moreover, both parameters were not intercorrelated with quarry size. Overall, the Shannon index based on habitat types is a relatively coarse measure of habitat heterogeneity, which does not reflect small-scale variability of environmental conditions within a certain habitat type, e.g. in vegetation structure, soil type or soil humidity. Consequently, we still explain the positive relationship between quarry size and species richness by the habitat heterogeneity hypothesis, which predicts that habitat area is a surrogate of habitat heterogeneity (Brose, 2001; Steinmann et al., 2011).

Besides suitable nesting sites, the number of different pollen sources is known to be the second important driver of bee species richness, since many species are oligolectic (e.g. Holzschuh et al., 2008; Twerd and Banaszak-Cibicka, 2019; Twerd et al., 2019; Kettermann et al., 2022). In line with this, overall bee species richness and those of threatened species increased with the number of pollen sources.

Additionally, forest cover adjacent to the quarries had a positive effect on threatened plant species. However, we hardly observed threatened forest species in the quarries. By contrast, forest cover was negatively correlated with those of arable land. Since the study area is characterized by very intensive agriculture and high fertilizer input, a high forest cover can be regarded as a proxy for low nutrient input from the surrounding. Most threatened plant species are less competitive and depend on the naturally nutrient-poor conditions of the sand quarries (see above).

Grasshoppers were the only indicator group for which we did not observe differences in species richness between disturbed and abandoned quarries, and for which the diversity of protected habitats favoured species richness. Overall, the oceanic northwest of Germany is characterized by a very species-poor grasshopper fauna and specialized species are usually rare (Fartmann and Poniatowski, 2025). In line with this, the grasshopper assemblages in the quarries included mainly habitat generalists and the few habitat specialists that occurred usually had a low frequency. According to Fartmann and Poniatowski (2025), only 8 (35 %) of the 23 detected species were habitat specialists and only two of them, *Chorthippus mollis* and *Tetrix subulata*, had a frequency of more than 40 % in the studied quarries. Accordingly, we explained the lack of differences in species richness between the disturbed and abandoned quarries by the overall low level of habitat specificity of the species. Protected habitats within the quarries comprised different types of dry sandy grasslands and open riparian vegetation (own observation). They are known to be key habitats of grasshoppers (Fartmann et al., 2024; Fartmann and Poniatowski, 2025). As a result, species richness of grasshoppers increased with the diversity of these protected habitats.

The studied quarries were not only hotspots of species richness in native plants and insects but also in non-native plants. Both (i) the large availability of early successional stages rich in bare soil and (ii) the allochthonous soils, mostly from urban areas rich in seed and plant material, used for backfilling fostered the establishment of alien plants (see above). Moreover, quarries are often used for illegal dumping of waste material (e.g. garden waste), which also promotes the establishment of synanthropic plant species, including non-native ones (Twerd et al., 2019). However, the assemblages of non-native plants were highly variable in species composition and most species had usually a low cover (own observation). Solely, *Fallopia japonica* and *Solidago gigantea* were dominant in patches on allochthonous soil in some of the quarries.

In conclusion, our study highlights the high value of sand quarries for the conservation of species richness in general and threatened species in particular. Overall, disturbance, either by mining or grazing, was identified as the main predictor of species richness. It fostered vascular plant and bee species richness by creating and maintaining nutrient-poor, early successional stages such as patches of bare ground and earthen banks/scarps.

5. Implications for conservation

For the conservation of species richness in abandoned (parts of) sand quarries in the long run, regular disturbance that maintains nutrient-poor, early-successional stages is required. Therefore, we recommend to introduce low-intensity grazing (e.g. by cattle) after cessation of mining (cf. Rupprecht et al., 2016; Henning et al., 2017), which is generally known to foster habitat heterogeneity and thus biodiversity (Fartmann, 2024). In quarries, where late successional stages already cover larger areas, bush clearance and topsoil removal represent suitable restoration measures for the creation of open habitats prior to the introduction of grazing (Henriksson et al., 2019; Poniatowski et al., 2020). Overall, conservation should primarily focus on large quarries where a high proportion of early successional stages is still available. As our studied showed, such quarries usually still host a high richness of species in general and threatened species in particular. The concentration on such quarries is especially important in intensively used landscapes, such as our study area, where other source populations in the surrounding are usually lacking (cf. Kettermann et al., 2022). For the same reasons, the expansion of existing quarries should be preferred to the establishment of new quarries far away from other quarries (Kettermann et al., 2022).

When the implementation of conservation measures such as grazing is not feasible in abandoned quarries, spontaneous revegetation should be prioritized over reclamation (e.g. by afforestation), since the latter promotes the rapid loss of species-rich habitats (Prach et al., 2011; Šebelíková et al., 2019). In general, the deposition of allochthonous soils within quarries should strictly be banned since it promotes a faster degradation and favours the establishment of non-native plant species that may become dominant such as *Fallopia japonica* and *Solidago gigantea* (Prach et al., 2011; own observation).

CRediT authorship contribution statement

Merle Streitberger: Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Thomas Fartmann:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Marcel Kettermann:** Writing – review & editing, Investigation. **Marco Drung:** Writing – review & editing, Investigation. **Dominik Poniatowski:** Writing – review & editing, Project administration, Methodology, Investigation, Conceptualization.

Funding

This work was carried out in the framework of the project “Vielfalt in Geest und Moor” (Grant No. 3520685E26). The project was funded within the Federal Programme for Biological Diversity by the Federal Agency for Nature Conservation with resources from the Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are very grateful to Helmut Schlarmann and Matthias Galle (both nature conservation authority Vechta), Tilla Schulte Ostermann (nature conservation authority Oldenburg) as well as Maike Hoberg (nature conservation authority Emsland) for providing detailed information on the studied sand quarries. Moreover, we would like to thank the mining companies and private landowners for making their land available for the study.

Appendix A. Univariable models

Table A.1
Univariable models: Singular effects of landscape and habitat quality on the species richness of the different indicator groups in sand quarries ($n = 25$). Effects were analyzed with (generalized) linear mixed-effects models (see section 2 for details). + = positive estimate, – negative estimate. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, n.s. = not significant ($P > 0.05$). n.a. = not analyzed.

	Vascular plants			Bees		Grasshoppers
	Native species	Non-native species	Threatened species	All species	Threatened species	All species
Landscape quality						
Arable land (%)	n.s.	n.s.	–*	n.s.	n.s.	n.s.
Forest (%)	n.s.	n.s.	+*	n.s.	n.s.	n.s.
Grassland (%)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Urban area (%)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Connectivity[a] (m)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Habitat quality						
Size (ha)	+***	+***	n.s.	+**	+**	+*
Age (a)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Disturbance type (Disturbed/Abandoned)	+Disturbed*	+Disturbed*	+Disturbed*	+Disturbed**	+Disturbed**	n.s.
Habitat diversity[b]	n.s.	n.s.	+*	n.s.	+*	n.s.

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Table A.1 (*continued*)

	Vascular plants			Bees		Grasshoppers
	Native species	Non-native species	Threatened species	All species	Threatened species	All species
Habitat diversity$_{protected}$[b]	+**	+*	n.s.	n.s.	+*	+**
No. of pollen sources (plant species)	n.a.	n.a.	n.a.	+**	+**	n.a.
Density of earthen banks/scarps (m^2/ha)	n.a.	n.a.	n.a.	n.s.	n.s.	n.a.
Bare ground (%)	n.s.	n.s.	n.s.	n.s.	+*	n.s.
Ruderal tall herb communities (%)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Psammophilous grassland/heathland (%)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Allochthonous soil (%)	n.s.	n.s.	n.s.	–*	n.s.	n.s.

[a] Mean of the distances to the three nearest sand quarries with early successional stages of a minimum size of 1.000 m^2.
[b] Shannon index.

Appendix B. Species lists

Table B.1
Frequencies (%) of native and non-native vascular plant species recorded in more than 50 % of the studied sand quarries (n = 25). Species classification as non-native: see section 2 for details. Nomenclature: Metzing et al. (2018).

Species	Non-native species	Frequency (%)
Acer campestre	.	60.0
Acer pseudoplatanus	.	68.0
Achillea millefolium	.	100.0
Aegopodium podagraria	.	80.0
Agrostis capillaris	.	100.0
Agrostis stolonifera	.	84.0
Alnus glutinosa	.	64.0
Anthoxanthum odoratum	.	68.0
Arabidopsis thaliana	.	92.0
Arenaria serpyllifolia	.	68.0
Arrhenatherum elatius	.	76.0
Artemisia vulgaris	.	100.0
Barbarea vulgaris	.	52.0
Betula pendula	.	100.0
Bromus hordeaceus	.	92.0
Bromus sterilis	.	76.0
Calamagrostis epigejos	.	80.0
Calystegia sepium	.	88.0
Capsella bursa-pastoris	.	64.0
Cardamine hirsuta	.	100.0
Carduus crispus	.	68.0
Carex hirta	.	88.0
Carex leporina	.	60.0
Cerastium glomeratum	.	96.0
Cerastium holosteoides	.	96.0
Cerastium semidecandrum	.	76.0
Chaerophyllum temulum	.	68.0
Chelidonium majus	.	68.0
Chenopodium album	.	80.0
Cirsium arvense	.	100.0
Cirsium vulgare	.	92.0
Claytonia perfoliata	x	64.0
Cornus sanguinea	.	88.0
Corylus avellana	.	60.0
Crataegus monogyna	.	68.0
Crepis capillaris	.	100.0
Cytisus scoparius	.	84.0
Dactylis glomerata	.	100.0
Daucus carota	.	64.0
Deschampsia flexuosa	.	68.0
Digitalis purpurea	.	84.0
Draba verna	.	92.0
Dryopteris carthusiana	.	60.0
Dryopteris filix-mas	.	88.0
Eleocharis palustris	.	52.0
Elymus repens	.	96.0
Epilobium ciliatum	x	60.0
Epilobium parviflorum	.	68.0
Epilobium tetragonum	.	72.0
Equisetum arvense	.	96.0
Erigeron annuus	x	80.0
Erigeron canadensis	x	96.0

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Table B.1 (*continued*)

Species	Non-native species	Frequency (%)
Erodium cicutarium	.	56.0
Eupatorium cannabinum	.	52.0
Fagus sylvatica	.	56.0
Fallopia convolvulus	.	80.0
Fallopia japonica	x	68.0
Festuca rubra agg.	.	100.0
Filago minima	.	84.0
Galeopsis tetrahit	.	52.0
Galium aparine	.	96.0
Geranium molle	.	84.0
Geranium pusillum	.	76.0
Geranium robertianum	.	64.0
Geum urbanum	.	52.0
Glechoma hederacea	.	100.0
Gnaphalium uliginosum	.	60.0
Hedera helix	.	56.0
Holcus lanatus	.	100.0
Humulus lupulus	.	64.0
Hypericum perforatum	.	100.0
Hypochaeris radicata	.	100.0
Juncus articulatus	.	72.0
Juncus bufonius	.	64.0
Juncus conglomeratus	.	100.0
Juncus effusus	.	96.0
Juncus tenuis	x	84.0
Lactuca serriola	.	64.0
Lapsana communis	.	56.0
Larix spec.	x	64.0
Leucanthemum ircutianum	.	56.0
Lolium perenne	.	88.0
Lotus corniculatus	.	56.0
Lotus pedunculatus	.	88.0
Lupinus polyphyllus	x	88.0
Luzula campestris	.	56.0
Luzula multiflora	.	84.0
Lycopus europaeus	.	76.0
Matricaria chamomilla	.	64.0
Matricaria discoidea	x	68.0
Medicago lupulina	.	92.0
Melilotus albus	.	64.0
Myosotis arvensis	.	64.0
Oenothera biennis	x	100.0
Ornithopus perpusillus	.	92.0
Papaver dubium	.	84.0
Papaver somniferum	x	56.0
Persicaria amphibia	.	52.0
Persicaria maculosa	.	64.0
Phalaris arundinacea	.	52.0
Phleum pratense	.	52.0
Phragmites australis	.	80.0
Picea abies	x	64.0
Pinus sylvestris	.	92.0
Plantago lanceolata	.	100.0
Plantago major	.	88.0
Poa annua	.	76.0
Poa palustris	.	80.0
Poa trivialis	.	100.0
Polygonum aviculare agg.	.	76.0
Populus balsamifera agg.	x	56.0
Populus tremula	.	96.0
Potentilla anserina	.	80.0
Prunella vulgaris	.	88.0
Prunus serotina	x	88.0
Prunus spinosa	.	64.0
Quercus robur	.	100.0
Ranunculus repens	.	96.0
Robinia pseudoacacia	x	76.0
Rorippa palustris	.	64.0
Rosa canina	.	68.0
Rosa rubiginosa	x	52.0
Rubus fruticosus agg.	.	100.0
Rubus idaeus	.	80.0
Rumex acetosella	.	100.0
Rumex crispus	.	52.0
Rumex obtusifolius	.	96.0
Sagina procumbens	.	84.0

(*continued on next page*)

Table B.1 (*continued*)

Species	Non-native species	Frequency (%)
Salix alba	.	92.0
Salix aurita	.	64.0
Salix caprea	.	100.0
Salix cinerea	.	100.0
Salix viminalis	.	88.0
Sambucus nigra	.	60.0
Scrophularia nodosa	.	64.0
Senecio inaequidens	x	100.0
Senecio jacobaea	.	96.0
Senecio vulgaris	.	64.0
Silene latifolia	.	84.0
Sisymbrium altissimum	x	60.0
Sisymbrium officinale	.	56.0
Solidago gigantea	x	100.0
Sonchus asper	.	88.0
Sorbus aucuparia	.	80.0
Stellaria graminea	.	64.0
Stellaria media	.	72.0
Tanacetum vulgare	.	100.0
Taraxacum sect. *Ruderalia*	.	96.0
Trifolium arvense	.	100.0
Trifolium dubium	.	100.0
Trifolium hybridum	x	56.0
Trifolium pratense	.	56.0
Trifolium repens	.	100.0
Tripleurospermum perforatum	.	84.0
Tussilago farfara	.	92.0
Typha latifolia	.	68.0
Urtica dioica	.	100.0
Verbascum nigrum	.	52.0
Verbascum thapsus	.	88.0
Veronica arvensis	.	92.0
Veronica serpyllifolia	.	72.0
Vicia angustifolia	.	100.0
Vicia cracca	.	88.0
Vicia hirsuta	.	96.0
Vicia tetrasperma	.	88.0
Vulpia myuros	.	96.0

Table B.2
Frequencies (%) of threatened vascular plant species (according to Garve, 2004; see section 2 for details) in the studied sand quarries (n = 25). Nomenclature: Metzing et al. (2018).

Species	Frequency (%)
Agrimonia eupatoria	8.0
Aira caryophyllea	20.0
Blechnum spicant	4.0
Bromus secalinus	4.0
Carex flacca	4.0
Carex panicea	4.0
Carex viridula	4.0
Centaurium erythraea	20.0
Chaenorhinum minus	16.0
Cynoglossum officinale	4.0
Dactylorhiza majalis	4.0
Dianthus armeria	8.0
Dianthus deltoides	8.0
Drosera rotundifolia	4.0
Echium vulgare	28.0
Empetrum nigrum	4.0
Equisetum sylvaticum	4.0
Equisetum telmateia	4.0
Erica tetralix	4.0
Eriophorum angustifolium	12.0
Filago germanica	16.0
Galium verum	12.0
Helichrysum luteoalbum	20.0
Huperzia selago	4.0
Hypericum maculatum	8.0
Isolepis setacea	20.0

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Table B.2 (*continued*)

Species	Frequency (%)
Juncus squarrosus	8.0
Leontodon saxatilis	36.0
Limosella aquatica	4.0
Lycopodiella inundata	16.0
Malva sylvestris	20.0
Montia arvensis	8.0
Myosotis discolor	24.0
Myosotis ramosissima	24.0
Ononis spinosa agg.	4.0
Orobanche rapum-genistae	4.0
Osmunda regalis	8.0
Peplis portula	20.0
Pilularia globulifera	4.0
Plantago coronopus	4.0
Rhamnus cathartica	8.0
Salix pentandra	4.0
Setaria pumila	4.0
Thymus pulegioides	4.0
Trifolium medium	8.0
Turritis glabra	4.0
Valerianella locusta	8.0
Veronica maritima	8.0
Vicia lathyroides	8.0
Viola tricolor	4.0

Table B.3
Frequencies (%) of all bee species in the studied sand quarries ($n = 25$). Nomenclature: Scheuchl et al. (2023). Threatened species: Theunert (2002); see section 2 for details.

Species	Threatened species	Frequency (%)
Andrena afzeliella	.	16.0
Andrena barbilabris	.	80.0
Andrena batava	.	8.0
Andrena carantonica	.	20.0
Andrena cineraria	.	12.0
Andrena clarkella		68.0
Andrena denticulata	x	84.0
Andrena dorsata	.	92.0
Andrena flavipes	.	100.0
Andrena fulva	.	16.0
Andrena fuscipes	x	4.0
Andrena gravida	x	16.0
Andrena haemorrhoa	.	76.0
Andrena helvola	.	4.0
Andrena humilis	x	12.0
Andrena minutula	.	52.0
Andrena minutuloides	x	28.0
Andrena mitis	x	4.0
Andrena nigroaenea	.	36.0
Andrena nitida	.	32.0
Andrena nycthemera	x	20.0
Andrena ovatula	.	8.0
Andrena praecox	.	84.0
Andrena propinqua	.	16.0
Andrena proxima	x	16.0
Andrena ruficrus	x	8.0
Andrena strohmella	.	24.0
Andrena subopaca	.	16.0
Andrena tibialis	x	4.0
Andrena vaga	.	96.0
Andrena ventralis	x	16.0
Andrena wilkella	x	12.0
Anthidiellum strigatum	x	80.0
Anthidium manicatum	.	8.0
Anthidium punctatum	x	16.0
Anthophora plumipes	x	4.0
Bombus bohemicus	.	48.0
Bombus hortorum	x	52.0
Bombus hypnorum	.	44.0
Bombus jonellus	x	4.0
Bombus lapidarius	.	100.0
Bombus lucorum-complex	.	100.0

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Table B.3 (*continued*)

Species	Threatened species	Frequency (%)
Bombus norvegicus	x	28.0
Bombus pascuorum	.	100.0
Bombus pratorum	.	44.0
Bombus rupestris	x	8.0
Bombus sylvestris	.	20.0
Bombus vestalis	x	80.0
Chelostoma campanularum	.	8.0
Coelioxys mandibularis	x	12.0
Colletes cunicularius	.	100.0
Colletes daviesanus	.	72.0
Colletes fodiens	.	100.0
Colletes similis	x	56.0
Dasypoda hirtipes	.	76.0
Epeoloides coecutiens	.	4.0
Epeolus variegatus	.	100.0
Halictus confusus	x	12.0
Halictus quadricinctus	x	8.0
Halictus rubicundus	.	48.0
Halictus scabiosae	.	28.0
Halictus tumulorum	.	80.0
Heriades truncorum	.	92.0
Hoplitis claviventris	x	4.0
Hoplitis leucomelana	x	32.0
Hoplitis tridentata	.	4.0
Hylaeus brevicornis	.	68.0
Hylaeus communis	.	88.0
Hylaeus confusus	.	24.0
Hylaeus cornutus	.	32.0
Hylaeus difformis	x	24.0
Hylaeus dilatatus	.	88.0
Hylaeus gibbus	x	4.0
Hylaeus gredleri	x	28.0
Hylaeus hyalinatus	.	36.0
Hylaeus incongruus	.	4.0
Hylaeus moricei	.	8.0
Hylaeus paulus	.	28.0
Hylaeus pectoralis	x	4.0
Hylaeus rinki	x	12.0
Hylaeus signatus	x	40.0
Lasioglossum brevicorne	x	4.0
Lasioglossum calceatum	.	80.0
Lasioglossum fulvicorne	x	12.0
Lasioglossum laticeps	.	36.0
Lasioglossum lativentre	x	4.0
Lasioglossum leucopus	.	40.0
Lasioglossum leucozonium	.	88.0
Lasioglossum limbellum	.	4.0
Lasioglossum lucidulum	.	80.0
Lasioglossum minutissimum	x	56.0
Lasioglossum morio	.	100.0
Lasioglossum parvulum	x	48.0
Lasioglossum pauxillum	x	76.0
Lasioglossum punctatissimum	.	36.0
Lasioglossum quadrinotatulum	.	56.0
Lasioglossum quadrinotatum	x	32.0
Lasioglossum rufitarse	x	8.0
Lasioglossum sexnotatum	x	12.0
Lasioglossum sexstrigatum	.	80.0
Lasioglossum tarsatum	x	4.0
Lasioglossum villosulum	.	84.0
Lasioglossum zonulum	x	4.0
Macropis europaea	.	16.0
Macropis fulvipes	x	12.0
Megachile circumcincta	x	4.0
Megachile ericetorum	x	32.0
Megachile versicolor	.	56.0
Megachile willughbiella	.	32.0
Melecta albifrons	x	4.0
Nomada alboguttata	.	48.0
Nomada bifasciata	x	16.0
Nomada fabriciana	x	12.0
Nomada femoralis	.	4.0
Nomada ferruginata	x	28.0
Nomada flava	.	40.0
Nomada flavoguttata	.	36.0
Nomada fucata	.	80.0

(*continued on next page*)

Table B.3 (*continued*)

Species	Threatened species	Frequency (%)
Nomada fuscicornis	x	12.0
Nomada goodeniana	.	28.0
Nomada lathburiana	.	64.0
Nomada leucophthalma	x	24.0
Nomada marshamella	.	32.0
Nomada moeschleri	.	4.0
Nomada panzeri	.	8.0
Nomada roberjeotiana	x	8.0
Nomada ruficornis	.	32.0
Nomada rufipes	x	44.0
Nomada sheppardana	.	64.0
Nomada signata	.	16.0
Nomada succincta	.	36.0
Nomada zonata	x	36.0
Osmia aurulenta	x	8.0
Osmia bicornis	.	44.0
Osmia cornuta	x	4.0
Osmia leaiana	x	4.0
Panurgus banksianus	x	8.0
Panurgus calcaratus	.	68.0
Sphecodes albilabris	.	96.0
Sphecodes crassus	.	72.0
Sphecodes ephippius	.	52.0
Sphecodes geofrellus	.	56.0
Sphecodes gibbus	.	60.0
Sphecodes longulus	.	40.0
Sphecodes marginatus	x	4.0
Sphecodes miniatus	.	92.0
Sphecodes monilicornis	.	56.0
Sphecodes niger	x	8.0
Sphecodes pellucidus	.	80.0
Sphecodes puncticeps	.	16.0
Sphecodes reticulatus	.	36.0
Stelis breviuscula	.	24.0
Stelis phaeoptera	x	4.0

Table B.4
Frequencies (%) of all grasshopper species in the studied sand quarries ($n = 25$). Nomenclature: Fischer et al. (2020). Threatened species: Grein (2005).

Species	Threatened species	Frequency (%)
Chorthippus albomarginatus	.	40.0
Chorthippus apricarius	.	28.0
Chorthippus biguttulus	.	100.0
Chorthippus brunneus	.	96.0
Chorthippus dorsatus	x	88.0
Chorthippus mollis	x	76.0
Chrysocharon dispar	.	44.0
Conocephalus dorsalis	.	28.0
Conocephalus fucus	.	28.0
Gryllotalpa gryllotalpa	x	16.0
Leptophyes punctatissima	.	64.0
Myrmeleotettrix maculatus	.	24.0
Oedipoda caerulescens	x	8.0
Omocestus rufipes	x	4.0
Omocestus viridulus	.	20.0
Phaneroptera falcata	.	92.0
Pholidoptera griseoaptera	.	72.0
Pseudochorthippus parallelus	.	36.0
Roeselinana roeselii	.	88.0
Tetrix ceperoi	x	36.0
Tetrix subulata	x	80.0
Tetrix undulata	.	92.0
Tettigonia viridissima	.	92.0

Data availability

The authors do not have permission to share data.

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