

Quarry ponds are hotspots of amphibian species richness

Marcel Kettermann^{a,*}, Thomas Fartmann^{a,b}

^a Department of Biodiversity and Landscape Ecology, Osnabrück University, Barbarastraße 11, 49076 Osnabrück, Germany

^b Institute of Biodiversity and Landscape Ecology (IBL), An der Kleimannbrücke 98, 48157 Münster, Germany

ARTICLE INFO

Keywords:

Biodiversity conservation
Early-successional stage
Global change
Habitat quality
Mining site
Warm microclimate

ABSTRACT

Amphibians are among the most severely declining taxonomic group worldwide. Recent studies have shown that quarries may have a high conservation value for biodiversity conservation. However, well-replicated research on the importance of quarry ponds for amphibian assemblages has been scarce thus far. The aim of this study was to compare the environmental conditions and composition of amphibian assemblages of 15 randomly selected quarry ponds with those of 15 control ponds in the surrounding landscape. For each pond, we assessed several parameters of habitat and landscape quality. The effects of environmental conditions on overall species richness and number of threatened species were analysed using Generalized Linear Mixed-effects Models. Our study revealed strong differences in habitat quality and composition of amphibian assemblages between quarry and control ponds. In particular, a larger area of the semi-aquatic zone, a longer sunshine duration and the absence of fish were typical of quarry ponds, whereas a taller vegetation at the shoreline characterized control ponds. As a result, overall species richness and number of threatened species were higher in quarry ponds compared with control ponds. Overall, quarry ponds had a higher habitat quality than control ponds. In particular, (i) the large area of sunlit and warm microhabitats and (ii) the absence of fish predators favoured species richness of amphibians at the quarry ponds. Consequently, quarry ponds —thanks to their early-successional stages—have a high conservation value for amphibians.

1. Introduction

Biodiversity loss is accelerating continuously and, therefore, is one of the most critical global issues of our time (Rockström et al., 2009; Butchart et al., 2010; Naeem et al., 2012). The worldwide rate of extinction is currently estimated to be 1000 times higher than the natural background rate (Pimm et al., 2014; De Vos et al., 2015). In terrestrial biomes, land-use change is seen as the main driver of the recent biodiversity crisis (Newbold et al., 2015; Cardoso et al., 2020). In particular, intensification and abandonment of traditional land use have led to a dramatic loss of natural and semi-natural habitats. As a result, the remaining habitat fragments and their biodiversity are often highly isolated and suffer from the deterioration of habitat quality (Arntzen et al., 2017; Poniatowski et al., 2018; Münsch et al., 2019).

For a long time, quarries had a bad image among conservationists and were associated with negative effects on biodiversity (Beneš et al., 2003; Tropek et al., 2010). Indeed, quarrying results in fundamental changes of the environmental conditions, since existing vegetation and top soil are removed (Bétard, 2013; Kalarus et al., 2019). However, it

also creates vast areas of early-successional stages. Such seral stages are among the most rapidly declining habitats in our landscapes and often harbour assemblages rich in thermophilic and threatened species (Köppel, 1995; Poschlod and Braun-Reichert, 2017; Fartmann et al., 2021). So far, recent studies have shown that quarries may have a high conservation value for birds (Šálek, 2012; Salgueiro et al., 2020), arthropods (Beneš et al., 2003; Tropek et al., 2008; Tropek et al., 2010; Münsch and Fartmann, 2022; Kettermann et al., 2022) and vascular plants (Tropek et al., 2010; Rehounková et al., 2020). For quarry ponds, there are data from large-scale surveys of amphibian distributions in anthropogenic landscapes showing their value for species-rich amphibian assemblages (e.g., Günther, 1996). However, well-replicated research on quarry ponds and their species assemblages is still lacking.

Amphibians are among the most severely declining taxonomic groups worldwide (Stuart et al., 2004; Wake and Vredenburg, 2008; Grant et al., 2016; Cordier et al., 2021). It is assumed that approximately 50% of the global amphibian species are threatened by extinction (González-del-Pliego et al., 2019). One of the main drivers of this

* Corresponding author.

E-mail address: mkettermann@uos.de (M. Kettermann).

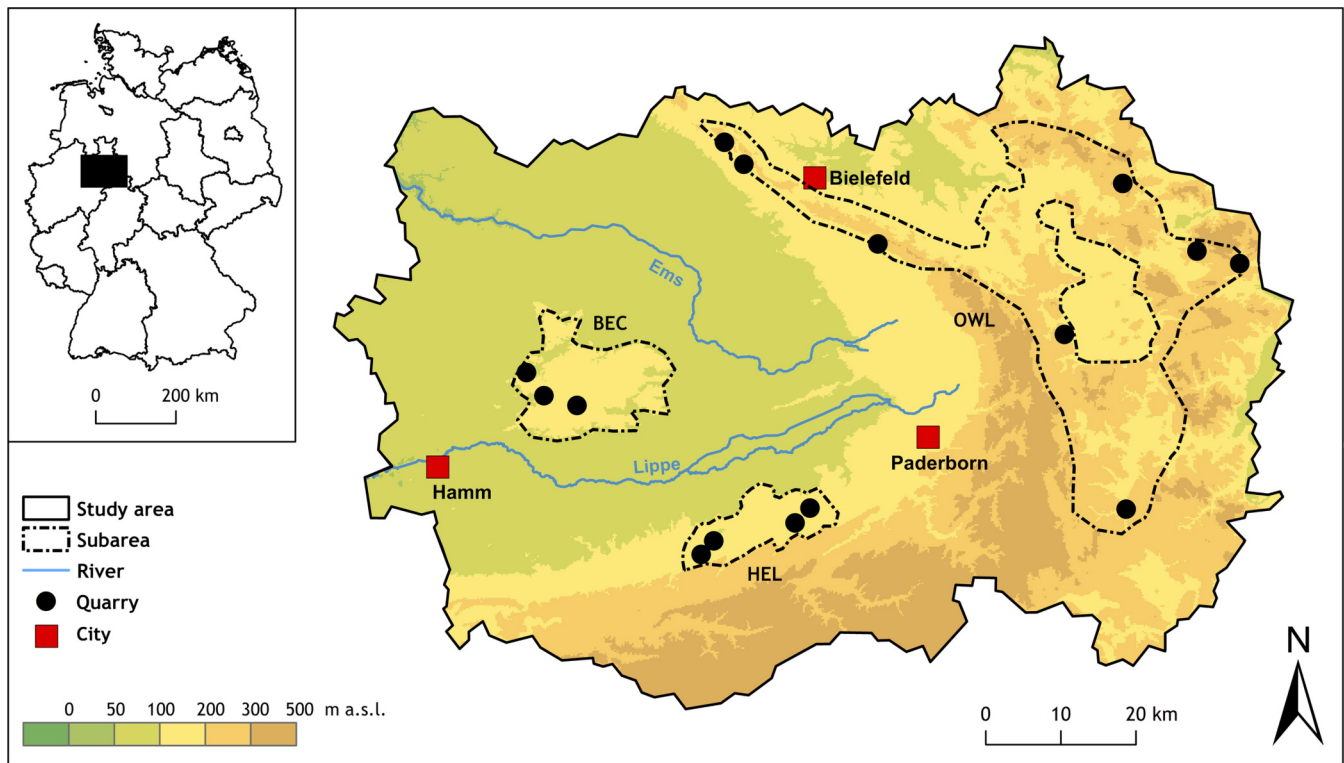


Fig. 1. Location of the study area in the eastern part of North Rhine-Westphalia in central Germany (inlay) and of the three subareas Beckumer Berge (BEC), Ostwestfalen-Lippe (OWL) and Hellweg (HEL) with its ponds in limestone quarries (Quarry). Due to the overlap between quarry ponds and control ponds at this scale the latter are not shown.

dramatic decline is habitat loss (Cushman, 2006; Hof et al., 2011; Arntzen et al., 2017; Murray et al., 2020; Cordier et al., 2021). Additionally, amphibians suffer from climate change (Hof et al., 2011; Murray et al., 2020), introduced alien species (Kats and Ferrer, 2003) and infectious diseases (Yap et al., 2017; DiRenzo and Grant, 2019). Amphibians are dependent on a high habitat quality of the water bodies used for breeding (Unglaub et al., 2018, 2021). In particular, sunlit and warm water bodies with low predator densities, such as fish, are of crucial importance for successful reproduction of most species (cf. Van Buskirk, 2003; Hartel et al., 2007; Shulze et al., 2012; Drayer and Richter, 2016; Holtmann et al., 2017; Rannap et al., 2020; Cox et al., 2017). Since temperate amphibians usually have a complex life cycle

with aquatic and terrestrial stages (Stuart et al., 2004; Cushman, 2006), landscape quality also plays a significant role in overall yearly survival (Cox et al., 2017; Holtmann et al., 2017).

The aim of this study was to compare the environmental conditions and composition of amphibian assemblages of 15 randomly selected quarry ponds with those of 15 control ponds in the surrounding landscape. For each pond, we assessed several parameters of habitat and landscape quality. The effects of environmental conditions on overall species richness and number of threatened species were analysed using Generalized Linear Mixed-effects Models. Finally, based on the results of this study, we developed management recommendations for quarry ponds to enhance amphibian species richness.



Fig. 2. Examples of a quarry pond (a) and a control in the study area (Photos: M. Kettermann).

Table 1

Overview of environmental parameters (mean $\pm$ SE, minimum and maximum). Differences in parameters between quarry ponds (Quarry, $N = 15$) and control ponds (Control, $N = 15$) were analysed using Generalized Linear Mixed-effects Models (Poisson error structure for count data, proportional binomial error structure for cover data) with ‘subarea’ as a random intercept (for details see Section 2.5). n.s. = not significant, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	Quarry		Control		P
	Mean ($\pm$ SE)	Min.–Max.	Mean ($\pm$ SE)	Min.–Max.	
Habitat quality					
Pond size (m ²) ¹	1443 $\pm$ 394	729–5811	868 $\pm$ 161	106–1763	n.s.
pH ²	7.6 $\pm$ 0.1	7.1–8.0	7.4 $\pm$ 0.1	7.1–8.0	n.s.
Conductivity (μ S/cm) ²	436 $\pm$ 136	261–682	528 $\pm$ 52	255–918	n.s.
Sunshine duration spring (h/day) ³	10.4 $\pm$ 0.5	6–12	8.1 $\pm$ 0.7	4–13	**
Sunshine duration summer (h/day) ³	12.8 $\pm$ 0.5	9–15	6.8 $\pm$ 1.1	2–14	***
Cover semi-aquatic zone (%) ⁴	80.0 $\pm$ 5.2	30–100	37.6 $\pm$ 9.1	10–100	***
<i>Vegetation cover shoreline (%)</i>					
Trees	2.3 $\pm$ 0.8	0–10	23.0 $\pm$ 6.0	0–65	**
Shrubs	16.8 $\pm$ 3.2	2.5–45.0	14.3 $\pm$ 4.0	0–40	n.s.
Field layer	16.0 $\pm$ 2.6	2.5–35.0	22.3 $\pm$ 4.7	5–60	n.s.
Litter	39.3 $\pm$ 4.4	5–65	40.0 $\pm$ 2.9	20–60	n.s.
Bare soil	30.0 $\pm$ 6.9	0–90	3.2 $\pm$ 1.1	0–15	***
Vegetation height shoreline (cm)	32.7 $\pm$ 3.0	19–58	50.1 $\pm$ 5.4	20–102	**
Cover submerged macrophytes (%)	29.3 $\pm$ 6.4	0–80	20.7 $\pm$ 5.0	0–50	n.s.
Landscape quality					
Elevation (m a.s.l.) ⁵	167 $\pm$ 13	98–273	147 $\pm$ 14	91–259	n.s.
Annual temperature (°C) ⁶	9.3 $\pm$ 0.1	8.8–9.8	9.4 $\pm$ 0.1	8.5–9.9	n.s.
Pond connectivity (m) ⁷	789 $\pm$ 222	39–2479	481 $\pm$ 115	29–1306	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 = amphibious zone.

⁵ Elevation was taken from topographic maps.

⁶ Long-term mean (1981–2010) from 1-km² grid datasets of Germany’s National Meteorological Service (DWD, 2021).

⁷ Geometric mean of the distance to the next three water bodies.

2. Material and methods

2.1. Study area

The study area was located in the eastern part of the German Federal State of North Rhine-Westphalia (Central Europe) and covered approximately 1516 km². Due to differences in elevation, and, hence, climate it was divided into three subareas: (i) Beckumer Berge, (ii) Ostwestfalen-Lippe and (iii) Hellweg (Fig. 1). The climate is suboceanic with a mean annual temperature of 9.5 °C and a mean annual precipitation of 951 mm (meteorological station Bad Lippspringe [157 m a.s.l.]; period:

1981–2010; DWD, 2021). The subarea Ostwestfalen-Lippe comprises a mosaic of forested hills and ridges as well as flat valleys mainly covered by grassland at an elevation of 250 to 350 m a.s.l. The subareas Beckumer Berge and Hellweg are located in the Westphalian Basin and have an elevation range of 100 to 197 m a.s.l. In both subareas, agriculture is the dominant type of land use. The limestone is mined in quarries and used for the production of gravel, bricks, building material or cement.

In the study area, we randomly selected a total of 15 ponds within limestone quarries (Figs. 1 and 2). For each quarry ($N_{\text{Active}} = 5$, $N_{\text{Abandoned}} = 10$), we used the pond closest to a random point by applying the ‘create random points’ tool in ArcGIS 10.2. As a control, the closest pond

Table 2

Absolute and relative frequencies of the categorical variable ‘occurrence of fish’ at quarry ponds and control ponds. Differences in absolute frequencies between the two groups were analysed with Fisher’s Exact test. * $P < 0.05$.

Parameter	Quarry		Control		P
	N	%	N	%	
Fish					*
Present	1	6.7	7	46.7	
Absent	14	93.3	8	53.3	

to the respective quarry pond was chosen in the surrounding landscape (Fig. 2).

2.2. Sampling design

During the breeding period of the amphibians from the beginning of March to early May 2019, each pond was visited four times, twice at night and twice during the day. Different methods were used due to the varying phenology and activity patterns of each species (Glandt, 2014). *Rana temporaria* was detected by egg masses during the day in early March (Hachtel et al., 2009; Holtmann et al., 2017). Green frogs (*Pelophylax esculentus*, *P. lessonae*) were recorded at daytime through visual and acoustic observation in early May. In accordance with Hachtel et al. (2009), the two night surveys were conducted between sunset and midnight. *Bufo bufo* were surveyed using a torch at the end of March and the beginning of April (Hachtel et al., 2009). *Alytes obstetricans*, *Epidalea calamita* and *Hyla arborea* were recorded by call surveys during warm nights in April. *Salamandra salamandra* was detected during each of the four surveys by turning wood and stones near the shoreline. Additionally, newt species (*Ichthyosaura alpestris*, *Lissotriton helveticus*, *Lissotriton vulgaris* and *Triturus cristatus*) were caught by using bottle traps (Kronshage et al., 2014). For this purpose, five bottle traps were placed

once in each pond in early April for one night.

Amphibian species were classified in the field according to Glandt (2011) and Tetzlaff (2007). For statistical analysis, we used two response variables: number of (i) all and (ii) threatened species. Amphibians were considered ‘threatened’ if they were listed as critically endangered, endangered, vulnerable or near threatened in the red data book of North Rhine-Westphalia (LANUV NRW, 2011).

2.3. Environmental parameters

For each studied pond, we sampled several environmental parameters of habitat quality and landscape quality (Table 1). The pH and conductivity were measured during each of the four visits. Prior to statistical analysis, the data were averaged per parameter and pond. Sunshine duration was measured at the first (spring) and the last visit (summer) by using a horizontoscope (Holtmann et al., 2017). Occurrence of fish in shallow or clear ponds was assessed by visual inspection during each survey. In deep or murky ponds, ground motions were generated on warm days in May at all four shoreline sides (N, E, S, W) by jumping up to create visible water movement through fleeing fish (Table 2). In addition, information about fish stock was obtained from quarry operators and/or pond owners. Data on annual temperature (°C) (long-term mean: 1981–2010) were available from 1-km² grid datasets of Germany’s National Meteorological Service (DWD, 2021) (Table 1). All other field parameters were recorded once between the end of April and early May. For spatial analyses, we used ArcGIS 10.3.1 and aerial photographs. We calculated the distance to the next three water bodies (geometric mean) as a measure of pond connectivity (Thomas et al., 2001; Compton et al., 2007; Eichel and Fartmann, 2008; Poniatowski and Fartmann, 2010; Holtmann et al., 2017; Winiarski et al., 2020).

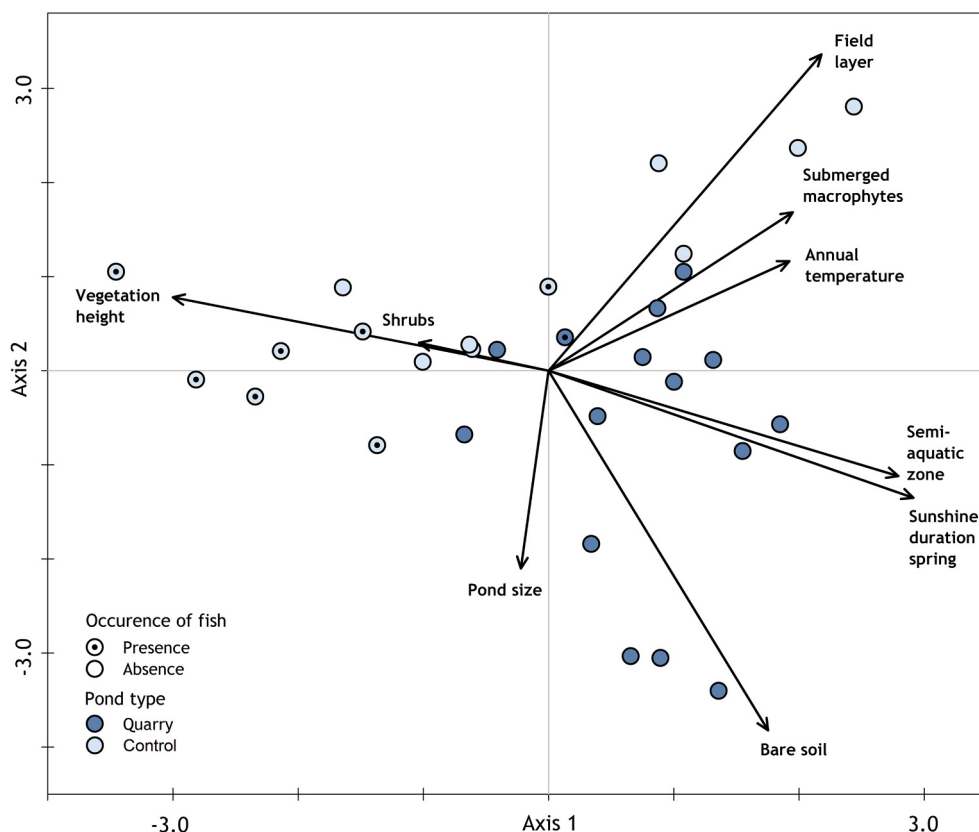


Fig. 3. Principal Component Analysis (PCA): Biplot based on the two pond types and sampled environmental parameters.

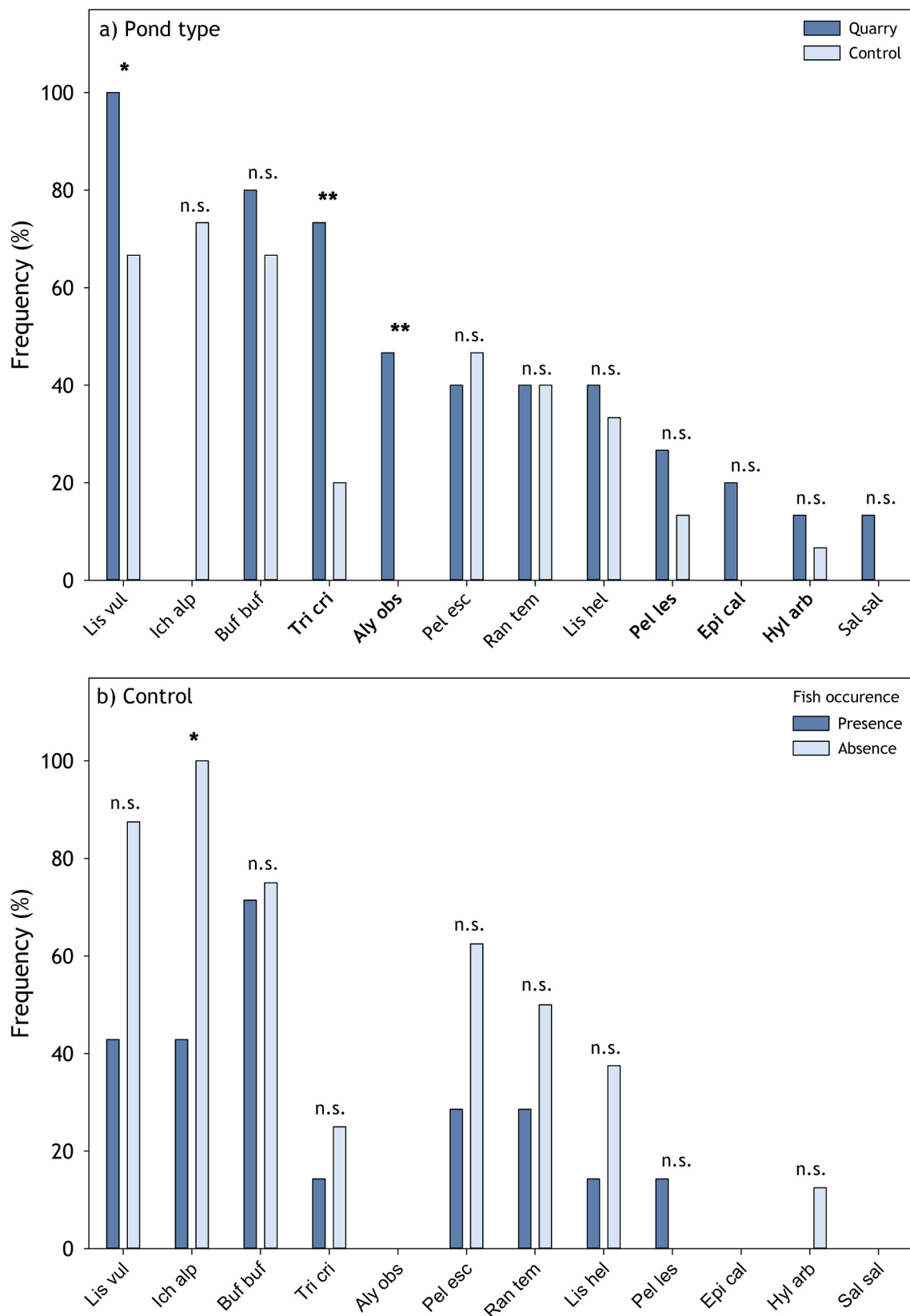


Fig. 4. Frequency of amphibian species a) at the two pond types (Quarry, $N = 15$; Control, $N = 15$) and b) control ponds in dependence of fish occurrence (Presence, $N = 7$; Absence, $N = 8$). Differences in absolute frequencies were tested by Chi-squared test. Abbreviations of species names: Lis vul = *Lissotriton vulgaris*, Ich alp = *Ichthyosaura alpestris*, Buf buf = *Bufo bufo*, Tri cri = *Triturus cristatus*, Aly obs = *Alytes obstetricans*, Pel esc = *Pelophylax esculentus*, Ran tem = *Rana temporaria*, Lis hel = *Lissotriton helveticus*, Pel les = *Pelophylax lessonae*, Epi cal = *Epidalea calamita*, Hyl arb = *Hyla arborea*, Sal sal = *Salamandra salamandra*. Threatened species (LANUV, 2011) are highlighted in bold type. n.s. = not significant; * $P < 0.05$; ** $P < 0.01$.

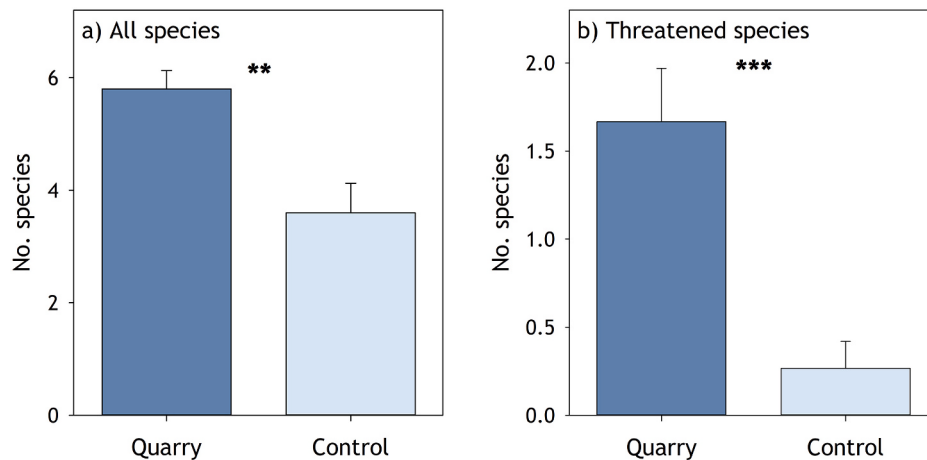


Fig. 5. Mean ($\pm$ SE) number of all species (a) and number of threatened species (b) in quarry ponds (Quarry, $N = 15$) and control ponds (Control, $N = 15$). Differences between pond types were analysed using Generalized Linear Mixed-effects Models (Poisson error structure) with 'subarea' as a random intercept (for details see Section 2.4). Statistical significance is indicated as follows: ** $P < 0.01$; *** $P < 0.001$.

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., 2021).

Since our study was based on a paired design, all metric environmental parameters (see Section 2.4) and the two response variables (number of all and threatened species; see Section 2.3) were tested for significant differences between quarry and control ponds as well as fish presence/absence in control ponds by using univariable GLMMs. Poisson 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).

In order to detect environmental parameters that explain species richness of all and threatened species, we conducted multivariable GLMMs. All predictor variables were standardized prior to the calculations to ensure the comparability of the model coefficients (cf. Le Provost et al., 2021). To avoid multicollinearity in the models, we applied Spearman's rank correlations (Spearman rank correlation $|r_s| > 0.5$; see Table A1) prior to the multivariable analyses. If two or more variables

were intercorrelated just one—the ecologically comprehensible variable—was used for statistical modelling (Dormann et al., 2013). In a second step, univariable GLMMs were fitted for all combinations of response and predictor variables in order to detect which predictor variables had an impact on the given response variable (Likelihood Ratio Tests, $P < 0.05$) (see Table A2). In the last step, the multivariable models were calculated incorporating all significant variables of the univariable models. In order to identify the most relevant environmental parameters within our 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) and only included top-ranked models within $\Delta AIC_c < 3$ (cf. Grueber et al., 2011). 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 observation-level random effect. This formatted factor can account for moderate overdispersion in models with a Poisson error structure (Harrison, 2014, 2015).

A Principal Component Analysis (PCA) was conducted to assess the relationship between environmental parameters and pond type. Differences in nominal variables were tested using Fisher's Exact test. Differences in absolute frequencies of each species between the two pond

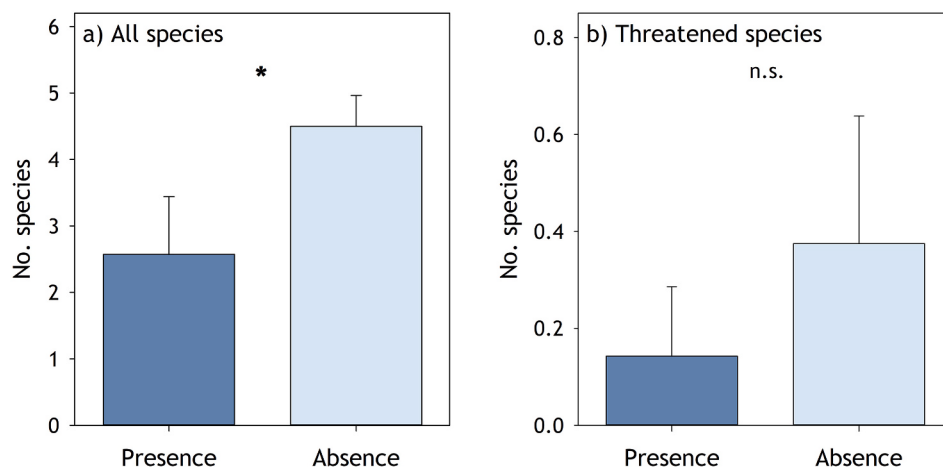


Fig. 6. Mean ($\pm$ SE) number of all species (a) and number of threatened species (b) in control ponds with fish presence ($N = 7$) and absence ($N = 8$). Differences between pond types were analysed using Generalized Linear Mixed-effects Models (Poisson error structure) with 'subarea' as a random intercept (for details see Section 2.5). Statistical significance is indicated as follows: n.s. = not significant; * $P < 0.05$.

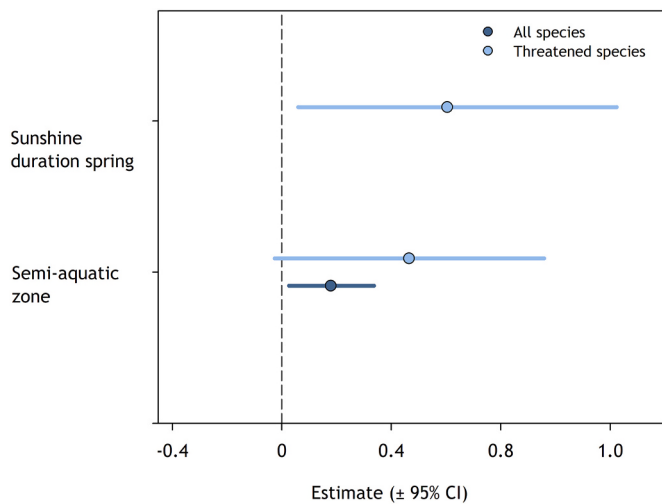


Fig. 7. Parameter estimate between the number of all and threatened species (Poisson error structure) and environmental parameters using multivariable GLMM including 'subarea' as a random intercept. Model-averaged coefficients (Standardized estimates $\pm$ 95% confidence intervals = CI) derived from the top-ranked models ($\Delta AIC_c < 3$) are shown. Confidence intervals of significant predictors ($P < 0.05$) do not cross $x = 0$ (for more details see Table A4).

types were analysed with a Chi-squared test.

3. Results

3.1. Environmental parameters

Our study revealed clear differences in habitat quality but not in landscape quality between quarry and control ponds (Table 1). At quarry ponds, the semi-aquatic zone accounted for most of the pond area and overall, it was more extended compared with those of control ponds. Additionally, the sunshine duration (spring and summer) was generally higher and, along the shoreline, the cover of trees was lower, the cover of bare soil higher and vegetation shorter at quarry ponds than at control ponds. Occurrence of fish also differed between both types of ponds (Table 2, Fig. 3). Quarry ponds were, with one exception, never occupied by fish. By contrast, fish were present in nearly one half of the control ponds.

The strong differences in environmental conditions between the two pond types were confirmed by the PCA, which showed a clear separation

of control and quarry ponds along the first axis (Fig. 3, Table A3). In particular, a taller vegetation at the shoreline was characteristic of control ponds, whereas a larger area of the semi-aquatic zone (which was negatively correlated with presence of fish), a longer sunshine duration in spring and more bare soil at the shoreline were typical of quarry ponds.

3.2. Response of amphibian assemblages to environmental conditions

Altogether, we detected 12 amphibian species, including five threatened species (*Alytes obstetricans*, *Epidalea calamita*, *Hyla arborea*, *Pelophylax lessonae* and *Triturus cristatus*) (Fig. 4a). Three species, *A. obstetricans*, *Lissotriton vulgaris* and *T. cristatus*, had a higher frequency in quarry ponds compared with control ponds (Fig. 4a), and there were even three species observed only in quarry ponds (*A. obstetricans*, *E. calamita* and *Salamandra salamandra*). Overall species richness and number of threatened species were higher in quarry ponds compared with control ponds (Fig. 5). Moreover, control ponds with presence of fish had a lower overall species richness and frequency of *Ichthyosaura alpestris* (Fig. 4b, Fig. 6).

In the GLMM analyses, assemblage composition was only determined by habitat quality, not landscape quality—more precisely by the area of the semi-aquatic zone and sunshine duration in spring (Figs. 7 and 8, Table A4). Overall species richness increased with the extent of the semi-aquatic zone. By contrast, the number of threatened species was fostered by sunshine duration.

4. Discussion

Our study revealed strong differences in habitat quality and composition of amphibian assemblages between quarry and control ponds. In particular, a larger area of the semi-aquatic zone, a longer sunshine duration, more bare soil at the shoreline and the absence of fish was typical of quarry ponds, whereas a taller vegetation at the shoreline characterized control ponds. As a result, overall species richness and number of threatened species were higher in quarry ponds compared with control ponds.

The 12 amphibian species observed in the quarry ponds and generally in this study comprise 80% of the amphibian fauna of the whole study area (cf. Hachtel et al., 2011). Of the three remaining species occurring within the study area, two are extremely rare (*Bombina variegata* and *Pelobates fuscus*) and one has very localized and often allochthonous populations (*Pelophylax ridibundus*). Accordingly, the high completeness of detected species already highlights the high conservation value of quarry ponds for amphibians.

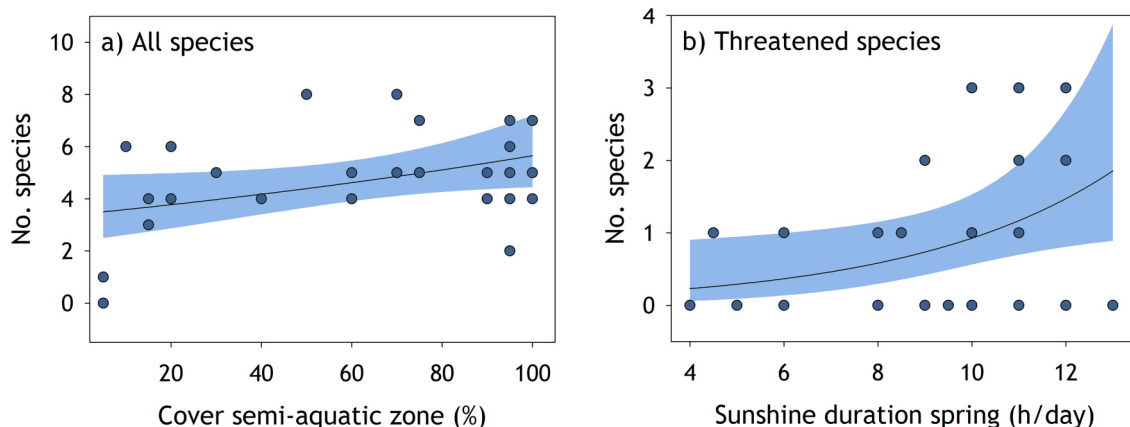


Fig. 8. Relationship between the number of all species (a) and number of threatened species (b) with significant parameters from the multivariable models ($N = 30$). For statistics see Table A4. (a) $\log(y) = 1.228947 + 0.00504 \times (\text{Semi-aquatic zone})$, $P < 0.05$, $R_m^2 = 0.12$, $R_c^2 = 0.12$; (b) $\log(y) = -2.39122 + 0.02316 \times (\text{Sunshine duration spring})$, $P < 0.05$, $R_m^2 = 0.16$, $R_c^2 = 0.23$. Blue bands indicate 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The comparison of environmental conditions between the two types of ponds provided further insights into the importance of quarry ponds for amphibians. Quarry ponds exhibited two characteristics that are of crucial importance for species-rich amphibian assemblages: (i) sunlit and warm microhabitats and (ii) the absence of fish (cf. Hartel et al., 2007; Shulze et al., 2012; Drayer and Richter, 2016; Rannap et al., 2020; Holtmann et al., 2017). A larger area of the semi-aquatic zone and longer sunshine duration (spring and summer) together with a more sparse (lower cover of trees, more bare soil) and shorter vegetation at the shoreline were typical of quarry ponds in comparison with control ponds. Such conditions are known to result in a generally warmer microclimate and higher water temperatures, in particular in the shallow water of the extensive semi-aquatic zone of the quarry ponds (cf. Stoutjesdijk and Barkman, 1992). The majority of the Central European amphibian species (Günther, 1996) and especially those that are thermophilic and threatened, such as *Alytes obstetricans*, *Epidalea calamita*, *Hyla arborea* or *Triturus cristatus* (Günther, 1996; Richter-Boix et al., 2006), depend on warm water bodies for breeding. In line with this, the number of threatened species increased with sunshine duration in spring and a higher cover of the semi-aquatic zone fostered overall species richness. Additionally, the favourable microclimatic conditions were probably at least partly responsible for the higher frequency of *A. obstetricans* and *T. cristatus* as well as the exclusive occurrence of *E. calamita* in quarry ponds.

Fish stock has negative effects on amphibian populations due to predation of eggs and larvae and, especially concerning newts, also of adults (Scheffer et al., 2006; Hartel et al., 2007; Rannap et al., 2020). However, in quarry ponds, predation by fish was generally unimportant since fish were only present in one of the ponds. By contrast, fish occurred in almost one half of the control ponds. Although we did not determine fish to species level, the occurrence of fish in control ponds had a negative effect on overall species richness and frequency of *Ichthyosaura alpestris*. In general, a large area of the semi-aquatic zone was a surrogate for water bodies free of fish (see Table A1), because they had a higher likelihood of drying out (temporary ponds) in the course of the growing season (own observation) and, hence, hampering the establishment of a permanent fish population. Additionally, in the shallow water of the semi-aquatic zone, eggs, larvae or adults are generally sheltered against predation by larger fish (Caballero-Diaz et al., 2020). Consequently, the positive effect of the cover of the semi-aquatic zone may not only reflect the importance of warm microclimates but also of microhabitats that are free of fish predators. Therefore, based on the aforementioned, we attribute the higher overall species richness and number of threatened species in quarry ponds to both the favourable microclimatic conditions and the lack of fish predators. More sophisticated sampling techniques (e.g., using environmental DNA) (Brys et al., 2021; Thomsen et al., 2012) would possibly have provided additional insights.

To sum up, quarry ponds had a higher habitat quality than control ponds. In particular, (i) the large area of sunlit and warm microhabitats and (ii) the absence of fish predators favoured species richness of amphibians (overall and threatened species) at the quarry ponds. Overall, quarry ponds—thanks to their early-successional stages—have a high conservation value for amphibians.

5. Implications for conservation

In quarries, succession is usually delayed due to the lack of topsoil (Münsch and Fartmann, 2022). Additionally, active quarrying regularly creates new and in particular temporary ponds in wheel tracks or excavation depressions and slows down successional speed through driving by construction vehicles (Gilcher and Tränkle, 2005; Baumbach et al., 2013). Such ephemeral ponds are especially important as breeding habitats for *Epidalea calamita* (Günther, 1996). Populations of both

species have strongly declined in recent decades (Rote-Liste-Gremium Amphibien und Reptilien, 2020), and quarry ponds are nowadays often the last refuge for the species in our landscapes (this study; Rote-Liste-Gremium Amphibien und Reptilien, 2020). However, due to climate warming, some of the temporary ponds dry out too early in the growing season to enable successful completion of the amphibian metamorphosis (own observation; Streitberger et al., 2016), even for a species with fast development such as *E. calamita* (Günther, 1996). Accordingly, we recommend creating additional ponds in the quarries that contain water until the end of summer, even in times of climate change. Moreover, artificial ponds that can be drained to prevent the establishment of fish are another possibility (Schenkenberger, 2023).

During our study, we regularly detected fresh tracks of raccoons (*Procyon lotor*) at muddy shorelines of the studied ponds and parts of dead amphibians, which were likely killed by the species. The raccoon is a non-native, omnivorous predator with a strongly growing population in the study area (Klauer and Kriegs, 2015). It has already been shown that especially populations of small mammals, birds and amphibians can strongly suffer from raccoon predation (Salgado, 2018; Fiderer et al., 2019). To reduce predation by the raccoon, we recommend installing metal cages above the ponds, at least during the spawning season and around shallow parts of the ponds where amphibians are easily accessible for the species.

Still many reclamation concepts intend to fill, afforest or flood quarries after cessation of mining (Krauss et al., 2009; Tropek et al., 2010). Such measures should generally be prohibited since they do not only have negative effects on amphibians but also many other groups of conservation concern (Beneš et al., 2003; Tropek et al., 2010; Münsch and Fartmann, 2022). Additionally, in abandoned quarries, regular cutting and removal of shoreline vegetation should be implemented to create the preferred early-successional stages (Holtmann et al., 2017). There are many other taxonomic groups that are known to depend on early stages of pond succession and would benefit from such actions (e.g., dragon- and damselflies: Holtmann et al., 2018, 2019a; vascular plants: Holtmann et al., 2019b).

Funding

The study was funded by the German Federal Environmental Foundation (DBU, grant no. 34381/01).

CRediT authorship contribution statement

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

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.

Data availability

The authors do not have permission to share data.

Acknowledgements

We are very grateful to all quarry operators and districts for access and permits. Three anonymous reviewers made valuable comments on an earlier version of the manuscript.

Appendix A. Appendix

Table A1

Overview of environmental parameters used for Generalized Linear Mixed-effects Models and their inter-correlations with other environmental parameters (Spearman correlation $[r_s]$, $|r_s| > 0.5$). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	Surrogate for (Spearman Rank Order Correlation $[r_s]$)
Habitat quality	
Habitat type (%)	
Shrubs	.
Field layer	Litter (0.54**), conductivity (−0.51**)
Bare soil	Sunshine duration summer (0.61***), pH (0.53**), trees (−0.50**)
Submerged macrophytes	Conductivity (−0.51**)
Vegetation height (cm)	Trees (0.67***), sunshine duration summer (−0.56**), fish (0.52**)
Pond size (ha)	.
Sunshine duration spring (h/day)	Sunshine duration summer (0.68***), trees (−0.52**)
Semi-aquatic zone (%)	Fish (−0.71**)
Landscape quality	.
Annual temperature (°C)	Elevation (−0.93***), pond connectivity (−0.55**)

Table A2

Univariable models (Generalized Linear Mixed-effects Models, Poisson error structure): Influence of environmental parameters (predictor variables) on the number of all species and number of threatened species within both pond types ($N = 30$). n.s. = not significant, * $P < 0.05$.

Parameter	No. all species			No. threatened species		
	Estimate	SE	P	Estimate	SE	P
Habitat quality						
Pond size	6.95×10^{-2}	7.98×10^{-2}	n.s.	1.49×10^{-1}	2.22×10^{-1}	n.s.
Sunshine duration spring	1.79×10^{-1}	9.23×10^{-2}	n.s.	5.93×10^{-1}	2.63×10^{-1}	*
Semi-aquatic zone	1.79×10^{-1}	8.94×10^{-2}	*	5.30×10^{-1}	2.64×10^{-1}	*
Submerged macrophytes	1.27×10^{-1}	8.28×10^{-2}	n.s.	1.23×10^{-1}	2.28×10^{-1}	n.s.
Shrubs	7.57×10^{-2}	8.37×10^{-2}	n.s.	-1.17×10^{-1}	2.46×10^{-1}	n.s.
Field layer	2.31×10^{-2}	8.46×10^{-2}	n.s.	-7.03×10^{-2}	2.42×10^{-1}	n.s.
Bare soil	6.32×10^{-2}	8.16×10^{-2}	n.s.	3.63×10^{-1}	1.96×10^{-1}	n.s.
Vegetation height	-4.56×10^{-2}	8.84×10^{-2}	n.s.	-3.24×10^{-1}	2.55×10^{-1}	n.s.
Landscape quality						
Annual temperature	2.29×10^{-2}	8.62×10^{-2}	n.s.	1.82×10^{-1}	2.44×10^{-1}	n.s.

Table A3

Summary of PCA results based on the two pond types and environmental parameters ($N = 30$).

Parameter	Axis	
	1	2
Habitat quality		
Pond size	−0.22	−2.10
Sunshine duration spring	2.91	−1.35
Semi-aquatic zone	2.79	−1.12
Submerged macrophytes	1.95	1.68
Shrubs	−1.04	0.30
Field layer	2.18	3.36
Bare soil	1.75	−3.82
Vegetation height	−3.00	0.78
Landscape quality		
Annual temperature	1.92	1.16
Explained variance (cumulative)	21.8	42.0

Table A4

Results of Generalized Linear Mixed-effects Models (GLMM) (Poisson error structure, with 'subarea' as a random intercept): Influence of environmental parameters (predictor variables) on the number of all species (a) and on the number of threatened species (b). Model-averaged coefficients (conditional average) were derived from the top-ranked GLMM ($\Delta AIC_C < 3$). R_m^2 = variance explained by fixed effects, R_c^2 = variance explained by both fixed and random effects (Nakagawa et al., 2017) ($N = 30$). n.s. = not significant; * $P < 0.05$; *** $P < 0.001$.

Parameter	Estimate	SE	Z	P
-----------	----------	----	---	---

(continued on next page)

Table A4 (continued)

Parameter	Estimate	SE	Z	P
a) No. all species ($R^2m = 0.12$, $R^2c = 0.12$)				
(Intercept)	1.53	0.09	17.78	***
Semi-aquatic zone	1.79×10^{-1}	8.94×10^{-2}	2.00	*
b) No. threatened species ($R^2m = 0.12-0.30$, $R^2c = 0.23-0.30$)				
(Intercept)	-0.28	0.27	1.00	n.s.
Sunshine duration spring	6.05×10^{-1}	2.76×10^{-1}	2.08	*
Semi-aquatic zone	4.65×10^{-1}	2.46×10^{-1}	1.80	n.s.

References

Arntzen, J.W., Abrahams, C., Meilink, W.R., Iosif, R., Zuiderwijk, A., 2017. Amphibian decline, pond loss and reduced population connectivity under agricultural intensification over a 38 year period. *Biodivers. Conserv.* 26 (6), 1411–1430. <https://doi.org/10.1007/s10531-017-1307-y>.

Bartoń, K., 2021. Package ‘MuMin’. Retrieved from. <https://cran.r-project.org/web/packages/MuMin/MuMin.pdf> (accessed 23 November 2021).

Bates, D., Maechler, M., Bolker, B., Walker, S., 2021. Linear Mixed-Effects Models using ‘Eigen’ and S4 (Package lme4, version 1.1.21). <https://cran.r-project.org/web/packages/lme4> (accessed 23 November 2021).

Baumbach, H., Sanger, H., Heinze, M., 2013. Bergbaufolgelandschaften Deutschlands: Geobotanische Aspekte und Rekultivierung. Weissdorn-Verlag Jena.

Beneš, J., Kepka, P., Konvicka, M., 2003. Limestone quarries as refuges for European xerophilous butterflies. *Conserv. Biol.* 17, 1058–1069. <https://doi.org/10.1046/j.1523-1739.2003.02092.x>.

Betard, F., 2013. Patch-scale relationships between geodiversity and biodiversity in hard rock quarries: case study from a disused quartzite quarry in NW France. *Geoderma* 5 (2), 59–71. <https://doi.org/10.1007/s12371-013-0078-4>.

Brys, R., Haegeman, A., Halmaert, D., Neyrinck, S., Staelens, A., Auwerx, J., Ruttkink, T., 2021. Monitoring of spatiotemporal occupancy patterns of fish and amphibian species in a lentic aquatic system using environmental DNA. *Mol. Ecol.* 30 (13), 3097–3110. <https://doi.org/10.1111/mec.15742>.

Butchart, S.H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P., Almond, R.E., Baillie, J.E., Bomhard, B., Brown, C., Bruno, J., 2010. Global biodiversity: indicators of recent declines. *Science* 328 (5982), 1164–1168. <https://doi.org/10.1126/science.1187512>.

Caballero-Diaz, C., Sanchez-Montes, G., Butler, H.M., Vredenburg, V.T., Martinez-Solano, I., 2020. The role of artificial breeding sites in amphibian conservation: a case study in rural areas in Central Spain. *Herpetol. Conserv. Biol.* 15 (1), 87–104. <http://hdl.handle.net/10261/240044>.

Cardoso, P., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J., Hallmann, C.A., Hill, M., Hochkirch, A., Kwak, M.L., Mammola, S., Noriega, J.A., Orfinger, A.B., Pedraza, F., Pryke, J.S., Roque, F.O., Settele, J., Simaika, J.P., Stork, N.E., Suhling, F., Vorster, C., Samways, M.J., 2020. Scientists’ warning to humanity on insect extinctions. *Biol. Conserv.* 242, 108426. <https://doi.org/10.1016/j.biocon.2020.108426>.

Compton, B.W., McGarigal, K., Cushman, S.A., Gamble, L.R., 2007. A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conserv. Biol.* 21 (3), 788–799. <https://doi.org/10.1111/j.1523-1739.2007.00674.x>.

Cordier, J.M., Aguilar, R., Lescano, J.N., Leynaud, G.C., Bonino, A., Miloch, D., Loyola, R., Nori, J., 2021. A global assessment of amphibian and reptile responses to land-use changes. *Biol. Conserv.* 253, 108863. <https://doi.org/10.1016/j.biocon.2020.108863>.

Cox, K., Maes, J., Van Calster, H., Mergeay, J., 2017. Effect of the landscape matrix on gene flow in a coastal amphibian metapopulation. *Conserv. Genet.* 18 (6), 1359–1375. <https://doi.org/10.1007/s10592-017-0985-z>.

Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol. Conserv.* 128 (2), 231–240. <https://doi.org/10.1016/j.biocon.2005.09.031>.

De Vos, J.M., Joppa, L.N., Gittleman, J.L., Stephens, P.R., Pimm, S.L., 2015. Estimating the normal background rate of species extinction. *Conserv. Biol.* 29 (2), 452–462. <https://doi.org/10.1111/cobi.12380>.

DiRenzo, G.V., Grant, E.H.C., 2019. Overview of emerging amphibian pathogens and modeling advances for conservation-related decisions. *Biol. Conserv.* 236, 474–483. <https://doi.org/10.1016/j.biocon.2019.05.034>.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Marquez, J.R.G., Gruber, B., Lafourcade, B., Leitao, P.J., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36 (1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.

Drayer, A.N., Richter, S.C., 2016. Physical wetland characteristics influence amphibian community composition differently in constructed wetlands and natural wetlands. *Ecol. Eng.* 93, 166–174. <https://doi.org/10.1016/j.ecoleng.2016.05.028>.

DWD (German Meteorological Service), 2021. Climate data center: grids of climate over Germany. https://opendata.dwd.de/climate_environment/CDC/grids_germany/ (accessed 23 November 2021).

Eichel, S., Fartmann, T., 2008. Management of calcareous grasslands for Nickerl’s fritillary (*Melitaea aurelia*) has to consider habitat requirements of the immature stages, isolation, and patch area. *J. Insect Conserv.* 12 (6), 677–688. <https://doi.org/10.1007/s10841-007-9110-9>.

Fartmann, T., Jedicke, E., Streitberger, M., Stuhldreher, G., 2021. Insektensterben in Mitteleuropa. Ursachen und Gegenmanahmen, Eugen Ulmer, Stuttgart.

Fiderer, C., Gottert, T., Zeller, U., 2019. Spatial interrelations between raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), and ground-nesting birds in a special Protection Area of Germany. *Eur. J. Wildl. Res.* 65 (1), 14. <https://doi.org/10.1007/s10344-018-1249-z>.

Gilcher, S., Trankle, U., 2005. Steinbruche und Gruben in Bayern und ihre Bedeutung fur den Arten- und Biotopschutz. *Bayerischer Industrieverband Steine und Erden e. V. und Bayerisches Landesamt fur Umwelt*, Munchen, Germany.

Glandt, D., 2011. Grundkurs Amphibien- und Reptilienbestimmung: Beobachten, Erfassen und Bestimmen aller europaischen Arten. Quelle & Meyer, Wiebelsheim.

Glandt, D., 2014. Wasserfallen als Hilfsmittel der Amphibienerfassung – eine Standortbestimmung. Wasserfallen fur Amphibien – praktische Anwendung im Artmonitoring. Abhandlungen aus dem Westfalischen Museum fur Naturkunde 77, 9–50.

Gonzalez-del-Piego, P., Freckleton, R.P., Edwards, D.P., Koo, M.S., Scheffers, B.R., Pyron, R.A., Jetz, W., 2019. Phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. *Curr. Biol.* 29 (9), 1557–1563. <https://doi.org/10.1016/j.cub.2019.04.005>.

Grant, E.H.C., Miller, D.A.W., Schmidt, B.R., Adams, M.J., Amburgey, S.M., Chambert, T., Cruickshank, S.S., Fisher, R.N., Green, D.M., Hossack, B.R., Johnson, P.T.J., Joseph, M.B., Rittenhouse, T.A.G., Ryan, M.E., Waddle, J.H., Walls, S.C., Bailey, L.L., Fellers, G.M., Gorman, T.A., Ray, A.M., Pilliod, D.S., Price, S. J., Saenz, D., Sadinski, W., Muths, E., 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Sci. Rep.* 6 (1), 1–9. <https://doi.org/10.1038/srep25625>.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24 (4), 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>.

Gunther, R., 1996. Die Amphibien und Reptilien Deutschlands. Gustav Fischer Verlag, Jena.

Hachtel, M., Schlupmann, M., Thiesmeier, B., Weddelling, K., 2009. Methoden der Feldherpetologie: Laurenti-Verlag.

Hachtel, M., Schlupmann, M., Weddelling, K., Thiesmeier, B., Geiger, A., Willigalla, C., 2011. Handbuch der Amphibien und Reptilien Nordrhein-Westfalens. Band 1. Laurenti Verlag, Bielefeld.

Harrison, X.A., 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2, e616. <https://doi.org/10.7717/peerj.616>.

Harrison, X.A., 2015. A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology and evolution. *PeerJ* 3, e1114. <https://doi.org/10.7717/peerj.1114>.

Hartel, T., Nemes, S., Cogalniceanu, D., Ollerer, K., Schweiger, O., Moga, C.-I., Demeter, L., 2007. The effect of fish and aquatic habitat complexity on amphibians. *Hydrobiologia* 583 (1), 173–182. <https://doi.org/10.1007/s10750-006-0490-8>.

Hof, C., Araujo, M.B., Jetz, W., Rahbek, C., 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* 480 (7378), 516–519. <https://doi.org/10.1038/nature10650>.

Holtmann, L., Philipp, K., Becke, C., Fartmann, T., 2017. Effects of habitat and landscape quality on amphibian assemblages of urban stormwater ponds. *Urban Ecosyst.* 20 (6), 1249–1259. <https://doi.org/10.1007/s11252-017-0677-y>.

Holtmann, L., Juchem, M., Bruggeshemke, J., Mohlmeier, A., Fartmann, T., 2018. Stormwater ponds promote dragonfly (Odonata) species richness and density in urban areas. *Ecol. Eng.* 118, 1–11. <https://doi.org/10.1016/j.ecoleng.2017.12.028>.

Holtmann, L., Bruggeshemke, J., Juchem, M., Fartmann, T., 2019a. Odonate assemblages of urban stormwater ponds: the conservation value depends on pond type. *J. Insect Conserv.* 23, 123–132. <https://doi.org/10.1007/s10841-018-00121-x>.

Holtmann, L., Kerler, K., Wolfart, L., Schmidt, C., Fartmann, T., 2019b. Habitat heterogeneity determines plant species richness in urban stormwater ponds. *Ecol. Eng.* 138, 434–443. <https://doi.org/10.1016/j.ecoleng.2019.07.035>.

Kalarus, K., Halecki, W., Skalski, T., 2019. Both semi-natural and ruderal habitats matter for supporting insect functional diversity in an abandoned quarry in the city of Krakow (S Poland). *Urban Ecosyst.* 22 (5), 943–953. <https://doi.org/10.1007/s11252-019-00869-3>.

Kats, L.B., Ferrer, R.P., 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Divers. Distrib.* 9 (2), 99–110. <https://doi.org/10.1046/j.1472-4642.2003.00013.x>.

Kettermann, M., Poniatowski, D., Fartmann, T., 2022. Active management fosters species richness of wild bees in limestone quarries. *Ecol. Eng.* 182, 106733. <https://doi.org/10.1016/j.ecoleng.2022.106733>.

- Klauser, F., Kriegs, J.O., 2015. Zur Verbreitung und Häufigkeit des Waschbären *Procyon lotor* (Linnaeus, 1758) in der Westfälischen Bucht in den Jahren 2000 bis 2011. *Nat. Heimat* 75 (1), 121–130.
- Köppel, C., 1995. Kiesgruben – ein Ersatz für Flussauen. *Naturschutz Landschaftsplanung* 27 (1), 7–11.
- Krauss, J., Alfert, T., Steffan-Dewenter, I., 2009. Habitat area but not habitat age determines wild bee richness in limestone quarries. *J. Appl. Ecol.* 46 (1), 194–202. <https://doi.org/10.1111/j.1365-2664.2008.01582.x>.
- Kronshage, A., Schlüpman, M., Beckmann, C., Weddelling, K., Geiger, A., Haacks, M., Böll, S., 2014. Empfehlungen zum Einsatz von Wasserfällen bei Amphibienerfassungen Wasserfällen für Amphibien – praktische Anwendung im Artenschutz. *Abhandlungen aus dem Westfälischen Museum für Naturkunde* 77, 293–358.
- LANUV NRW (Landesamt für Natur, Umwelt- und Verbraucherschutz Nordrhein-Westfalen), 2011. Rote Liste und Artenverzeichnis der Lurche – Amphibia – in Nordrhein-Westfalen. 4. Fassung. Retrieved from <https://www.lanuv.nrw.de> (accessed 18 March 21).
- Le Provost, G., Thiele, J., Westphal, C., Penone, C., Allan, E., Neyret, M., van der Plas, F., Ayasse, M., Bardgett, R.D., Birkhofer, K., Boch, S., Bonkowski, M., Buscot, F., Feldhaar, H., Gaulton, R., Goldmann, K., Gossner, M.M., Klaus, V.H., Kleinebecker, T., Krauss, J., Renner, S., Scherrei, P., Sikorski, J., Baulechner, D., Blüthgen, N., Bolliger, R., Börschig, C., Busch, V., Chisté, M., Fiore-Donno, A.M., Fischer, M., Arndt, H., Hoelzel, N., John, K., Jung, K., Lange, M., Marzini, C., Overmann, J., Pašalić, E., Perović, D.J., Prati, D., Schäfer, D., Schöning, I., Schürpf, M., Sonnemann, I., Steffan-Dewenter, I., Tschapka, M., Türke, M., Vogt, J., Wehner, K., Weiner, C., Weisser, W., Wells, K., Werner, M., Wolters, V., Wubet, T., Wurst, S., Zaitsev, A.S., Manning, P., 2021. Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. *Nat. Commun.* 12 (1), 3918. <https://doi.org/10.1038/s41467-021-23931-1>.
- Münsch, T., Fartmann, T., 2022. Limestone quarries are the most important refuge for a formerly widespread grassland butterfly. *Insect. Conserv. Diversity*. <https://doi.org/10.1111/icad.12544>.
- Münsch, T., Helbing, F., Fartmann, T., 2019. Habitat quality determines patch occupancy of two specialist Lepidoptera species in well-connected grasslands. *J. Insect Conserv.* 23, 247–258. <https://doi.org/10.1007/s10841-018-0109-1>.
- Murray, A.H., Nowakowski, A.J., Frishkoff, L.O., 2020. Climate and land-use change severity alter trait-based responses to habitat conversion. *Glob. Ecol. Biogeogr.* 30 (3), 598–610. <https://doi.org/10.1111/geb.13237>.
- Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. *Science* 336 (6087), 1401–1406. <https://doi.org/10.1126/science.1215855>.
- Nakagawa, S., Johnson, P.C., Schielzeth, H., 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* 14 (134). <https://doi.org/10.1098/rsif.2017.0213>.
- Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520 (7545), 45–50. <https://doi.org/10.1038/nature14324>.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P. H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344 (6187). <https://doi.org/10.1126/science.1246752>.
- Poniatowski, D., Fartmann, T., 2010. What determines the distribution of a flightless bush-cricket (*Metrioptera brachyptera*) in a fragmented landscape? *J. Insect Conserv.* 14 (6), 637–645. <https://doi.org/10.1007/s10841-010-9293-3>.
- Poniatowski, D., Stuhldreher, G., Löffler, F., Fartmann, T., 2018. Patch occupancy of grassland specialists: Habitat quality matters more than habitat connectivity. *Biol. Conserv.* 225, 237–244. <https://doi.org/10.1016/j.biocon.2018.07.018>.
- Poschlod, P., Braun-Reichert, R., 2017. Small natural features with large ecological roles in ancient agricultural landscapes of Central Europe – history, value, status, and conservation. *Biol. Conserv.* 211, 60–68. <https://doi.org/10.1016/j.biocon.2016.12.016>.
- R Development Core Team, 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rannap, R., Kaart, M.M., Kaart, T., Kill, K., Uuemaa, E., Mander, Ü., Kasak, K., 2020. Constructed wetlands as potential breeding sites for amphibians in agricultural landscapes: a case study. *Ecol. Eng.* 158, 106077. <https://doi.org/10.1016/j.ecoleng.2020.106077>.
- Řehounková, K., Vítovcová, K., Prach, K., 2020. Threatened vascular plant species in spontaneously revegetated post-mining sites. *Restor. Ecol.* 28 (3), 679–686. <https://doi.org/10.1111/rec.13027>.
- Richter-Boix, A., Llorente, G.A., Montori, A., 2006. Breeding phenology of an amphibian community in a Mediterranean area. *Amphibia-Reptilia* 27 (4), 549–559. <https://doi.org/10.1163/156853806778877149>.
- Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., Lambin, E.F., Lenton, T. M., Scheffer, M., Folke, C., Schellnhuber, H.J., 2009. A safe operating space for humanity. *Nature* 461 (7263), 472–475. <https://doi.org/10.1038/461472a>.
- Rote-Liste-Gremium Amphibien und Reptilien, 2020. Rote Liste und Gesamtartenliste der Amphibien (Amphibia) Deutschlands. *Naturschutz Biologische Vielfalt* 170 (4), 1–86.
- Šálek, M., 2012. Spontaneous succession on opencast mining sites: implications for bird biodiversity. *J. Appl. Ecol.* 49 (6), 1417–1425. <https://doi.org/10.1111/j.1365-2664.2012.02215.x>.
- Salgado, I., 2018. Is the raccoon (*Procyon lotor*) out of control in Europe? *Biodivers. Conserv.* 27 (9), 2243–2256. <https://doi.org/10.1007/s10531-018-1535-9>.
- Salgueiro, P.A., Silva, C., Silva, A., Sá, C., Mira, A., 2020. Can quarries provide novel conditions for a bird of rocky habitats? *Restor. Ecol.* 28 (4), 988–994. <https://doi.org/10.1111/rec.13080>.
- Scheffer, M., Van Geest, G., Zimmer, K., Jeppesen, E., Søndergaard, M., Butler, M., Hanson, M., Declercq, S., De Meester, L., 2006. Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos* 112 (1), 227–231. <https://doi.org/10.1111/j.0030-1299.2006.14145.x>.
- Schenkenberger, J., 2023. Arbeitsgruppe für Tierökologie und Planung – Asphalt für Amphibien. *Naturschutz Landschaftsplanung* 55 (1), 42–45.
- Shulse, C.D., Semlitsch, R.D., Trauth, K.M., Gardner, J.E., 2012. Testing wetland features to increase amphibian reproductive success and species richness for mitigation and restoration. *Ecol. Appl.* 22 (5), 1675–1688. <https://doi.org/10.1890/11-0212.1>.
- Stoutjesdijk, P., Barkman, J.J., 1992. Microclimate, vegetation and fauna. *Opulus Press, Upsala*.
- Streitberger, M., Ackermann, W., Fartmann, T., Kriegl, G., Ruff, A., Balzer, S., Nehring, S., 2016. Artenschutz unter Klimawandel: Perspektiven für ein zukunftsfähiges Handlungskonzept. *Naturschutz Biologische Vielfalt* 147, 1–367.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306 (5702), 1783–1786. <https://doi.org/10.1126/science.1103538>.
- Tetzlaff, I., 2007. *Froschlurche: die Stimmen aller heimischen Arten; inklusive Beiheft mit Texten, Farbfotos, Oszillo- und Spektrogrammen*. Musikverl. Ed. AMPLE.
- Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R., Goodger, B., 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 268 (1478), 1791–1796. <https://doi.org/10.1098/rspb.2001.1693>.
- Thomsen, P.F., Kielgast, J.O.S., Iversen, L.L., Wiuf, C., Rasmussen, M., Gilbert, M.T.P., Orlando, L., Willerslev, E., 2012. Monitoring endangered freshwater biodiversity using environmental DNA. *Mol. Ecol.* 21 (11), 2565–2573. <https://doi.org/10.1111/j.1365-294X.2011.05418.x>.
- Tropek, R., Spitzer, L., Konvicka, M., 2008. Two groups of epigeic arthropods differ in colonising of piedmont quarries: the necessity of multi-taxa and life-history traits approaches in the monitoring studies. *Commun. Ecol.* 9 (2), 177–184. <https://doi.org/10.1556/ComEc.9.2008.2.6>.
- Tropek, R., Kadlec, T., Karesova, P., Spitzer, L., Kocarek, P., Malenovsky, I., Banar, P., Tuf, I.H., Hejda, M., Konvicka, M., 2010. Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. *J. Appl. Ecol.* 47 (1), 139–147. <https://doi.org/10.1111/j.1365-2664.2009.01746.x>.
- Unglaub, B., Steinfartz, S., Kühne, D., Haas, A., Schmidt, B.R., 2018. The relationships between habitat suitability, population size and body condition in a pond-breeding amphibian. *Basic Appl. Ecol.* 27, 20–29. <https://doi.org/10.1016/j.baee.2018.01.002>.
- Unglaub, B., Cayuela, H., Schmidt, B.R., Preißler, K., Glos, J., Steinfartz, S., 2021. Context-dependent dispersal determines relatedness and genetic structure in a patchy amphibian population. *Mol. Ecol.* 30 (20), 5009–5028. <https://doi.org/10.1111/mec.16114>.
- Van Buskirk, J., 2003. Habitat partitioning in European and north American pond-breeding frogs and toads. *Divers. Distrib.* 9 (5), 399–410. <https://doi.org/10.1046/j.1472-4642.2003.00038.x>.
- Wake, D.B., Vredenburg, V.T., 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc. Natl. Acad. Sci.* 105 (Supplement 1), 11466–11473. <https://doi.org/10.1073/pnas.0801921105>.
- Winiarski, K.J., Peterman, W.E., Whiteley, A.R., McGarigal, K., 2020. Multiscale resistant kernel surfaces derived from inferred gene flow: an application with vernal pool breeding salamanders. *Mol. Ecol. Resour.* 20 (1), 97–113. <https://doi.org/10.1111/1755-0998.13089>.
- Yap, T.A., Nguyen, N.T., Serr, M., Shepack, A., Vredenburg, V.T., 2017. *Batrachochytrium salamandrivorans* and the risk of a second amphibian pandemic. *EcoHealth* 14 (4), 851–864. <https://doi.org/10.1007/s10393-017-1278-1>.