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RESEARCH

The return of natural fish communities in Bohemian Forest watercourses after acidification recovery

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Abstract

Following decades of atmospheric acidification, the Bohemian Forest watercourses are now witnessing a remarkable resurgence of natural fish communities. This study presents the most comprehensive ichthyological survey of the region to date, covering 168 watercourse sites across the Czech and Bavarian parts of the Bohemian Forest. Using standardized electrofishing methods, we assessed species composition, density, and the presence of young-of-the-year individuals in relation to environmental characteristics. Fish were detected at 165 sites, with brown trout (*Salmo trutta*) and bullhead (*Cottus gobio*) being the dominant species. The widespread occurrence of young-of-the-year individuals indicates successful natural reproduction. Multivariate analyses revealed that fish community structure was significantly influenced by altitude, watercourse morphology, and substrate composition. Species richness increased with watercourse size and habitat heterogeneity. Acidification-sensitive species were found even in high-altitude headwaters, suggesting substantial ecosystem recovery. The near absence of invasive species further supports the high ecological quality of these watercourses. The fish fauna of the Bohemian Forest nowadays reflects the natural recovery of aquatic ecosystems after decades of atmospheric acidification. This study highlights the importance of preserving natural processes in mountain freshwater ecosystems.

Keywords Brown trout · Electrofishing · Stream ecology · Environmental gradients · Freshwater biodiversity

Introduction

Fish communities are at the top of the aquatic food webs, integrating the ecological characteristics of the environment (Hoeinghaus et al. 2007), and individual species or ecological groups are therefore used as ecological indicators of water quality (Karr 1981). Fish communities can be classified by altitude, slope, geographic position, temperature regime, catchment, and watercourse size (Melcher et al. 2007). In addition to the presence of a particular species, the age group(s), especially the cohort of young-of-the-year (0+), should also be considered, as they indicate the natural reproduction and sustainability of the population of that species (Jurajda et al. 2010). Fish are a relatively long-lived, diverse group that respond to natural environmental parameters and anthropogenic stressors (Schmutz et al. 2007). Among the most important stressors currently are nutrient enrichment, habitat modification and the spread of non-native species (Reid et al. 2019). In the past, acidification

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was also a major pressure, most significant in the Northern Hemisphere in the second half of the last century (Haines 1981), leading locally to the disappearance of many aquatic organisms, including fish (Muniz 1990).

A low mountain range of the Bohemian Forest (Šumava in Czech, Böhmerwald respectively Bayerischer Wald in German) forms a natural border between Czechia and southeast Germany, with eight glacial lakes serving as significant ecological features. Beginning in the mid-twentieth century and peaking in the 1980 s, a massive influx of acidifying substances depleted the natural buffering capacity of these lakes, causing the pH drop to levels as low as 4 (Vrba et al. 2003). As a result, after leaching, toxic chemical compounds are formed, fish and other biota became extinct from all the lakes (Vrba et al. 2003) and surrounding headwater watercourses (Čihař and Švátora 1998). Recovery, however, has been slow and uneven, with some species taking decades to return, depending on site conditions and migratory abilities (Petruželová et al. 2023).

In the past, political restrictions on both sides of the border limited access to the area, especially after the construction of the Iron Curtain on the Czech side, which effectively halted many forms of development and disturbance. During this period, the Šumava protected landscape area was established in 1963, followed by the declaration of the Bavarian Forest National Park in 1970 and the Šumava National Park in 1991. This led to the preservation of natural processes, but also to limited data collection on the biological recovery of ecosystems from acidification.

Despite the political barriers, most limnological data for the Bohemian Forest are available from the eight glacial lakes (Vrba et al. 2003). For instance, while the two Arbersee lakes in the Bavarian Forest were artificially stocked with brook trout, the Rachelsee was left to develop naturally, with no fish present to date (pers. obs.). Due to a dam, natural repopulation in the Great Arbersee is not possible. On the Czech side, the brown trout has gradually recolonized the outflow stream of Lake Laka (Matěna et al. 2017) and successfully recolonized Lake Laka, where a stable population has been established (Blabolil et al. 2024b). However, due to the steep slopes and low water levels in the watercourses, the fish cannot naturally return to the other lakes, although brown trout and bullhead have been recorded in the outflow streams below the lakes (Blabolil et al. 2024a).

Historical records of fish distribution in the Czech side of the Bohemian Forest headwaters are available from Frič´s map (Frič 1988), which classified all upper reaches as belonging to the brown trout zone, followed downstream by grayling and barbel zones. Due to the low productivity of the headwaters, fisheries are limited to the downstream parts of the watercourses, where the number of stocked fish corresponds to the anglers' catches (Lyach 2021). In the post-acidification period, fish communities in the headwaters are therefore expected to consist primarily of native populations or migratory individuals and be shaped by natural environmental characteristics such as stream morphology, fragmentation, and substrate (Baldigo et al. 2019; Heard et al. 1997). Rheophilic fish communities are under significant anthropogenic pressure worldwide, and knowledge of their distribution and recovery abilities after long lasting acidification period is essential for conserving these fragile ecosystems (Grill et al. 2019).

The aim of the study was to conduct ichthyological monitoring across the Bohemian Forest in Czechia and Bavaria using a uniform method. Specifically, we sought to map the occurrence of fish species, determine the extent of occurrence of young-of-the-year fish, and assess how community indicators and individual species respond to key environmental characteristics. We hypothesized that the retreat of acidification would enable fish to recolonize the majority of watercourses in the Bohemian Forest (Blabolil et al. 2024a, b). We expected brown trout to be the dominant species due to its migratory abilities. Additionally, we anticipated that populations would not be significantly affected by invasive species due to difficult area accessibility for humans. Finally, we predicted that environmental characteristics would have a major influence on the distribution and density of different fish species across the area.

Material and methods

Study sites

Studied sites were located across the entire Bohemian Forest in Czechia and Bavaria, along the European divide between the Black Sea and North Sea basins. The area has low population density, mostly covered by spruce forest or locally pastures, and heavy industry is completely missing. Sampling was performed from September to October in the years 2023 and 2024. In total, 168 sites (124 in Czechia and 44 in Bavaria) were sampled (Fig. 1, Online resource: Table A1). The Bohemian Forest region shares similar conditions at both countries (Table 1). The range of altitudes was 440–1182 with an average of 749.4 m above sea level. Most sites lie on small streams with Strahler (1957) classification 1 to 7 (mean 3), depth 3–60 cm (mean 28 cm) and width 0.5–30 m (mean 4.3 m). The watercourses are situated in the mountain to foothill regions, characterized by fast water flow and the bottoms mostly covered with stones, gravel, rocks and possibly other substrates (Online resource: Table A1).

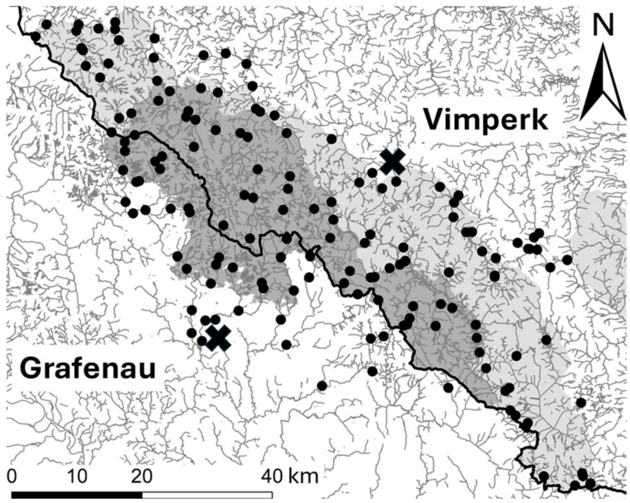

Fig. 1 Map of the Czech (above diagonal bold line = state border) and Bavarian (below diagonal) studied sites (black circles) within the Šumava and Bavarian national parks (dark grey), protected landscape area (light grey in Czechia), and in areas without specific protection. The administrative centres of both national parks are marked by crosses

Table 1 Environmental characteristics of studied sites in Bavaria and Czechia

Characteristics	Bavaria	Czechia
Altitude m a. s. l	725 (440–1143)	755 (476–1182)
Stream order (Strahler)	2 (1–3)	3 (1–7)
Average depth (cm)	30 (10–60)	27 (3–60)
Average width (m)	3.9 (0.5–10)	4.5 (0.5–30)
pH	7.0 (5.9–7.8)	7.1 (6.0–7.6)
Current (%)*	25 (18–35)	22 (10–38)
Rock (%)	25 (0–80)	12 (0–90)
Stones (%)	46 (0–90)	40 (0–96)
Gravel (%)	17 (0–65)	28 (0–95)
Sand (%)	11 (0–65)	16 (0–80)
Mud (%)	1 (0–15)	4 (0–100)

*Current was calculated as weighted average of relative contribution (%) of cascades (weight 4), rapids (weight 3), gentle watercourse (weight 2) and stagnant pool (weight 1) within each studied site

Environmental characteristics

At each sampling site, a representative 100 m long transect was selected, and contributions (%) to cascades, rapids, stagnant, and gentle watercourses were assessed relative to each transect. A weighted average with weights based on water flow rates (cascades evaluated as 4, rapids as 3, gentle watercourse as 2, and stagnant pool as 1) was calculated for each site as follows:

$$Current\,flow = (\%\ of\ cascades \times 4, \%\ of\ rapids \times 3, \%\ of\ gentle\ watercourse \times 2\ and\ \%\ of\ stagnant\ pool \times 1)/10$$

Within the same transect, the range of substrates classified to rock (> 25 cm), stones (6–25 cm), gravel (0.2–6 cm), sand (0.1–2 mm), and mud (< 0.1 mm) were evaluated and expressed as percentage cover (Table 1). Finally, pH was measured in situ using a multimetre (HI98494, Hanna Instruments, Woonsocket, RI, USA). The water pH was around neutral, as determined during the surveys.

Fish sampling and processing

Fish sampling was conducted by electrofishing (backpack motor-powered electric unit Hans-Grassl ELT60IIHI, 1.3 kW, 300/500 V, 25–100 Hz, Germany) by wading the watercourses. In watercourses ≤ 8 m width, continual sampling of the whole profile (all available habitats) was conducted. The length of a transect was 100 m, and its entire width was fished. Each transect was sampled twice consecutively, with captured fish being released after the second sampling. In wider watercourses, in a zigzag pattern along the transect to minimize disturbance and avoid startling the fish, point sampling was conducted. The transect for point sampling was 200 m long, with 200 points. One point represents an area of 1.5 m^2 (5 s current activation). All samplings were processed from the lower part towards the upstream.

Captured fish were kept in a spacious water container, processed separately for each sampling event, and released in accordance with the laws immediately after the second sampling at each site. All fish were identified to species and standard length measured (SL, 1 mm precision). Fish density per 1 ha of each watercourse was calculated in case of continuous electrofishing as $N = N_1^2 / (N_1 - N_2)$, where N_1 is number of fish of a species captured during first sampling and N_2 is number of fish of a species captured during second sampling (Zippin 1956). In case of point sampling the number of fish in a sampled area was recalculated per 1 ha. For evaluation of natural reproduction, based on the fish-size distribution (histogram of number of individuals in given lengths) fish were determined to 0 + and older.

Statistical analyses

Data from Czechia and Bavaria were combined in all analyses. Prior the statistical analyses, ichthyofaunal population density data were log(x + 1) transformed, and the relative cover of substrate were arcsine square root transformed to improve normality and homoscedasticity. For the community and species comparisons with environmental characteristics only samples with detection of fish were used.

The relationships between community characteristics (species richness, Simpson diversity index, total fish population density, density of Cottidae, Cyprinidae, Salmonidae) and environmental characteristics (altitude, watercourse order, mean depth, mean width, current flow, pH and relative cover of substrates: rock, stones, gravel, sand and mud) were evaluated by Spearman's rank correlation test in R software version 4.3.2 (R Development Core Team 2023). Potential redundant metrics ($\rho > 0.70$) were kept in the analyses as their ecological interpretation is different.

Multivariate analysis was performed in CANOCO 5 software (Šmilauer and Lepš 2014) to test whether fish communities were influenced by environmental characteristics using a redundancy analysis (RDA). The relationship between density of individual species and environmental characteristics was tested by Monte-Carlo permutation test with 9,999 permutations. Species density data were $\log(x + 1)$ transformed, response data centered and standardized by a norm.

Ethical statement

The animal handling within the project complied with the Czech Republic animal welfare laws, guidelines, and policies as approved by Ministry of Environment of the Czech Republic under number MZP/2023/630/2193. Fish sampling was approved by the Šumava National Park authorities (NSP07981/2023), Bavarian Wald National Park (BWP3656/2024), South Bohemian Territorial Association of the Czech Fishing Association (JCUS526/23), West Bohemian Territorial Association of the Czech Fishing Association (ZCUS233/23) and Bezirk Niederbayern Fachberatung für Fischerei (BN20.3.5).

Results

Species composition and presence of 0 + fish in the studied sites

Fish were detected at 165 of 168 sites. Two Czech and one Bavarian site was fishless, because they were located upstream of high (> 3 m) waterfalls ($N = 2$) and a muddy low-water watercourse ($N = 1$). In total, 11,836 fish of 15 species were captured. The dominant species was brown trout (all sites with fish, abundance 66.9% of all fish). The second most common was bullhead (126 sites, abundance 22.5%). The third most common was common minnow (23 sites, 5.1%). Other species were captured in < 10% sites, and their relative abundance was < 5% (i.e., < 300 individuals) (Table 2, Online resource: Table A1).

The occurrence of 0 + fish was detected for all species with the exception of rare common dace ($N = 2$ older than 0 +), gudgeon ($N = 3$), and stone moroko ($N = 1$). The relative contribution of 0 + fish was species dependent. The only captured rainbow trout was 0 +. The highest proportions were for northern pike (7 out of 8 specimens were 0 +), European perch (193/296), and grayling (24/47). The minor contribution of 0 + to older specimens was in roach with 3 0 + out of a total of 67 specimens (Table 2).

Community indicators

Strong correlations ($\rho > 0.70$) were observed between two community indicators: species richness with the Simpson diversity index and total ichthyofaunal population density with the density of Salmonidae (Table 3). Most environmental characteristics were significantly correlated with total fish density ($N = 8$). Fish density increased with altitude, and relative coverage of gravel, sand, and mud ($\rho = 0.18$ to 0.24) and decreased with watercourse order, mean depth, mean width, and relative coverage of rock ($\rho = -0.39$ to -0.19). Six characteristics were significantly correlated with species richness, a positive relationship was for watercourse order, mean width, and relative rock cover ($\rho = 0.16$ to 0.24), and a negative relationship for altitude, current flow, and relative sand cover ($\rho = -0.26$ to -0.23). The same number was correlated with Salmonidae density, with positive relationships for altitude and relative mud coverage ($\rho = 0.26$, 0.31) and negative relationships for watercourse order, mean depth, mean width, and relative rock coverage ($\rho = -0.48$ to -0.17). On the contrary, only two characteristics were significantly correlated with Cottidae density: a positive relationship was with current flow ($\rho = 0.17$) and a negative relationship with relative sand cover ($\rho = -0.17$).

Four explanatory characteristics (altitude, mean width, current flow, and relative sand coverage) were significantly correlated with four community indicators. None of the community indicators was significantly correlated with relative stone coverage. pH was significantly positively correlated only with Simpson diversity index ($\rho = 0.19$). Relative gravel coverage was significantly positively correlated only with total ichthyofaunal population density (Table 3).

Species responses

The RDA permutation test shows a significant response of the fish species on selected environmental characteristics (test on all axes pseudo-F = 2.4, df = 11, $p < 0.001$). The first axis explained 8.00% of the variation, and the second one 4.04%. Based on the ordination score, the first axis was mostly correlated with altitude gradient (Fig. 2). The strongest positive association with the axis had observed in brown trout, compared with the negative association in bullhead

Table 2 Occurrence and abundance of fish species detected in Bohemian Forest watercourses, with emphasis on young-of-the-year (0+) individuals

English name	Scientific name	Site-level occurrence (%)	0+site-level occurrence (%)	Relative abundance (%)	0+within species (%)
Brook trout	*Salvelinus fontinalis* Mitchill, 1814	7.14	4.17	0.74	38.64
Brown trout	*Salmo trutta* Linnaeus, 1758	98.21	92.86	66.89	36.71
Bullhead	*Cottus gobio* Linnaeus, 1758	75.00	60.12	22.45	34.32
Burbot	*Lota lota* Linnaeus, 1758	8.33	3.57	0.47	48.21
Chub	*Squalius cephalus* Linnaeus, 1758	3.57	2.38	0.51	50.00
Common dace	*Leuciscus leuciscus* Linnaeus, 1758	1.19	0	0.02	0
Common minnow	*Phoxinus phoxinus* Linnaeus, 1758	13.69	6.55	5.08	26.12
European perch	*Perca fluviatilis* Linnaeus, 1758	6.55	2.98	2.50	65.20
Grayling	*Thymallus thymallus* Linnaeus, 1758	4.17	1.79	0.40	51.06
Gudgeon	*Gobio gobio* Linnaeus, 1758	1.79	0	0.03	0
Northern pike	*Esox lucius* Linnaeus, 1758	2.38	2.38	0.07	87.50
Rainbow trout	*Oncorhynchus mykiss* Walbaum, 1792	0.60	0.60	0.01	100
Roach	*Rutilus rutilus* Linnaeus, 1758	4.17	1.19	0.57	4.48
Stone loach	*Barbatula barbatula* Linnaeus, 1758	6.55	2.38	0.27	21.88
Stone moroko	*Pseudorasbora parva* Temminck & Schlegel, 1846	0.60	0	0.01	0

Explanations: Shown are the English and scientific names of recorded species, species occurrence across sites (%), 0+occurrence across sites (%), relative species abundance (%), and proportion of 0+within each species (%)

and the negative trends in brook trout and chub. The second axis demonstrated an increase of watercourse area with the main predictor, mean watercourse width, with positively associated watercourse order, mean depth, and relative coverage of sand. The opposite trend in direction to watercourse reduction was mostly connected with an increase in relative rock coverage and current flow. Species with increasing density in wider watercourses were northern pike, grayling, common dace, roach, European perch, burbot, and common minnow.

Discussion

Fish distribution in the Bohemian Forest

The study analysed a robust data set covering practically important watercourses in the Bohemian Forest. Sampling was consistent in method and effort over two consecutive years. The results confirmed the natural recovery of the ecosystem from acidification and all-over distribution of fish throughout the Bohemian Forest. The recovery of the headwater watercourses lasted almost 40 years. Besides acidification itself, the recovery process was further delayed by recent bark beetle outbreaks, which caused forest disturbance, release of acidic compounds, and temporary re-acidification (Blabolil et al. 2024b; Kopáček et al. 2023).

Due to the non-intervention regime and overall isolation of many sites in the Bohemian Forest, ichthyological studies from this area have been rare. Earlier surveys by Čihař and Švátora (1998) reported no fish above 1000 m a.s.l. (i.e., in Luzenský, Březnický or Modravský streams), confirming that these headwaters were not suitable for fish occurrence during strong acidification in the 1970s. More recently, Slavík et al. (2018) captured and monitored brown trout in these same streams, illustrating ongoing recolonization. The process was significantly supported by the restoration of the river continuum in the past three decades, especially on the Bavarian side. Fish were found in all suitable environments accessible for natural migration. Sensitive species have returned to all watercourses and reproduce naturally, confirming that suitable habitat and water chemistry have been restored.

This study, therefore, provides a unique dataset for Central Europe, showing that fish communities have spontaneously recovered from acidification. The results also emphasize the importance of maintaining or restoring longitudinal connectivity for fish migration and protecting headwater habitats, which serve as critical spawning and nursery areas.

Species diversity

Species diversity was relatively low, as is typical for north-flowing rivers, where the ice ages strongly influenced river

Table 3 Spearman's rank correlation tests between fish community indicators (species richness, diversity, standardised densities of all species, Cottidae, Cyprinidae, and Salmonidae) and environmental characteristics. Correlation coefficients are shown above the diagonal, and *p*-values below

	Species richness	Simpson diversity index	All	Cottidae	Cyprinidae	Salmonidae	Altitude	Stream order	Mean depth	Mean width	Current	pH	Rock	Stones	Gravel	Sand	Mud
Species richness	x	0.75	0.20	0.53	0.65	−0.14	−0.23	0.18	0.10	0.24	−0.26	0.15	−0.23	0.00	0.10	0.16	0.07
Simpson diversity index	< 0.001	x	0.13	0.68	0.36	−0.23	−0.24	0.08	−0.02	0.14	−0.20	0.19	−0.13	−0.05	0.06	0.25	0.06
All	0.010	0.094	x	0.55	0.13	0.78	0.24	−0.26	−0.19	−0.39	−0.14	−0.05	−0.27	−0.09	0.19	0.18	0.22
Cottidae	< 0.001	< 0.001	< 0.001	x	0.03	0.13	−0.13	−0.08	−0.13	−0.08	−0.17	0.10	−0.12	−0.04	0.11	0.17	0.08
Cyprinidae	< 0.001	< 0.001	0.086	0.725	x	0.00	0.01	0.15	0.13	0.17	−0.18	0.02	−0.18	−0.01	−0.01	0.13	0.12
Salmonidae	0.072	0.003	< 0.001	0.097	0.949	x	0.31	−0.32	−0.17	−0.48	−0.08	−0.12	−0.25	−0.05	0.14	0.15	0.26
Altitude	0.003	0.002	0.002	0.107	0.887	< 0.001	x	−0.16	−0.25	−0.28	0.19	−0.14	0.02	0.10	−0.07	0.11	0.02
Stream order	0.019	0.329	0.001	0.290	0.051	< 0.001	0.040	x	0.35	0.58	−0.16	−0.07	−0.01	0.05	0.01	0.06	−0.13
Mean depth	0.180	0.764	0.015	0.095	0.086	0.032	0.001	< 0.001	x	0.50	−0.40	−0.10	−0.04	−0.16	0.16	0.09	0.06
Mean width	0.002	0.077	< 0.001	0.322	0.027	< 0.001	< 0.001	< 0.001	< 0.001	x	0.11	−0.02	0.24	0.13	−0.15	0.03	−0.29
Current	0.001	0.009	0.066	0.027	0.024	0.302	0.013	0.036	< 0.001	0.161	x	−0.01	0.53	0.27	−0.43	−0.21	−0.27
pH	0.057	0.014	0.550	0.189	0.832	0.132	0.066	0.354	0.184	0.819	0.897	x	0.05	−0.09	0.01	0.03	0.03
Rock	0.002	0.108	< 0.001	0.135	0.018	0.001	0.841	0.911	0.655	0.002	< 0.001	0.493	x	0.09	−0.47	−0.38	−0.36
Stones	0.998	0.535	0.227	0.600	0.927	0.508	0.202	0.518	0.041	0.102	< 0.001	0.271	0.230	x	−0.47	−0.31	−0.24
Gravel	0.204	0.452	0.013	0.158	0.903	0.065	0.387	0.852	0.041	0.058	< 0.001	0.880	< 0.001	< 0.001	x	0.21	0.09
Sand	0.040	0.001	0.018	0.029	0.086	0.062	0.167	0.434	0.262	0.691	0.006	0.668	< 0.001	< 0.001	0.008	x	0.22
Mud	0.406	0.419	0.005	0.329	0.119	0.001	0.809	0.109	0.437	< 0.001	< 0.001	0.668	< 0.001	0.002	0.248	0.005	x

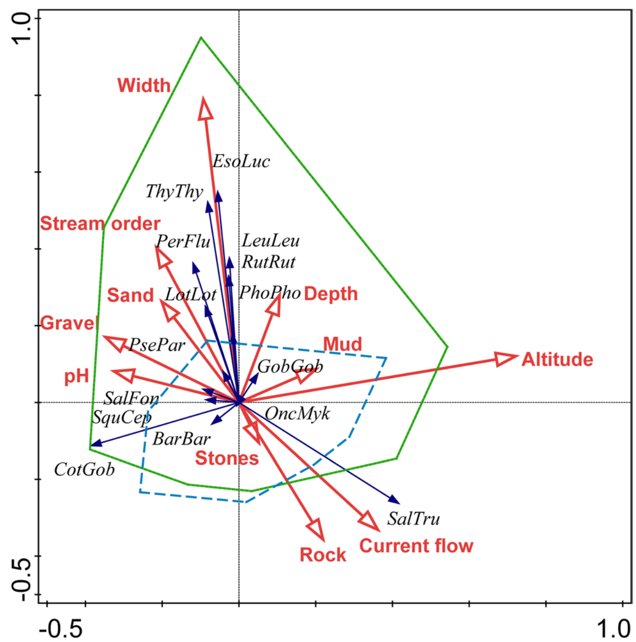

Fig. 2 Redundancy analysis (RDA) biplot of fish species detected in Bohemian Forest watercourses, showing correlations with environmental characteristics (first and second axes). The green solid polygon represents Czech sites, and the blue dashed polygon represents Bavarian sites. Species abbreviations are created from the first three letters of genus and species names according to the scientific name (see Table 2)

basins and migratory species recolonized only after warming (Griffiths 2006). In addition, the low diversity of standing waters in Central Europe, often centres of endemism (Schluter 1996) contributes to this pattern. Species richness was similar in the Elbe and Danube basins, and no species were found exclusively associated with the Danube. This probably reflects the high altitude that the Danube fish cannot reach, and comparable environmental conditions in both basins. Alternatively, the uniform communities may be due to a similar history of management, including logging, modification of watercourses for timber floating, and certainly exploitation of water resources, including fish (Vašíčková et al. 2024).

The dominant species in the area was the brown trout. Its prevalence is not surprising, as most watercourses flow through well-oxygenated trout zones. Brown trout characteristically migrate in smaller streams to breed, and smaller individuals occupy these sections for a longer period (Aarestrup et al. 2017; Simonović et al. 2020). In numerous sites, we found both adults and 0 + individuals, confirming successful reproduction and survival of young fish during the first growing season. In both national parks, natural processes are respected, and no stocking took place for decades. In larger watercourses outside the parks, anglers introduce catchable-size trout (~ 250 mm SL) in spring. Most are later caught, drift downstream, or may be eaten by piscivores (Šlapanský et al. 2024). Depending on the existing community and environment, some of the introduced fish may survive and mix with native populations (Hansen 2002).

Bullhead was the second-most-common species. Unlike trout, the small-bodied bullhead is not a commercially important species, and there have been no introductions, and none are likely to have occurred in the past. This is one of the reasons why the species is often used as an ecological indicator and is listed as Near Threatened on the Czech Red List (Lusk et al. 2017). The Šumava mountains (the Czech side of the Bohemian Forest) were declared as a site of European importance for the protection of, among others, the bullhead (NATURA 2000, No. CZ0314024). The migratory abilities of the bullhead are very limited; it has no gas bladder, is typically associated with the bottom, and a barrier of only 20 cm is reported as an insurmountable barrier (Utzinger et al. 1998). Bullhead is dependent on high oxygen concentration, cannot tolerate low pH, and requires a substrate with shelters (Davey et al. 2005; Kłosiński et al. 2025; McCahon and Pascoe 1989). The correlation matrix showed a positive relationship with current flow and a negative relationship with the relative abundance of sandy substrate cover. Bullhead were detected at most sites, indicating a "healthy" environment of most watercourses in the Bohemian Forest. The fact that no bullhead was recorded at some sites was rather due to the unsuitability of the site conditions (too high altitude, unsuitable sediment, insurmountable obstacles) than water chemistry. As a lithophilic species, the bullhead needs shelters under rocks and the presence of rocks to breed, so this may play a role in its distribution. The results of this study confirmed the more abundant occurrence of bullhead at lower altitudes, where there is a lower slope of watercourses and a higher diversity of bottom substrates where bullhead find shelter and food.

The common minnow was also relatively abundant. Its occurrence is linked to the specific habitat of downstream watercourses with deeper pools alternating with shallow alluvial deposits and shelter opportunities. Populations of this species are declining in Czechia and Bavaria, and it is therefore listed as vulnerable on the Red Lists. There are few watercourses with naturally wider floodplains in the Bohemian Forest, especially in the Blanice basin. Suitable habitat is now emerging in areas where the European beaver (*Castor fiber* Linnaeus, 1758), which has been spreading across the Bohemian Forest in recent decades, has settled (Vorel et al. 2014). Of course, the common minnow has to be present in the basin to take advantage of beaver pools in establishing local abundant population (Hägglund and Sjöberg 1999).

Other important indicator species were the grayling (a vulnerable species on the Czech Red List and endangered in the German Red List) and the burbot (a near-threatened species on the Czech Red List and endangered in the German

Red List). Both species are supported by local introductions into larger, downstream watercourses in the Šumava National Park and into fishing grounds. Stocking of the 0 + category takes place in late spring and summer. The relatively higher density of 0 + may thus be an artefact of stocking management, and the capture of older individuals may in turn be evidence of fish survival (Avramović et al. 2024). Thus, the species find suitable living conditions in the Bohemian Forest watercourses and, if abundant enough, they can establish stable populations.

Community structure and environmental drivers

During the summer season, brown trout are territorial and undertake upstream spawning migrations in autumn (Héland 1999). Sampling was performed in autumn when changes in solar radiation, flow and water temperature stimulate brown trout for spawning migration (García-Vega et al. 2017), and a positive relationship was found between the characteristics of the spawning grounds (faster-flowing rocky/stone substrate) and trout density. Thus, catches captured both migrating adults and 0 + individuals that likely hatched and persisted here since the spring or were flushed from even higher elevations. The observed standardized density appears to be higher than during the summer season.

Reproduction of most species was successful, indicating suitable habitats throughout the system. Only the very rarely captured common dace, gudgeon, and stone moroko lacked 0 + individuals. In common dace and gudgeon, the 0 + are very small and may have been overlooked in the watercourse or were in different parts of the watercourse than the sampled. In the case of stone moroko, it was likely an individual flushed from a pond in the catchment. Suitable habitats for stone moroko are standing water or slow-moving watercourses (Adámek et al. 2024). It is an invasive species that tend spreading both upstream and downstream (Gozlan et al. 2010). Recording even one individual is important information for the nature protection agency to identify its occurrence in a catchment and reduce the potential for invasion. The almost absolute absence of invasive fish in Bohemian Forest watercourses, however, is further evidence of a healthy environment with good ecological potential shortly after recovery from acidification (Ritterbusch et al. 2022).

Of the other non-native species, the most frequently detected was the brook trout. The stocking of the brook trout has a tradition of more than 100 years in the Bohemian Forest. The first documented introductions occurred in 1890 in Černé Lake, where they established a stable population (Frič and Vávra 1897). Nowadays, brook trout are not stocked into open waters but are kept in hatcheries or as live food for brown trout or for market (e.g., Annín, Borová Lada, Dobišův Mlýn, Lindbergmühle), from where they can escape at higher flows. Brook trout compete with brown trout for food and space, and in good conditions, the brown trout will displace the brook trout, but if conditions deteriorate (e.g., decrease of pH or oxygen concentration, hydromorphological deficits), the more resistant brook trout will outcompete the brown trout (Fausch and White 1981; Lovén Wallerius et al. 2022). In addition, interbreeding and interspecific hybrids can occur in nature (Cucherousset et al. 2008). Given the clear dominance of brown trout over brook trout in the Bohemian Forest watercourses, it cannot be assumed that, under the conditions suitable for brown trout life and reproduction, brook trout would pose any significant threat to the stable brown trout population.

In Czechia, fishermen in the spring introduce non-native rainbow trout of catchable size (~ 250 mm SL) into larger watercourses. These fish are reared for long periods in sets and fed pellets, and typically remain in watercourses for only a short time before being caught by anglers (or piscivorous predators) or drifting downstream (Lyach 2023). Rainbow trout have been commercially reared for a long time, and several breeds can be bred at different times of the year. Reproduction in hatcheries is entirely artificial, and natural reproduction has been observed rarely (Stanković et al. 2015). The only one 0 + individual found was caught under the fishponds in Volary, likely having escaped from them.

Brown trout strongly influenced overall fish density patterns. Their abundance was highest at higher elevations with coarse substrates suitable for spawning and lowest in larger, deeper, and wider watercourses. Headwaters, which depend on allochthonous production, provide ideal habitat for trout and other insectivores (Dekar et al. 2012), while lower reaches support a greater diversity of feeding traits (Wang et al. 2019).

Species diversity decreased with elevation and current flow and increased with watercourse size and width. This is not surprising because in larger watercourses there are more habitats on which different species or life stages can specialise (Tracy et al. 2022), and environmental heterogeneity is a key to high species diversity (Allouche et al. 2012). Lower reaches can host a variety of habitats in terms of alternating depths, flow paths, associated bottom substrates, and shelters (roots, wood in the water, rocks). Higher nutrient availability and stable water flow in the lower reaches, as well as flushing of fish from higher standing water, can also play a role. Multiple reproductive strategies, not only lithophilic or psamophilic but also phytophilic species, can apply in lower reaches and larger watercourses, and lower reaches are also fishing grounds, where fishermen stock commercially important species. Finally, larger watersheds can host more food sources and have greater capacity to dilute negative effects (e.g., low pH). Multivariate analysis demonstrates trends in the dependence of fish on individual environmental factors. Important factors are geographical features, morphology and bottom substrate. Species with specific ecological requirements, especially larger watercourse size and associated environmental diversity, are northern pike, grayling, ide, European perch, roach, common minnow, and burbot. No specific relationships were found for other species, so their occurrence could appear to be coincidental or significant factors for these species were not documented in this study. These were invariably relatively low abundance species.

The ordination polygons of Czech and Bavarian sites overlapped in their centre, indicating similar environmental conditions (smaller mountain watercourses). The Czech polygon significantly extended along the gradient of watercourse size. On the Czech side of the Bohemian Forest, we sampled larger watercourses, such as the Vltava River, which flow through the alluvial plain. In Bavaria, watercourses flow rapidly down steeper slopes and almost individually head into the Danube (Janík and Romportl 2017).

Synthesis and conservation implications

This study provided the most detailed ichthyological monitoring of the Bohemian Forest at the border area of Czechia and southeast Germany watercourses to date, documenting the current distribution of fish on both the Czech and Bavarian sides. These high-altitude systems, severely affected by atmospheric acidification, now host self-sustaining populations of brown trout and bullhead, with natural reproduction confirmed for most species. Less abundant species like grayling, northern pike, European perch, and roach occupy especially deeper, wider, sandier reaches, corresponding to Frič (1988) ichthyological zonation.

The widespread recovery of native fish communities represents a successful case of natural ecosystem restoration without major human intervention. Future research should focus on the genetic structure of brown trout populations to assess local adaptation and legacy effects of past acidification. Long-term monitoring will be essential to detect emerging threats, such as climate change or renewed anthropogenic pressures, and to guide adaptive conservation strategies aimed at preserving these ecologically valuable mountain streams.

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Data availability Data will be made available on request.

Declarations

Competing interest The authors declare no competing interests.

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