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Original Research Article

Ponds in quarries have a higher plant species richness than those in the surrounding landscape

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A R T I C L E I N F O

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A B S T R A C T

Habitat loss is one of the main drivers of the current global biodiversity crisis, with freshwater ecosystems among those that suffer most. The aim of this study was to compare the environmental conditions and assemblages of semi-aquatic and aquatic plants (vascular plants, mosses, stoneworts) of 15 randomly selected ponds in limestone quarries with those of 15 control ponds in the surrounding landscape. Our study revealed clear differences in habitat quality and plant species composition between quarry and control ponds. The number of all and threatened species was for both vascular plants and mosses higher in quarry than in control ponds. Moreover, threatened moss species were even restricted to quarry ponds, and stoneworts generally only occurred in this type of pond. A higher habitat quality was the key for the increased species richness in quarry ponds compared to control ponds. Particularly, sunlit early-successional stages, a heterogeneous submerged and a large semi-aquatic zone accounted for the higher number of plant species in quarry ponds. Across the 30 studied ponds, sunshine duration and pond diversity were the most important predictors of species richness, followed by the cover of the semi-aquatic zone. All three had a positive effect. Backfilling, afforestation or flooding of quarries after the cessation of mining should generally be avoided. In times of climate change, it is recommended to create a variety of water bodies, including both temporary and permanent ones, within quarries. Where thick topsoil layers and woody plants may establish, they should be removed locally.

1. Introduction

Habitat loss is one of the main drivers of the current global biodiversity crisis (Johnson et al., 2017; Pykälä, 2019; Caro et al., 2022), with freshwater ecosystems among those that suffer most (Janse et al., 2015; Hill et al., 2021). According to Davidson (2014), globally more than 60 % of the wetlands have been modified since the early 20th century and loss rates are even accelerating. This is particularly worrying given that freshwater ecosystems occupy only 1 % of the Earth's land surface but exhibit a disproportionately high density of species per unit area compared to terrestrial and marine ecosystems (Grooten and Almond, 2018).

Small water bodies are known to be important habitats for semi-aquatic and aquatic plants. Compared to other types of water bodies, they tend to have a higher phytodiversity, especially concerning rare and threatened species (Nicolet et al., 2004; Davies et al., 2008; Holtmann et al., 2019). By contrast, larger and deeper water bodies are usually less rich in species, but if they have low nutrient

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contents and are calcareous, they can represent important habitats for threatened stonewort species (Rey-Boissezon and Joye, 2015; O'Reilly and Shimwell, 2017; Seelen et al., 2021). Due to their great importance for nature conservation, such lakes are protected by the EU Habitats Directive (European Commission, 2007).

Quarries often have a negative reputation in the general public and are associated with habitat destruction and adverse effects on biodiversity (Beneš et al., 2003; Tropek et al., 2010). Indeed, quarrying leads to fundamental alterations of a habitat by removing vegetation and topsoil (Bétard, 2013; Kalarus et al., 2019). For a long time, the only post-mining measure considered was the reclamation and afforestation of quarries. However, recent studies reveal that quarries can host exceptionally high biodiversity. In quarries, active mining continuously creates sunlit, early-successional stages, which are essential for overall species richness and many species of conservation concern (Baumbach et al., 2013; Řehounková et al., 2016; Kettermann et al., 2022; Münsch and Fartmann, 2022). Additionally, quarries exhibit another peculiarity: due to the lack of topsoil, the successional speed is very low, and thus the early-successional stages have a high durability even without further management (Řehounková and Prach, 2010; Prach et al., 2011; Münsch and Fartmann, 2022). Both characteristics also apply to water bodies in quarries (Kettermann et al., 2023). By contrast, small water bodies outside quarries usually lack any disturbance that creates early-seral stages and successional speed is mostly high due to deep soils and the general eutrophication of the landscape (Nijssen et al., 2017; Kettermann et al., 2023).

The aim of this study was to compare the environmental conditions and assemblages of semi-aquatic and aquatic plants of 15 randomly selected ponds in limestone quarries with those of 15 control ponds in the surrounding landscape. For each pond, we assessed several environmental parameters of habitat and landscape quality. The environmental predictors of overall species richness and number of threatened species of vascular plants, mosses and stoneworts were analysed using Generalized Linear Mixed-effects Models. Based on the results of this study, we make management recommendations to enhance plant species richness in quarry ponds.

2. Material and methods

2.1. Study area

The study area was located in the northeast of the German Federal State of North Rhine-Westphalia (Central Europe) and covered an area of approximately 1520 km^2. It has a suboceanic climate with an average annual temperature of 9.5 °C and a mean annual precipitation of 951 mm (Bad Lippspringe meteorological station, 157 m a.s.l, period: 1981–2010; DWD, 2023). However, due to variation in landscape configuration but also slight differences in elevation and therefore in climate, we divided the study area into four distinct subareas to account for possible spatial autocorrelation: (i) Beckumer Berge, (ii) Hellweg, (iii) Teutoburger Wald and (iv) Ostwestfalen-Lippe (Fig. 1). The subareas Ostwestfalen-Lippe and Teutoburger Wald comprise a diverse landscape featuring a mix of forested hills, ridges and flat valleys primarily covered by grassland. The elevation ranges from 250 to 350 m a.s.l. By contrast, the subareas Beckumer Berge and Hellweg are situated within the Westphalian Basin, characterized by elevations varying from 100 to

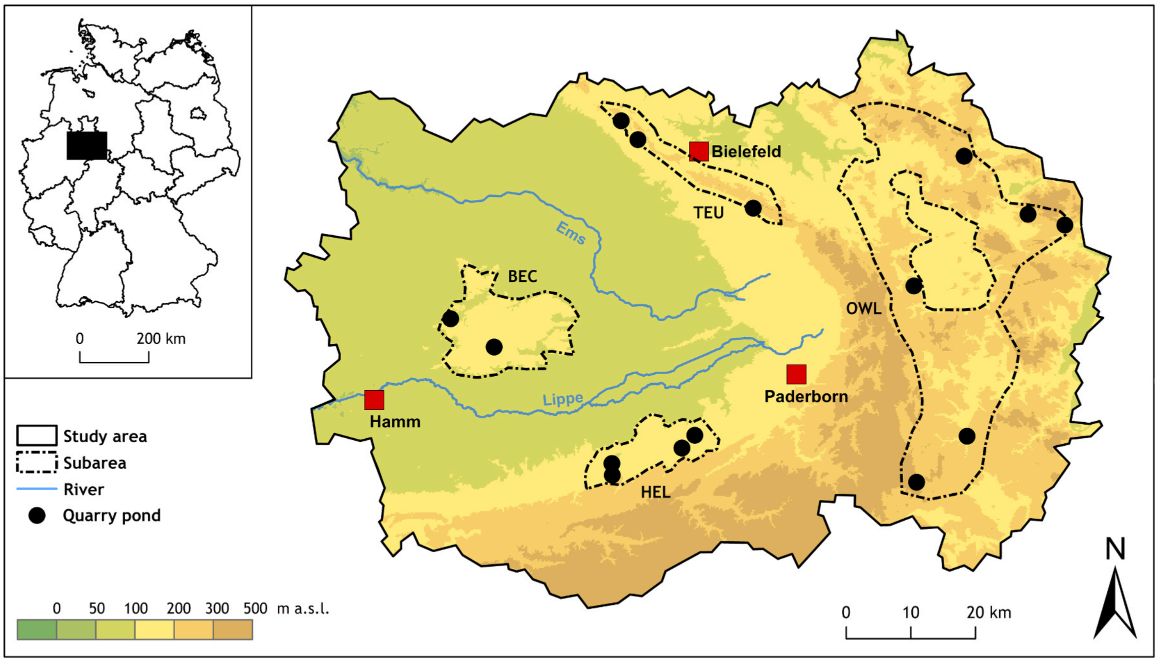

Fig. 1. The study area in the eastern part of North Rhine-Westphalia in central Germany (inlay) and the location of the four subareas Beckumer Berge (BEC), Hellweg (HEL), Teutoburger Wald (TEU), and Ostwestfalen-Lippe (OWL) with its ponds in limestone quarries (Quarry pond). Control ponds are not shown since they are overlapping at this scale.

197 m a.s.l. There, agriculture is the predominant type of land use. Across the study area, limestone is extracted from quarries and is used for manufacturing of gravel, bricks, construction materials and cement. Each of the four subareas included both quarry and control ponds, allowing for paired comparisons within each region.

2.2. Sampling design

Within our study area, we conducted a random selection of 15 ponds located within limestone quarries (Figs. 1 and 2). For each quarry, the nearest pond in the surrounding landscape, located outside the quarry area but within the same subarea, was chosen as a control (Fig. 2).In each water body, we surveyed all species of vascular plants, mosses and stoneworts in the semi-aquatic and in the aquatic zone twice: once at the end of May and once in the beginning of July. During each visit, plants were surveyed for 2 h. Macrophytes in deeper areas of the water body were collected using a telescopic pole (3 m in length) equipped with a hook. Species identification was carried out using the guidebooks by Haeupler and Muer (2007), Oberdorfer et al. (2001) and Van de Weyer et al. (2018). For statistical analysis, all three groups of plants were treated separately. Moreover, we differentiated all three groups into all and threatened species (including near-threatened species). The threat status was derived from the most recent red data books in North Rhine-Westphalia: Verbücheln et al. (2021) for vascular plants, Schmidt et al. (2011) for mosses and Van de Weyer (2023) for stoneworts.

2.3. Environmental parameters

For each pond, we collected several environmental parameters to assess habitat and landscape quality (Table 1). Prior to statistical analysis, those parameters that were sampled more than once were averaged for each pond. Conductivity and pH measurements were taken during both visits. Sunshine duration was measured in May and July using a horizontoscope (Holtmann et al., 2017). Data on annual temperature (°C) (long-term average: 1981–2010) were obtained from 1-km^2 grid datasets provided by Germany's National Meteorological Service DWD (2023) (Table 1). All other parameters were recorded during the first visit in May. Four diversity indices were created as indicators of habitat heterogeneity. Each water body was divided into three sub-zones, and we determined which of the following layers were present per sub-zone: (i) submerged zone ($N_{max} = 3$) consisting of submerged herbs, stoneworts and other algae; (ii) emergent zone ($N_{max} = 6$) including open water surface, floating leaf plants, reed, Juncaceae, Cyperaceae, herbs and (iii) shoreline ($N_{max} = 4$) with trees, shrubs, field layer and bare soil. The number of layers per sub-zone represented the diversity index of the respective sub-zone. Subsequently, the sum of all layers per water body ($N_{max} = 13$) was summed up in the pond diversity index. For spatial analysis, we utilized ArcGIS 10.3.1 and aerial photographs. We calculated the distance to the nearest three water bodies (geometric mean) as a measure of pond connectivity, following methods described by Holtmann et al. (2017) and Kettermann and Fartmann (2023).

2.4. Statistical analysis

All statistical analyses were performed using R 4.1.2. (R Development Core Team, 2022). Generalized Linear Mixed-effects Models (GLMM) were fitted with 'subarea' (see Section 2.1) as a random intercept (lme4 package; Bates et al., 2011). Since we were only able to detect one species of threatened stoneworts (*Chara hispida*) in one pond, we refrained from further statistical analyses and model calculations for this group. As our study was based on a paired design, all metric environmental parameters (see Table 1) and the five response variables (number of all and threatened species; see Section 2.3) were tested for significant differences between quarry and

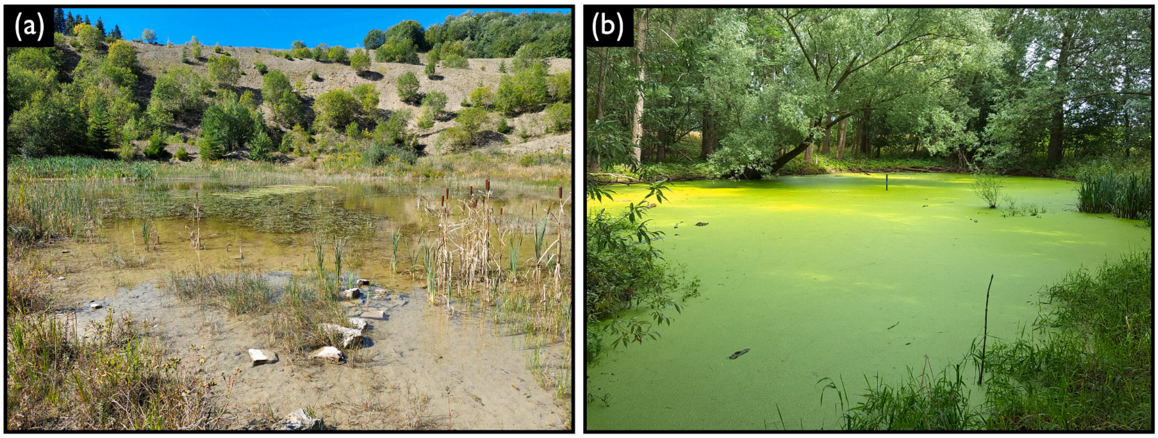

Fig. 2. Examples of the two studied pond types: a quarry pond (a), characterized by full sunlight, high habitat diversity, and a well-developed semi-aquatic zone; a control pond (b), with taller shoreline vegetation, strong shading of the water body, and dense cover of floating-leaved plants (Photos: M. Kettermann).

Table 1
Overview of the sampled environmental parameters (mean ± SE, minimum and maximum). Differences between quarry ponds (Quarry, $N = 15$) and control ponds (Control, $N = 15$) were analysed using Generalized Linear Mixed-effects Models (negative-binomial error structure for count data, proportional-binomial error structure for cover data) with 'subarea' as a random intercept (for details see Section 2.4). n.s. = not significant, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	Quarry		Control		*P*
	Mean (± SE)	Min.–Max.	Mean (± SE)	Min.–Max.	
Habitat quality					
Pond size (m^2)[1]	3033 ± 868	32–14,630	1064 ± 350	78–5527	n.s.
pH[2]	7.1 ± 0.1	7–8	6.9 ± 0.2	7–8	n.s.
Conductivity (μS/cm)[2]	456.1 ± 39.0	204–733	563 ± 60.9	218–974	n.s.
Sunshine July (h/day)[3]	13.9 ± 0.5	10–16	5.7 ± 1.0	1–16	***
Water level fluctuation (cm)[4]	29.9 ± 13.2	0–180	6.5 ± 1.8	0–25	**
Cover semi-aquatic zone (%)	65.0 ± 5.8	35–100	32.3 ± 6.9	5–100	**
Diversity index					
Pond	10.3 ± 0.4	7–12	8.7 ± 0.5	5–12	n.s.
Shoreline	3.2 ± 0.2	2–4	3.1 ± 0.2	2–4	n.s.
Emergent zone	4.6 ± 03	3–6	4.3 ± 0.3	2–6	n.s.
Submerged zone	2.5 ± 0.2	1–3	1.3 ± 0.2	0–2	*
Shoreline					
Cover (%)					
Trees	4.0 ± 1.3	0–15	30.0 ± 4.3	0–50	***
Shrubs	19.0 ± 4.1	5–65	21.2 ± 4.7	0–60	n.s.
Field layer	42.8 ± 6.2	2.5–70.0	45.3 ± 5.7	5–95	n.s.
Bare soil	35.0 ± 7.9	5–95	4.8 ± 2.0	0–30	***
Vegetation height (cm)	37.7 ± 4.4	4–64	55.2 ± 4.4	23–102	**
Water body					
Cover (%)					
Open water surface	45.3 ± 7.8	5–95	43.7 ± 9.1	0–95	n.s.
Floating leaf plants	6.8 ± 3.3	0–50	40.2 ± 8.7	2.5–90.0	**
Emergent vegetation	48.7 ± 7.4	5–95	16.8 ± 3.7	2.5–60.0	***
Reed	20.8 ± 5.3	0–70	4.2 ± 2.7	0–40	***
Juncaceae	13.3 ± 2.0	2.5–25.0	1.8 ± 0.7	0–10	***
Cyperaceae	9.8 ± 3.7	0–55	2.8 ± 0.9	0–10	n.s.
Emergent herbs	1.5 ± 0.5	0–5	5.2 ± 1.2	0–15	***
Submerged vegetation	44.7 ± 5.3	15–85	21.3 ± 6.4	5–90	**
Submerged herbs	18.3 ± 3.5	2.5–55.0	16.2 ± 5.9	0–80.0	n.s.
Characeae	21.0 ± 3.7	2.5–45.0	0 ± 0.0	0–0	***
Other algae	6.3 ± 0.9	2.5–15.0	5.7 ± 0.9	0–10.0	n.s.
Landscape quality					
Elevation (m a.s.l.)[5]	181.0 ± 14.3	98–289	158 ± 16.7	91–287	n.s.
Mean annual temperature (°C)[6]	9.2 ± 0.1	8.1–9.8	9.3 ± 0.1	8.5–9.9	n.s.
Mean annual precipitation (mm)[6]	907 ± 20	815–1088	947 ± 75	800–1945	n.s.
Pond connectivity (m)[7]	783 ± 223	47–2479	697 ± 137	27–1595	n.s.

[1] Calculated from aerial photographs by using ArcGIS 10.3.1.
[2] Measured by using a multi-parameter probe (Hanna HI 98129).
[3] Measured by using a horizontoscope; mean of four measures at N, E, S, W (Holtmann et al., 2017).
[4] Measured by using a water gauge.
[5] Elevation was taken from topographic maps.
[6] Long-term mean (1991—2020) from 1-km^2 grid datasets of Germany's National Meteorological Service DWD, 2023).
[7] Geometric mean of the distance to the next three water bodies.

control ponds by using univariable GLMMs (Fig. 3). Negative-binomial error structure was applied for count data, while proportional-binomial error structure was used for cover data. The corresponding pairs of quarry and control ponds were nested within 'subarea' and used as a random factor in all models. The significance of the predictor variable was assessed with likelihood-ratio tests (Type III tests). To prevent multicollinearity, all environmental variables were screened for pairwise correlations (Pearson's $|r| > 0.5$; see Table A1). When variables were intercorrelated, only the ecologically comprehensible variable was used for subsequent analyses (Dormann et al., 2013). Next, univariable GLMMs were fitted for all combinations of response and predictor variables to identify those predictors with a significant effect ($P < 0.05$; see Table A2). All variables that were significant in these univariable models were then included in the global multivariable GLMMs to explain species richness of all and threatened species. To identify the most relevant environmental parameters within these models, we applied model averaging based on an information-theoretic approach (Grueber et al., 2011). Model averaging was conducted using the dredge function (R package MuMIn; Bartoń, 2021), including only top-ranked models within $\Delta AICc < 3$ (cf. Grueber et al., 2011). Standardized model-averaged coefficients were calculated to assess the relative importance of predictors. The resulting multivariable models were used to identify and visualize the environmental parameters that significantly influenced species richness (see Figs. 4 and 5, Table A4). We evaluated the explanatory power of the models by calculating marginal (variance explained by fixed effects) and conditional (variance explained by both fixed and random effects) R_2 (Nakagawa et al., 2017). The ID of each water body in the data table was used to establish an observation-level random effect. This formatted factor

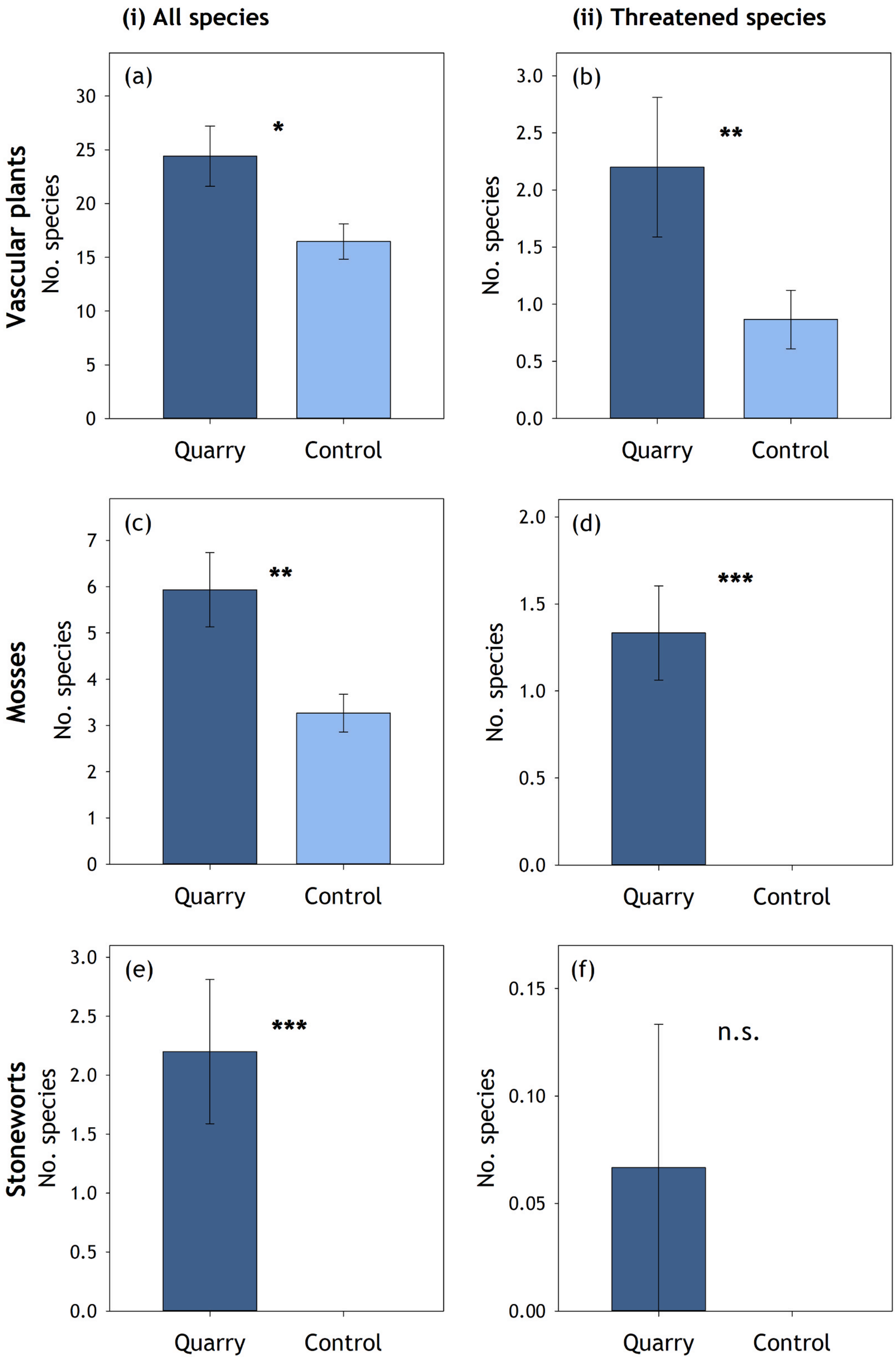

Fig. 3. Mean (± SE) number of all vascular plants (a), threatened vascular plants (b), all mosses (c), threatened mosses (d), all stoneworts (e) and threatened stoneworts (f) in quarry ponds (Quarry, $N = 15$) and control ponds (Control, $N = 15$). Differences between pond types were analysed using Generalized Linear Mixed-effects Models (negative-binomial error structure) with 'subarea' as a random intercept (for details see Section 2.4). Statistical significance is indicated as follows: * $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$.

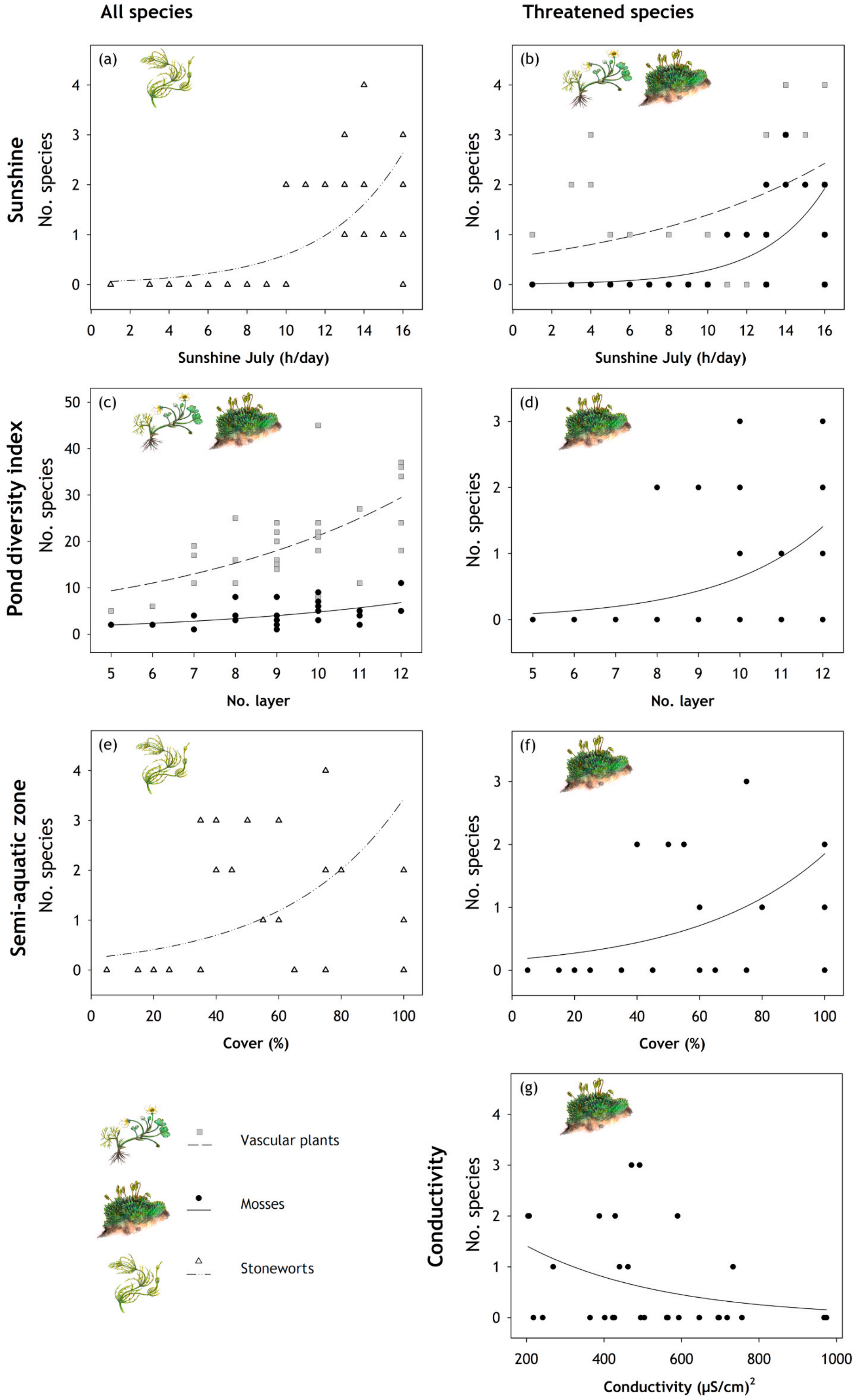

Fig. 4. Relationship between significant environmental parameters and the number of vascular plant, moss and stonewort species shown in two columns representing all species (left) and threatened species (right). Each row represents one significant environmental parameter retained in the final multivariable models (negative-binomial error structure, $N = 30$). The regression slopes were fitted using univariable Generalized Linear Mixed-effects Models with 'subarea' as a random intercept (for details, see Section 2.4). Red List stoneworts were excluded from the analyses because *Chara hispida* was recorded in only one pond.

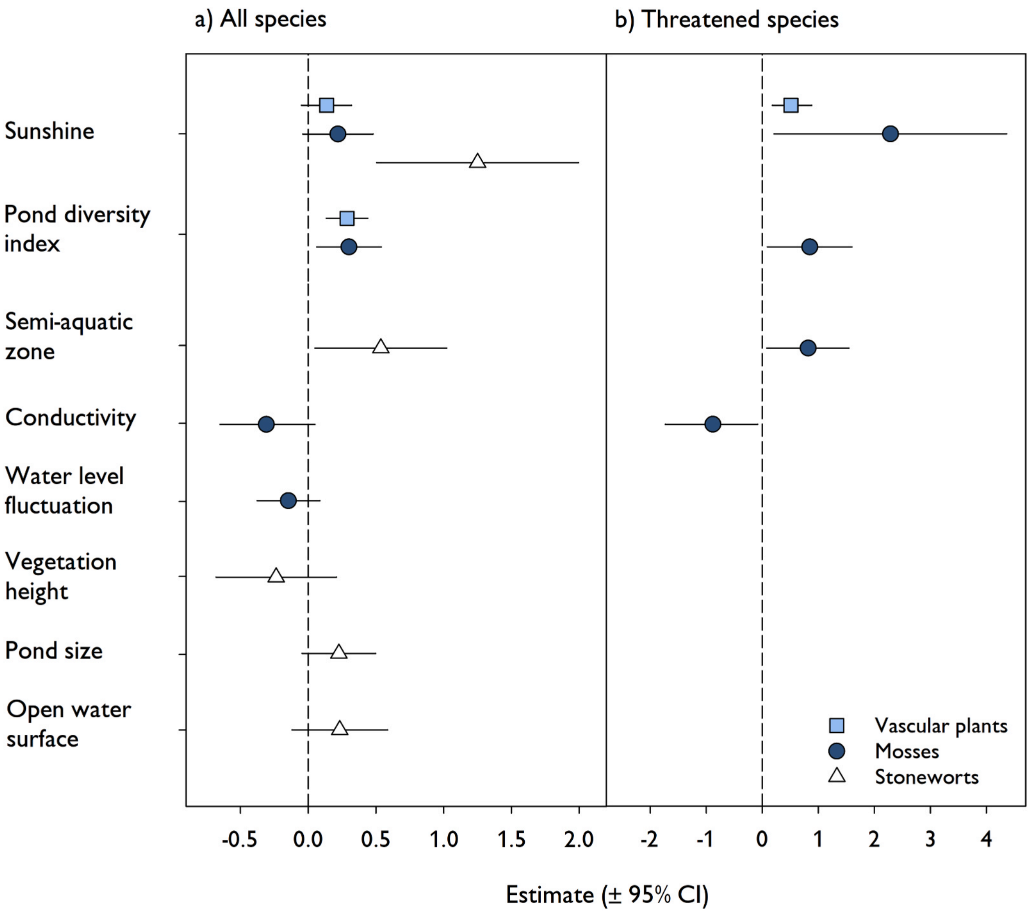

Fig. 5. Standardized estimates (± 95 % confidence intervals [CI]) of environmental predictors of the number of vascular plant, moss and stonewort species (divided into all and threatened species). Model-averaged coefficients were derived from the top ranked models (ΔAICc<3). The environmental variables were centred and standardized to allow direct comparison between them. Confidence intervals of significant predictors ($P < 0.05$) do not cross x = 0. For details of Generalized Linear Mixed-effects Model statistics see Table A4.

can account for moderate overdispersion in models (Harrison, 2014, 2015). To identify species that were characteristic either of quarry or control ponds, an Indicator Species Analysis (ISA) was carried out using the 'multipatt' function in the package 'indicspecies' (De Cáceres et al., 2010) and the association index "IndVal.g". The statistical significance of the indicator values was tested by a permutation test with 9999 permutations (De Cáceres et al., 2010).

3. Results

3.1. Environmental conditions

The two studied pond types strongly differed in habitat quality but not in landscape quality (Table 1). Regarding habitat quality, quarry ponds exhibited higher sunshine duration, stronger water level fluctuations, higher cover of the semi-aquatic zone and higher diversity of the submerged zone than control ponds. Moreover, shoreline vegetation at quarry ponds was more open (lower tree cover, more bare soil) and shorter (lower vegetation height) compared to those of control ponds. The water body of quarry ponds was characterized by a higher cover of the emergent vegetation (particularly reed and Juncaceae) and submerged vegetation (particularly Characeae) but a lower cover of floating leaf plants and emergent herbs than control ponds.

3.2. Response of plant species to environmental conditions

Overall, we identified 156 plant species (Table A3, Appendix), including 118 vascular plants (20 threatened ones), 33 mosses (10) and 5 stoneworts (1). The number of all and threatened species was for both vascular plants and mosses higher in quarry ponds than in control ponds (Fig. 3). Moreover, threatened mosses were even restricted to quarry ponds, and stoneworts generally only occurred in quarry ponds.

The ISA identified 14 vascular plants, five mosses and three stoneworts as indicator species for quarry ponds, including two threatened ones (the vascular plant *Centaurium pulchellum* and the moss *Fissidens adianthoides*) (Table 2). By contrast, for control ponds, only six vascular plants and three mosses were determined as indicator species. None of the species was threatened.

In the GLMM analyses, sunshine duration and pond diversity were the most important predictors, followed by the cover of the semi-aquatic zone (Figs. 4 and 5, Table A4). All three favoured species richness. Sunshine duration had a positive effect on the number of threatened vascular plant and moss species as well as on overall species richness of stoneworts. Pond diversity favoured overall species richness of vascular plants and mosses as well as the number of threatened mosses. The cover of the semi-aquatic zone promoted the overall number of stonewort species and those of threatened moss species. By contrast, conductivity had a negative effect on species richness of threatened moss species.

4. Discussion

Our study revealed clear differences in habitat quality and plant species composition between quarry and control ponds. Quarry ponds exhibited higher sunshine duration, stronger water level fluctuations, higher cover of the semi-aquatic zone and higher diversity of the submerged zone than control ponds. Moreover, shoreline vegetation at quarry ponds was more open (lower tree cover, more bare soil) and shorter (lower vegetation height) compared to control ponds. The water body of quarry ponds was characterized by a higher cover of the emergent and submerged vegetation but a lower cover of floating leaf plants and emergent herbs than control ponds. As a result, the number of all and threatened species was for both vascular plants and mosses higher in quarry than in control ponds. Moreover, threatened moss species were even restricted to quarry ponds, and stoneworts generally only occurred in this type of pond.

Light availability plays a key role in the composition of plant species assemblages. For example, it determines germination success, growth rates and overall species richness (Kotowski and van Diggelen, 2004; Lacoul and Freedman, 2006; Van Gerven et al., 2015). Usually, species richness decreases with shading (Schrautzer and Jensen, 2005; Hassall et al., 2011; Thornhill et al., 2017). The

Table 2

Results of the indicator species analysis: Plant indicator species of quarry ponds (Quarry, $N = 15$) and control ponds (Control, $N = 15$). Only species with significant indicator values (IV) are shown; dots indicate that no significant indicator value was found for the respective group. Threatened species are highlighted by bold type. A list of all species is provided in Table A3 (Appendix A). % = frequency. Statistical significance is indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Indicator species	*P*	Quarry		Control	
		IV	%	IV	%
i) Vascular plants					
Betula pendula	***	82	66.7	.	0.0
Calamagrostis epigejos	**	74	60.0	.	6.7
Centaurium pulchellum	*	58	33.3	.	0.0
Eleocharis vulgaris	*	72	66.7	.	20.0
Epilobium tetragonum	*	64	53.3	.	6.7
Eupatorium cannabinum	*	64	46.7	.	6.7
Juncus articulatus	***	93	93.3	.	0.0
Plantago major subsp. *major*	*	70	66.7	.	13.3
Prunella vulgaris	**	73	60.0	.	0.0
Salix caprea	***	90	93.3	.	6.7
Salix cinerea subsp. *cinerea*	*	72	73.3	.	20.0
Schoenoplectus lacustris	*	64	53.3	.	6.7
Typha latifolia	*	72	66.7	.	20
Zannichellia palustris subsp. *palustris*	*	63	40.0	.	0.0
Cardamine amara subsp. *amara*	*	.	0.0	58	33.3
Lemna minor	***	.	13.3	83	80.0
Myosotis scorpioides s. str.	**	.	0.0	68	46.7
Ranunculus repens	**	.	33.3	78	80.0
Ranunculus sceleratus	*	.	6.7	58	33.3
Spirodela polyrhiza	*	.	0.0	58	33.3
ii) Mosses					
Bryum bimum	**	68	46.7	.	0.0
Bryum spp.	*	58	33.3	.	0.0
Cratoneuron filicinum	*	64	46.7	.	6.7
Fissidens adianthoides	*	63	46.7	.	0.0
Pellia endiviifolia	**	68	46.7	.	0.0
Brachythecium rutabulum	*	.	6.7	64	46.7
Eurhynchium hians	*	.	0.0	58	33.3
Plagiomnium undulatum	*	.	0.0	63	40.0
iii) Stoneworts					
Chara contraria	*	58	33.3	.	0.0
Chara globularis	**	73	60.0	.	0.0
Chara vulgaris	***	97	100.0	.	0.0

paramount importance of light availability for plant species richness was also highlighted by our study. Across all studied ponds, sunshine duration, which was negatively correlated with tree cover (see Tab. A1), favoured overall species richness of stoneworts as well as the number of threatened vascular plant and moss species. Both stoneworts and many threatened plant species are well known to be less-competitive and very light-demanding (Ellenberg and Leuschner, 2010; Bornette and Puijalon, 2011; Sanjuan et al., 2017).

Quarry habitats are usually characterized by a low successional speed due the lack of topsoil (Řehounková and Prach, 2010; Prach et al., 2011; Münsch and Fartmann, 2022). Consequently, at quarry ponds, the cover of trees was negligible (4 %, see Fig. 2a) and hence the sunshine duration was very high (13.9 h). By contrast, the control ponds were characterized by a more than seven times higher cover of trees (30 %; see Fig. 2b) and a sunshine duration that was less than half as high (5.7 h). Moreover, control ponds exhibited a much higher cover of floating leaf plants (40 % vs. 7 %; particularly *Lemna minor* and *Spirodela polyrhiza*, see Fig. 2b and Tab. A3) and less open (bare ground: 5 % vs. 35 %) and taller shoreline vegetation (55 cm vs. 38 cm), which also resulted in substantial shading of the water body. Consequently, we argue that the much higher light availability was a main driver of the higher overall species richness in all three studied plant groups as well as of threatened vascular plant and moss species in quarry ponds compared to control ponds.

Habitat heterogeneity is another major driver of species richness (Steinmann et al., 2011; Poschlod and Braun-Reichert, 2016; Fartmann et al., 2021). According to the habitat heterogeneity hypothesis, a higher availability of microsites fosters species richness within a habitat. This has also been acknowledged for water bodies (e.g., Brose, 2001; Holtmann et al., 2019). In line with this, across all studied ponds, the pond diversity index—a measure of habitat heterogeneity—had a positive effect on species richness of vascular plants (all species) and mosses (all and threatened species). Since the diversity index of the submerged zone was higher at quarry ponds than at control ponds, we assume that it also contributed to the higher species richness of all (all three plant groups) and threatened species (vascular plants and mosses) in quarry ponds.

The semi-aquatic zone typically experiences seasonal water level fluctuations due to flooding during humid and grounding during dry periods. Disturbance by persistent flooding leads to dying of maladapted plant species, reducing competition for less-competitive ones and temporarily creating patches of bare soil for germination (Řehounková and Prach, 2008; Fleischer et al., 2013). Several studies have shown that these semi-aquatic zones have a high value for light-demanding, less competitive plant species (Baumbach et al., 2013; Řehounková et al., 2016; Holtmann et al., 2019; Müllerová et al., 2022). This was also the case in our study. Across all studied ponds, species richness of stoneworts and threatened moss species increased with the cover of the semi-aquatic zone. Moreover, the cover of the semi-aquatic zone was twice as high at quarry ponds compared to control ponds (65 % vs. 32 %). Consequently, we attribute the higher species richness of vascular plants and mosses (all and threatened species) in quarry ponds compared to control ponds as well as the exclusive occurrence of stoneworts in quarry ponds to the high cover of the semi-aquatic zone in this pond type. For example, Baumbach et al. (2013) also highlighted that extended semi-aquatic zones in quarries usually strongly fulfil the light and temperature requirements for the growth of stoneworts and provide suitable conditions for the persistence and germination of their oospores.

Species richness of semi-aquatic and aquatic plants usually peaks at intermediate levels of nutrient availability (Bornette and Puijalon, 2011). By contrast, threatened species are mostly more common under nutrient-poor conditions (Ellenberg and Leuschner, 2010). Our study corroborates this assumption. Across all studied ponds, species richness of threatened mosses decreased with conductivity.

The strong differences in plant species composition in quarry and control ponds was also confirmed by many different indicator species for each of the two pond types. Altogether, 22 plant species were characteristic of quarry ponds and nine were typical of control plots. However, threatened indicator species were only found in quarry ponds (the vascular plant *Centaurium pulchellum* and the moss *Fissidens adianthoides*). This additionally underlines the high conservation value of the quarry ponds.

To sum up, a higher habitat quality was the key for species-rich assemblages of vascular plants and mosses (all and threatened species) and the exclusive occurrence of stoneworts in quarry ponds compared to control ponds. Overall, quarry ponds had a high value for the conservation of plant species richness. Sunlit early-successional stages, a heterogeneous submerged and a large semi-aquatic zone particularly explained the high number of plant species in quarry ponds. Across the 30 studied ponds, sunshine duration and pond diversity were the most important predictors of species richness, followed by the cover of the semi-aquatic zone. All three had a positive effect.

5. Implications for conservation

Our study emphasized the great importance of quarry ponds for overall species richness and those of threatened species across three different groups of semi-aquatic and aquatic plants (vascular plants, mosses and stoneworts). Kettermann and Fartmann (2023) also acknowledged in a comparable study the high value of quarry ponds for amphibian species richness. Moreover, they also identified sunshine duration and the cover of the semi-aquatic zone as important predictors of species richness.

Unfortunately, despite the increasing awareness about the value of quarries for nature conservation in recent times, many reclamation concepts still intend to backfill, afforest or flood quarries after the cessation of mining (Krauss et al., 2009; Tropek et al., 2010). Such measures should be avoided in general, as they lead to an immediate loss of these valuable habitats. This has not only negative effects on phytodiversity but also on various other taxonomic groups, including insects (Kettermann et al., 2022; Münsch and Fartmann, 2022), amphibians (Kettermann and Fartmann, 2023) or birds (Šálek, 2012; Day et al., 2017).

Due to the ever-increasing impact of climate change, there is a growing risk of small water bodies drying up too early in the season, which can threaten local plant populations (Meerhoff and de los Ángeles González-Sagrario, 2022). Therefore, it is recommended to create a variety of water bodies, including both temporary and permanent ones within quarries. Temporary ponds with shallow shorelines promote many threatened plant species (Chester and Robson, 2013; Holtmann et al., 2019). By contrast, persistent, deep water bodies are typically species-poor but represent an important habitat for example for many rare stonewort species (Baumbach et al., 2013; Rey-Boissezon and Joye, 2015).

Although the successional speed is low in quarries (Řehounková and Prach, 2010; Prach et al., 2011; Münsch and Fartmann, 2022), over longer time periods, both thick topsoil layers and woody plants may establish. If this is the case, topsoil as well as shrubs or trees should be removed locally to create sunlit early-successional stages rich in bare ground and in favour of species richness (König, 2017; Holtmann et al., 2019; Münsch and Fartmann, 2022).

CRediT authorship contribution statement

Marcel Kettermann: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carsten Schmidt:** Writing – review & editing, Data curation. **Thomas Fartmann:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Conceptualization.

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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.

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Appendix

Table A1
Overview of environmental parameters used for Generalized Linear Mixed-effects Models (GLMM) and their intercorrelations (Pearson correlation [*r*], |*r*| > 0.5). Statistical significance is indicated as follows: $^{**}P < 0.01$; $^{***}P < 0.001$

Parameter	**Surrogate for** (Pearson correlation [*r*])
Habitat quality	
Pond size (m^2)	.
pH	Emergent herbs (–0.57***)
Conductivity	.
Sunshine July (h/day)	Trees (–0.87***), Characeae (0.63***), Juncaceae (0.63***), submerged zone diversity index (0.58***), bare soil (0.52**), floating leaf plants (–0.50**)
Water level fluctuation (cm)	Bare soil (0.56**), field layer (–0.50**)
Semi-aquatic zone (%)	Reed (0.54**), Juncaceae (0.53**)
Pond diversity index	Submerged herbs (0.80***), emergent zone diversity index (0.79***), submerged vegetation (0.77***), submerged zone diversity index (0.74***), emergent vegetation (0.64***), Juncaceae (0.63***), Cyperaceae (0.58***), shoreline diversity index (0.51**), reed (0.51**)
Shoreline	
Vegetation height (cm)	Bare soil (–0.61***)
Water body	
Open water surface (%)	Floating leaf plants (–0.62***), shrubs (–0.51**)
Other algae (%)	Reed (0.54**)
Landscape quality	
Annual temperature (°C)	Elevation (–0.93***), annual precipitation (–0.50**)
Pond connectivity (m)	.

Table A2
Univariable models: Influence of environmental parameters (standardized predictor variables) on the number of all vascular plant, threatened vascular plant, all moss, threatened moss, all stonewort and threatened stonewort species ($N = 30$). WLF = Water level fluctuation; DI = Diversity index. Differences were analysed using Generalized Linear Mixed-effects Models (negative-binomial structure). Statistical significance is indicated as follows: n.s. = not significant, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Vascular plants						Mosses						Stoneworts		
	All			Threatened			All			Threatened			All		
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Pond size	1.26×10^{-1}	9.79×10^{-2}	n.s.	2.19×10^{-1}	2.27×10^{-1}	n.s.	9.40×10^{-2}	1.01×10^{-1}	n.s.	2.24×10^{-1}	1.66×10^{-1}	n.s.	3.58×10^{-1}	1.66×10^{-1}	*
pH	8.37×10^{-2}	9.11×10^{-2}	n.s.	1.75×10^{-1}	2.53×10^{-1}	n.s.	-4.06×10^{-2}	1.14×10^{-1}	n.s.	9.80×10^{-2}	2.25×10^{-1}	n.s.	2.08×10^{-1}	2.73×10^{-1}	n.s.
Conductivity	-1.56×10^{-1}	9.59×10^{-2}	n.s.	-9.49×10^{-2}	2.49×10^{-1}	n.s.	-2.49×10^{-1}	1.12×10^{-1}	*	-5.22×10^{-1}	2.65×10^{-1}	*	-2.59×10^{-1}	2.77×10^{-1}	n.s.
Sunshine July	2.36×10^{-1}	8.01×10^{-2}	**	5.11×10^{-1}	1.78×10^{-1}	**	2.78×10^{-1}	9.44×10^{-2}	**	1.65	6.00×10^{-1}	**	1.25	3.07×10^{-1}	***
WLF	-7.51×10^{-2}	8.92×10^{-2}	n.s.	-1.37×10^{-1}	2.48×10^{-1}	n.s.	-3.03×10^{-1}	1.51×10^{-1}	*	-2.49×10^{-1}	4.02×10^{-1}	n.s.	2.48×10^{-1}	1.98×10^{-1}	n.s.
Pond DI	2.44×10^{-1}	7.74×10^{-2}	**	4.35×10^{-1}	2.31×10^{-1}	n.s.	4.20×10^{-1}	1.09×10^{-1}	***	1.05	3.55×10^{-1}	**	4.38×10^{-1}	2.66×10^{-1}	n.s.
Shoreline DI	1.20×10^{-1}	8.27×10^{-2}	n.s.	1.73×10^{-1}	2.25×10^{-1}	n.s.	2.73×10^{-1}	1.01×10^{-1}	**	4.52×10^{-1}	3.09×10^{-1}	n.s.	2.55×10^{-1}	2.33×10^{-1}	n.s.
Vegetation height	8.70×10^{-2}	8.70×10^{-2}	n.s.	-3.07×10^{-3}	2.15×10^{-1}	n.s.	4.03×10^{-2}	1.16×10^{-1}	n.s.	-1.36×10^{-1}	3.42×10^{-1}	n.s.	-5.21×10^{-1}	2.35×10^{-1}	*
Semi-aquatic zone	7.51×10^{-2}	9.19×10^{-2}	n.s.	2.90×10^{-1}	2.36×10^{-1}	n.s.	1.96×10^{-1}	1.06×10^{-1}	n.s.	5.94×10^{-1}	2.86×10^{-1}	*	7.82×10^{-1}	2.67×10^{-1}	**
Open water surface	3.93×10^{-2}	9.05×10^{-2}	n.s.	1.54×10^{-1}	2.35×10^{-1}	n.s.	-1.23×10^{-2}	1.18×10^{-1}	n.s.	1.29×10^{-1}	2.05×10^{-1}	n.s.	0.50	0.14	***
Cyperaceae	1.99×10^{-2}	1.02×10^{-1}	n.s.	3.56×10^{-2}	3.04×10^{-1}	n.s.	7.90×10^{-2}	1.09×10^{-1}	n.s.	2.21×10^{-1}	1.60×10^{-1}	n.s.	2.40×10^{-1}	2.07×10^{-1}	n.s.
Other algae	-9.41×10^{-3}	8.96×10^{-2}	n.s.	9.50×10^{-2}	2.50×10^{-1}	n.s.	1.31×10^{-1}	1.04×10^{-1}	n.s.	9.22×10^{-2}	2.84×10^{-1}	n.s.	-2.42×10^{-1}	2.59×10^{-1}	n.s.
Connectivity	2.76×10^{-2}	8.16×10^{-2}	n.s.	1.16×10^{-1}	3.08×10^{-1}	n.s.	9.01×10^{-2}	1.04×10^{-1}	n.s.	2.69×10^{-1}	2.08×10^{-1}	n.s.	-7.92×10^{-2}	2.23×10^{-1}	n.s.
Annual temperature	3.63×10^{-2}	9.09×10^{-2}	n.s.	3.51×10^{-1}	2.35×10^{-1}	n.s.	-4.01×10^{-2}	1.12×10^{-1}	n.s.	-1.67×10^{-1}	3.11×10^{-1}	n.s.	1.33×10^{-1}	2.53×10^{-1}	n.s.

Table A3
Frequency (%) of all observed plant species in quarry ponds and control ponds ($N = 30$). Threat status (TS): x = threatened species according to Verbücheln et al. (2021) for vascular plants, Schmidt et al. (2011) for mosses and Van de Weyer (2023) for stoneworts

Species	Quarry	Control	TS
Vascular plants			
Agrostis stolonifera s.str.	0.0	13.3	.
Alisma lanceolatum	13.3	0.0	.
Alisma plantago-aquatica s.str.	33.3	26.7	.
Alnus glutinosa	6.7	40.0	.
Alopecurus aequalis	6.7	13.3	.
Berula erecta	0.0	20.0	.
Betula pendula	66.7	0.0	.
Bolboschoenus laticarpus	6.7	0.0	.
Calamagrostis epigejos	60.0	6.7	.
Callitriche palustris s.str.	0.0	13.3	x
Callitriche spp.	6.7	0.0	.
Callitriche stagnalis	0.0	6.7	x
Cardamine amara subsp. *amara*	0.0	33.3	.
Carex acutiformis	13.3	6.7	.
Carex demissa	26.7	0.0	x
Carex distans	13.3	6.7	x
Carex flacca	26.7	13.3	.
Carex hirta	13.3	13.3	.
Carex muricata s.str.	6.7	20.0	.
Carex otrubae	13.3	20.0	.
Carex panicea	13.3	0.0	x
Carex paniculata	13.3	6.7	.
Carex pendula	0.0	6.7	.

(*continued on next page*)

Table A3 (*continued*)

Species	Quarry	Control	TS
Carex pseudocyperus	13.3	6.7	.
Carex remota	13.3	6.7	.
Carex riparia	6.7	0.0	x
Carex sylvatica	6.7	13.3	.
Carex vesicaria	6.7	6.7	x
Carex viridula	6.7	0.0	x
Centaurium pulchellum	33.3	0.0	x
Ceratophyllum demersum	0.0	6.7	.
Chenopodium glaucum	6.7	0.0	.
Cirsium palustre	20.0	0.0	.
Dactylorhiza incarnata	13.3	0.0	x
Dactylorhiza maculata agg.	6.7	0.0	x
Echinochloa crus-galli subsp. *crus-galli*	6.7	0.0	.
Eleocharis vulgaris	66.7	20.0	.
Epilobium hirsutum	46.7	40.0	.
Epilobium parviflorum	6.7	6.7	.
Epilobium tetragonum	53.3	6.7	.
Epipactis palustris	6.7	0.0	x
Equisetum fluviatile	13.3	13.3	.
Equisetum litorale	6.7	0.0	.
Equisetum palustre	33.3	6.7	.
Eupatorium cannabinum	46.7	6.7	.
Filipendula ulmaria	6.7	13.3	.
Frangula alnus	6.7	0.0	.
Fraxinus excelsior	13.3	13.3	.
Galium palustre	13.3	33.3	.
Glyceria fluitans s.str.	20.0	46.7	.
Glyceria maxima subsp. *maxima*	0.0	13.3	.
Iris pseudacorus	20.0	33.3	.
Juncus articulatus	93.3	0.0	.
Juncus bufonius s.str.	20.0	20.0	.
Juncus compressus	6.7	6.7	.
Juncus conglomeratus	26.7	13.3	.
Juncus effusus	26.7	33.3	.
Juncus inflexus	60.0	26.7	.
Lemna minor	13.3	80.0	.
Lemna trisulca	0.0	13.3	x
Limosella aquatica	6.7	0.0	.
Lycopus europaeus subsp. *europaeus*	60.0	60.0	.
Lysimachia nummularia	13.3	33.3	.
Lysimachia vulgaris	6.7	13.3	.
Lythrum salicaria	53.3	13.3	.
Mentha aquatica	13.3	40.0	.
Myosotis laxa	6.7	6.7	x
Myosotis scorpioides s.str.	0.0	46.7	.
Myriophyllum spicatum	20.0	0.0	.
Nasturtium officinale agg.	0.0	20.0	.
Persicaria amphibia	6.7	0.0	.
Persicaria lapathifolia subsp. *lapathifolia*	13.3	0.0	.
Persicaria maculosa	53.3	13.3	.
Persicaria minor	13.3	0.0	.
Phalaris arundinacea	6.7	33.3	.
Phragmites australis	46.7	26.7	.
Plantago major subsp. *major*	66.7	13.3	.
Poa trivialis	0.0	6.7	.
Populus tremula	6.7	0.0	.
Potamogeton crispus	13.3	6.7	.
Potamogeton natans	40.0	26.7	.
Potentilla anserina	20.0	13.3	.
Prunella vulgaris	60.0	0.0	.
Pulicaria dysenterica	6.7	6.7	x
Ranunculus aquatilis s.str.	0.0	6.7	x
Ranunculus peltatus s. l.	20.0	0.0	x
Ranunculus repens	33.3	80.0	.
Ranunculus sceleratus	6.7	33.3	.
Ranunculus trichophyllus agg.	40.0	26.7	x
Rorippa palustris	20.0	6.7	.
Rumex conglomeratus	20.0	6.7	.
Rumex crispus	13.3	0.0	.
Rumex obtusifolius subsp. *obtusifolius*	6.7	20.0	.

(*continued on next page*)

Table A3 (*continued*)

Species	Quarry	Control	TS
Rumex sanguineus	13.3	26.7	.
Salix alba	86.7	40.0	.
Salix aurita	6.7	0.0	.
Salix caprea	93.3	6.7	.
Salix cinerea subsp. *cinerea*	73.3	20.0	.
Salix fragilis s.str.	26.7	33.3	.
Salix purpurea	46.7	6.7	.
Salix viminalis	33.3	6.7	.
Schoenoplectus lacustris	53.3	6.7	.
Schoenoplectus tabernaemontani	6.7	0.0	x
Scirpus sylvaticus	6.7	26.7	.
Scutellaria galericulata	6.7	6.7	.
Solanum dulcamara	33.3	46.7	.
Sparganium emersum	6.7	0.0	.
Spirodela polyrhiza	0.0	33.3	.
Symphytum officinale s.str.	0.0	6.7	.
Typha angustifolia	20.0	0.0	.
Typha latifolia	66.7	20.0	.
Urtica dioica	0.0	20.0	.
Utricularia australis	13.3	0.0	x
Valeriana officinalis s.str.	0.0	6.7	.
Veronica anagallis-aquatica s.str.	13.3	0.0	.
Veronica beccabunga	6.7	20.0	.
Veronica catenata	6.7	0.0	.
Zannichellia palustris subsp. *palustris*	40.0	0.0	.
Mosses			
Amblystegium serpens	0.0	26.7	.
Brachythecium mildeanum	20.0	0.0	x
Brachythecium rutabulum	6.7	46.7	.
Bryum bimum	46.7	0.0	x
Bryum dichotomum	20.0	13.3	.
Bryum spec.	33.3	0.0	.
Calliergonella cuspidata	80.0	40.0	.
Campylium polygamum	6.7	0.0	x
Campylium stellatum var. *protensum*	33.3	0.0	.
Campylium stellatum var. *stellatum*	6.7	0.0	x
Ceratodon purpureus	0.0	6.7	.
Cratoneuron filicinum	46.7	6.7	.
Ctenidium molluscum	13.3	0.0	.
Dicranella varia	26.7	0.0	.
Didymodon fallax	33.3	6.7	.
Didymodon tophaceus	6.7	0.0	.
Drepanocladus aduncus	26.7	6.7	.
Eurhynchium hians	0.0	33.3	.
Eurhynchium praelongum	0.0	13.3	.
Eurhynchium speciosum	0.0	0.0	x
Fissidens adianthoides	46.7	0.0	x
Fontinalis antipyretica	6.7	0.0	.
Funaria hygrometrica	13.3	6.7	.
Leptodictyum riparium	20.0	60.0	.
Palustriella commutata	6.7	0.0	x
Pellia endiviifolia	46.7	0.0	
Philonotis calcarea	13.3	0.0	x
Plagiomnium undulatum	0.0	40.0	.
Platyhypnidium riparioides	0.0	6.7	.
Pohlia melanodon	0.0	6.7	.
Rhizomnium punctatum	0.0	6.7	.
Scorpidium scorpioides	6.7	0.0	x
Trichostomum crispulum	26.7	0.0	x
Stoneworts			
Chara contraria	33.3	0.0	.
Chara globularis	60.0	0.0	.
Chara hispida	6.7	0.0	x
Chara virgata	13.3	0.0	.
Chara vulgaris	100.0	0.0	.

Table A4
Multivariable models: Effects of environmental parameters (predictor variables) on the number of all vascular plant (a), threatened vascular plant (b), all moss (c), threatened moss (d) and all stonewort species (e) within all ponds ($N = 30$). Differences were analysed using Generalized Linear Mixed-effects Models (GLMM) (negative binomial error structure) with 'subarea' as a random intercept. Model-averaged coefficients (conditional average) were derived from the top-ranked GLMM (ΔAICc < 3). R^2_m = variance explained by fixed effects, R^2_c = varian$_c$e explained by both fixed and random effects (Nakagawa et al., 2017). Statistical significance is indicated as follows: n. s. = not significant; $P \geq 0.05$; *$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Parameter	Estimate	SE	Z	P
Vascular plants				
a) All species (R^2_m = 0.40–0.47, R^2_c = 0.40–0.47)				
(Intercept)	2.97	6.54×10^{-2}	43.19	***
Pond diversity index	2.87×10^{-1}	7.45×10^{-2}	3.68	***
Sunshine	1.36×10^{-1}	7.08×10^{-2}	1.83	n.s.
b) Threatened species (R^2_m = 0.18, R^2_c = 0.38)				
(Intercept)	1.64	2.38×10^{-1}	6.90×10^{-1}	n.s.
Sunshine	5.11×10^{-1}	1.78×10^{-1}	2.87	**
Moss species				
c) All species (R^2_m = 0.31–0.47, R^2_c = 0.41–0.57)				
(Intercept)	1.42	1.10×10^{-1}	12.31	***.
Pond diversity index	3.01×10^{-1}	1.16×10^{-1}	2.48	*
Water level fluctuation	-3.09×10^{-1}	1.50×10^{-1}	1.95	n.s.
Sunshine	2.20×10^{-1}	1.11×10^{-1}	1.90	n.s.
Conductivity	-1.45×10^{-1}	1.11×10^{-1}	1.23	n.s.
d) Threatened species (R^2_m 0.53–0.84, R^2_c = 0.53– 0.84)				
(Intercept)	−2.66	1.32	1.94	n.s.
Semi-aquatic zone	8.17×10^{-1}	3.55×10^{-1}	2.19	*
Sunshine	2.29	1.02×10^{-1}	2.16	*
Pond diversity index	8.47×10^{-1}	3.83×10^{-1}	2.09	*
Conductivity	-8.81×10^{-1}	4.12×10^{-1}	2.04	*
Stonewort species				
e) All species (R^2_m = 0.51–0.64, R^2_c = 0.51–0.64)				
(Intercept)	-7.42×10^{-1}	3.79×10^{-1}	1.86	n.s.
Sunshine	1.25	3.62×10^{-1}	3.29	**
Semi-aquatic zone	5.36×10^{-1}	2.36×10^{-1}	2.16	*
Pond size	2.27×10^{-1}	1.32×10^{-1}	1.63	n.s.
Open water surface	2.33×10^{-1}	1.71×10^{-1}	1.30	n.s.
Vegetation height	-2.36×10^{-1}	2.15×10^{-1}	1.04	n.s.

Data availability

The authors do not have permission to share data.

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