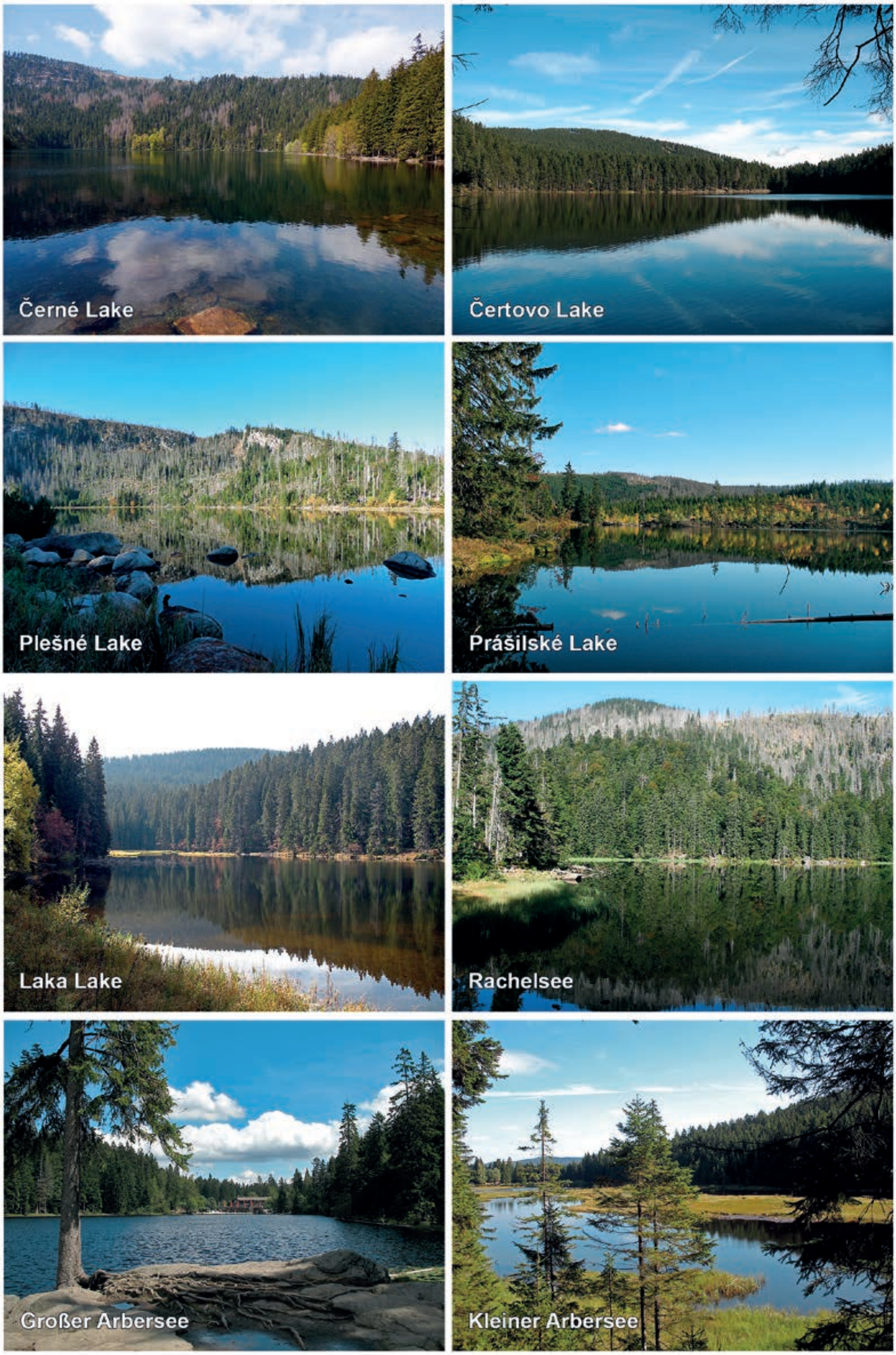
Brief history of long-term ecological research into aquatic ecosystems and their catchments in the Czech Republic

Part II: Glacial lakes



Černé Lake

Čertovo Lake

Plešné Lake

Prášilské Lake

Laka Lake

Rachelsee

Großer Arbersee

Kleiner Arbersee

Bohemian Forest lakes (2006–2014). Photos by Jiří Kopáček.

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Part II: Glacial lakes

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Long-term ecological research in the Czech Republic

Long-term ecological research provides valuable insights that can be obtained from other approaches only with difficulty. It facilitates testing of general ecological principles, which are essential for understanding the amazing complexity of ecosystems, and allows for prediction of future changes of the environment. The Czech long-term ecological research (LTER) network emerged during the early 1990s, following an initiative of US LTER scientists. The Czech LTER network coordinates efforts involving many scientists investigating ecological processes over long temporal and broad spatial scales. It was formally established from six UNESCO Biosphere Reserves and two reservoir sites in 1996, and has gradually evolved into the current network, which consists of more than twenty LTER sites covering various temperate forests, grasslands, wetlands, and freshwaters in the Czech Republic (**Fig. 1**). Long-term data series have indicated changes in land use, eutrophication, atmospheric sulphur and nitrogen deposition, and in climate. In addition, the Czech LTER network also includes a post-mining area to study soil formation and early succession, and an exterritorial LTER site of tropical rain forest at Papua-New Guinea. Here we present major findings of long-term ecological research into glacial lakes in the Bohemian Forest, the only natural lakes in the Czech Republic.

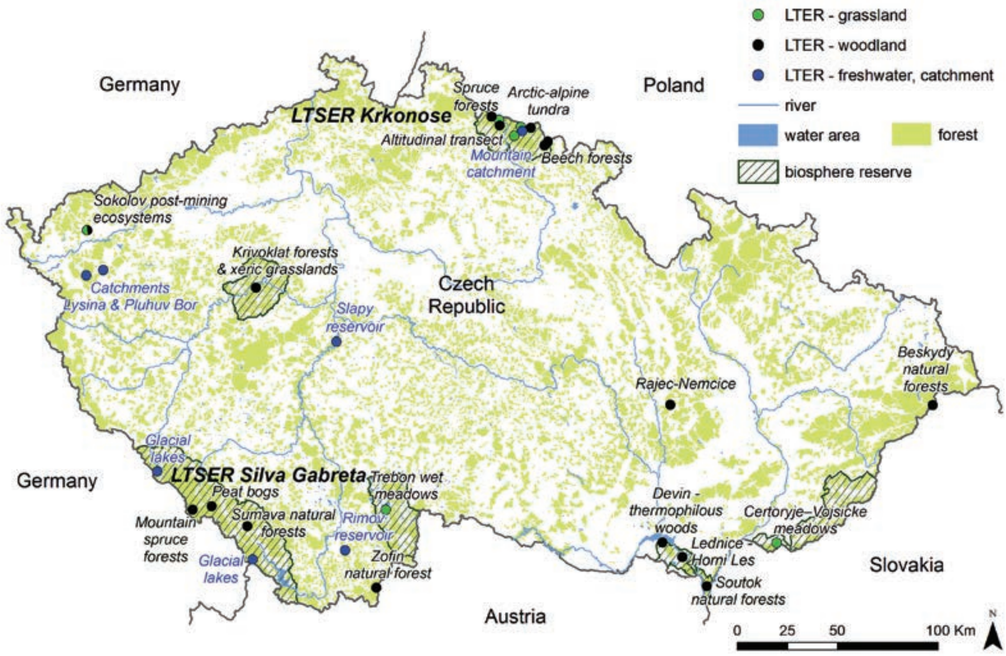

Fig. 1: Map of all sites included in the Czech LTER network (except for Wanang, Papua-New Guinea).

Basic characteristics of glacial lakes in the Bohemian Forest

There are eight lakes of glacial origin in the Bohemian Forest (Šumava in Czech, Böhmerwald in German; **Fig. 2**). Five of them (Černé, Čertovo, Plešné, Prášilské, and Laka) are in the Czech Republic and three others (Rachelsee, Großer Arbersee, and Kleiner Arbersee) are in Germany. Their bedrock is formed from metamorphic and crystalline rocks, sensitive to atmospheric acidification (**Table 1**). Thus, all the lakes became acidic in the last century (Vrba et al. 2003a, Kopáček et al. 2002a) and have a depleted carbonate buffering system or low acid-neutralising capacity at present (Nedbalová et al. 2006, Vrba et al. 2016).

Mean monthly air temperatures varied between −12.9 and 17.7°C in the Čertovo catchment at an elevation of 1057 m in the 1781–2012 period, with long-term averages between −3.5°C in January and 13.9°C in July (Turek et al. 2014). Annual precipitation in a treeless area averaged ~1300 mm in the Čertovo catchment at an elevation of 1180 m from 1992–2012 (Hruška et al. 2000, Kopáček et al. 2013b). The lakes are usually frozen for 4–5 months, from December to April.

Catchments of the Bohemian Forest lakes are steep (with maximum local

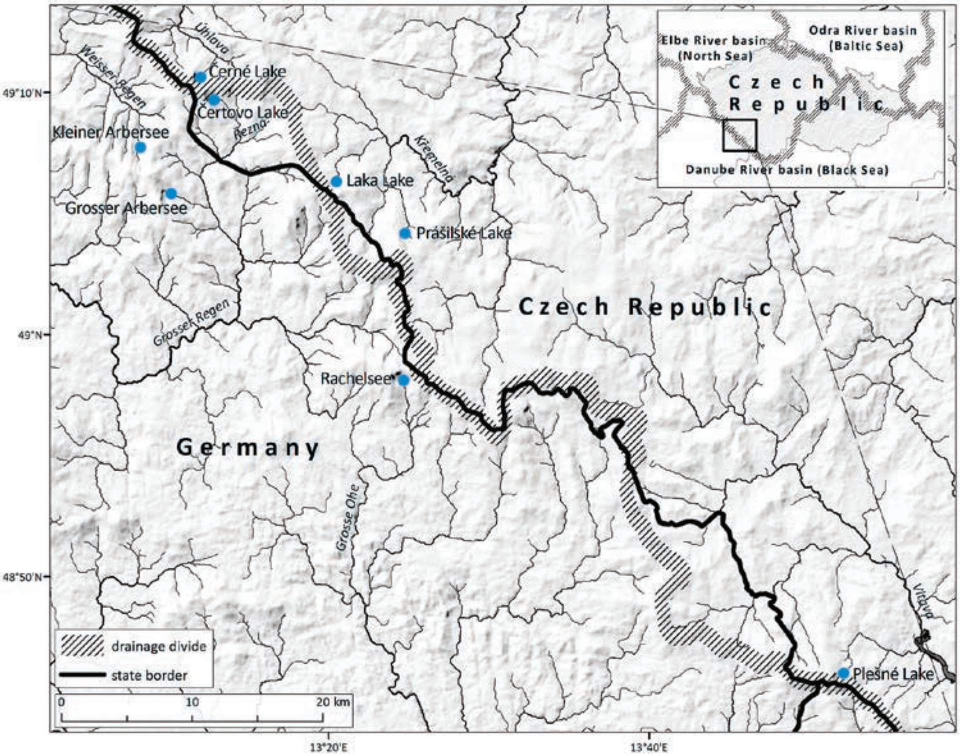

Fig. 2: Map of the LTER site Glacial Lakes showing their location in the Bohemian Forest.

Table 1. Basic characteristics of the Bohemian Forest lakes and their catchments.

Lake	Latitude (°N)	Longitude (°E)	Elevation (m)	Maximum depth (m)	Area (ha)	Volume ($10^6 m^3$)	Catchment area (ha)	Maximum elevation (m)	Dominant bedrock	Dominant forest [a]
Černé	49.183	13.183	1008	40	18.8	2.92	124	1343	mica schist, quartzite	spruce
Čertovo [b]	49.167	13.200	1027	35	10.7	1.86	89	1343	mica schist, quartzite	spruce
Plešné [b]	48.783	13.867	1087	18	7.2	0.55	67	1378	granite	spruce
Prášilské	49.067	13.400	1079	17	4.2	0.35	65	1314	mica schist, granite	spruce
Laka	49.117	13.333	1085	3.5	2.3	0.05	135	1336	gneiss	spruce
Rachelsee [c]	48.967	13.400	1071	13	4.8	0.25	58	1345	gneiss	spruce
Großer Arbersee [c]	49.100	13.150	935	17	7.9	0.49	258	1314	gneiss	spruce, beech
Kleiner Arbersee [c]	49.133	13.117	917	10	7.4	0.26	279	1260	gneiss	spruce, beech

[a] Norway spruce, with admixed European beech, white fir, or rowan
[b] LTER includes whole-catchment processes
[c] German lakes have also been included in LTER of all Bohemian Forest lakes

reliefs of 235–380 m) and covered with thin, acid lithosol, podzol, and cambisol (Kopáček et al. 2002b,c). Vegetation covers most of the catchment areas and is dominated by coniferous forests (**Table 1**). After World War II, access and most kinds of land use were restricted in most of the Czech part of the Bohemian Forest, which was behind the 'Iron Curtain', due to a rigid border control during the Cold War. The military zone was abolished in 1989, and since that time the area has become more accessible for scientific research. Most of the lakes belong to the core zone of the Šumava National Park and the Bavarian Forest National Park, declared in 1991 and 1970, respectively. Thus, free access or land use activities (like forestry) remain limited in the lake catchments, both in the Czech and German parts of the Bohemian Forest. Since the 1990s a large area of the Bavarian Forest and Šumava National Parks has been affected by bark beetle infestation and Norway spruce stands have been severely disturbed in some catchments (**Fig. 3**, Kopáček et al. 2009a, 2013c, Oulehle et al. 2013, Vrba et al. 2014).

Fig. 3: Forest dieback due to bark beetle infestation.

Over the last three decades the Bohemian Forest lakes have become a part of integrated studies on European lake ecosystems; they have been included in the International Cooperative Programme on Assessment and Monitoring of Acidification of Rivers and Lakes (ICP Waters) and established as an LTER site (see Glacial lakes in **Fig. 1**). The LTER has been coordinated by the Institute of Hydrobiology (BC CAS), working closely with the Czech Geological Survey and Charles University in Prague, University of South Bohemia in České Budějovice, and Masaryk University in Brno.

Overview of long-term ecological research into the lakes

Glacial lakes in the Bohemian Forest (**Figs. 4**) have attracted explorers for more than a century. Early hydrobiological research, starting more than 140 years ago (Frič 1872, 1874), sporadic research before the 1980s, and a few palaeolimnological studies provided a valuable background for long-term ecological research into the Bohemian Forest lake ecosystems (for review, see Vrba et al. 2000, 2003a, Kopáček and Vrba 2006, Soldán et al. 2012). Long-term data cover the natural (pre-acidification) status of the lakes, the period of their strong atmospheric acidification, which caused adverse impacts on lake water chemistry and aquatic communities, and a successive period of lake recovery from acidic stress (Vrba et al. 2003a).

Fig. 4: Aerial view of partly deforested southern slopes of Jezerní Hora Mt. with Černé (on the left) and Čertovo (on the right) lakes, 2015.

Atmospheric acidification of geologically sensitive areas has represented the most adverse anthropogenic impact on both aquatic and terrestrial headwater ecosystems in unmanaged regions since the mid-twentieth century. Increasing concentrations of sulphate, nitrate, and hydrogen ions in soil solutions due to long-range transport of acidic pollutants reduced acid-neutralizing capacity, depleted base cations in the soil, and mobilized ionic aluminium species (for review, see Norton et al. 2014). The elevated concentrations of ionic aluminium affected cycling and mobility of phosphorus (an important nutrient) in lakes (Kopáček et al. 2000, 2001a), while its toxicity degraded the health of forest and aquatic ecosystems, resulting in a deleterious reduction of freshwater biodiversity (Vrba et al. 2003a). Deposition of acidifying pollutants has substantially declined in Europe and North America after reductions in sulphur and nitrogen emissions since the late 1980s. While this abatement of atmospheric pollution caused significant changes in lake water composition and a partial recovery of their chemistry from acidification, their biological recovery remains remarkably delayed or even uncertain (Vrba et al. 2016).

Figure 5: Sampling at Prášilské Lake. Photo by Jana Hrdličková.

The regular monitoring of the Bohemian Forest lakes (**Fig. 5**) was initiated in 1984 and showed that the Bohemian Forest lake district was among the most acidified of European ecosystems. The original research focused on the development of lake water acidification (and/or recovery), and the increasing significance of nitrate in this process (Fott et al. 1987, Veselý et al. 1998a,b, Vrba et al. 2003a). The long-term monitoring provided the first step for the following integrated research into the Bohemian Forest lakes and enabled their acidification history to be reconstructed (Majer et al. 2003, Oulehle et al. 2012). It also helped disentangle effects of acidification and climate change on aluminium and of silica export from terrestrial to aquatic ecosystems (Veselý et al. 2003, 2005). Since the late 1990s, scientific interest in the Bohemian Forest lakes has expanded to include biogeochemical processes in their catchments (effects of soils and vegetation on water chemistry), chemistry of atmospheric deposition, hydrology and climate. The ongoing research thus provides a solid (and necessary) base for the systematic ecological research into the entire catchment–lake system (for review, see Kopáček and Vrba, 2006). Our recent review (Vrba et al. 2015) summarised the progress till now of this integrated research into the Bohemian Forest lakes and their catchments based on fourteen projects conducted during the past two decades. The major findings are presented in the next chapters.

Water chemistry, acidification and recovery of the lakes

The Bohemian Forest was exposed to heavy atmospheric pollution during the last century due to high central European anthropogenic emissions of sulphur (S) and nitrogen (N). Since the middle 1980s, emissions of S, N oxides, and ammonium in central Europe have declined by 93, 72, and 53 percent, respectively (Kopáček et al. 2016). Deposition of S and N compounds in the Bohemian Forest reflected their emission rates (Kopáček et al. 1998, 2001b). Deposition was relatively stable in the first half of the 20th century, rapidly increased between 1950 and 1980, and peaked in the early 1980s (**Fig. 6**).

During the 1990s, acid deposition decreased substantially, and its current level is similar to the late 19th century levels of sulphate and ammonium deposition, and to the mid-1960s levels of nitrate deposition (Kopáček et al. 2009b, 2011b). These changes in acidic deposition have led to a more significant recovery in the Bohemian Forest freshwaters compared to other European lake districts.

Lake water acidification of the Bohemian Forest lakes peaked in the mid-1980s and has been reversing ever since. From the 1980s to the late 1990s, the average sulphate and nitrate concentrations in the eight Bohemian Forest lakes decreased by 19 and 15 µmol l^{-1}, respectively (Kopáček et al. 2002c). The Bohemian Forest was the first lake district to exhibit a consistent decrease in nitrate concentrations (Veselý et al. 1998a). The decline in concentration of strong acid anions

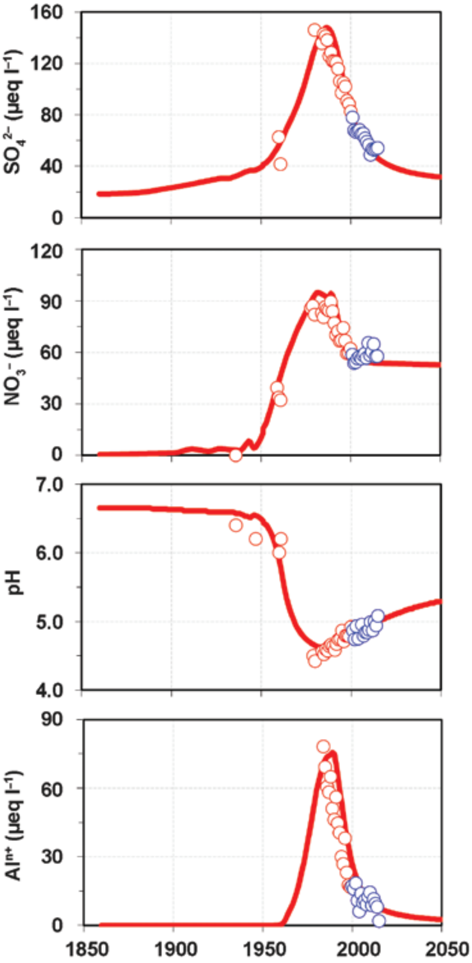

Fig. 6: Measured (open circles) and modelled (lines) trends in water chemistry of Černé Lake. The model (MAGIC 7) was calibrated on long-term data prior to year 2001 (red circles). Blue circles represent data measured in 2001–2010, which are in reasonable agreement with those predicted by the model. Except for pH, units are microequivalents (µeq l^{-1}; one equivalent is one mole of charge).

Figure 7: Anthropogenic emissions of sulphur and nitrogen caused acid rain, which decreased lake water pH. Photo by Martina Čtvrtlíková.

was compensated for by a fall in concentrations of aluminium, protons, and base cations (Kopáček et al. 2002a). The trend in lake water recovery from acidification is continuing, though more slowly than during the 1990s (Majer et al. 2003). The forest dieback due to bark beetle infestation delayed (and even temporally reversed) recovery of water chemistry in some lakes, particularly in Rachelsee and Plešné lakes (Kopáček et al. 2013a, Oulehle et al. 2013, Vrba et al. 2014).

The acidification history of the Bohemian Forest lakes is best documented for Černé Lake, the largest and deepest lake in the Bohemian Forest. The first reliable data on lake water chemistry, e.g. neutral pH (>6) and traces of nitrate (<2 µmol l^{-1}), come from 1936, while the first reliable sulphate data (20–30 µmol l^{-1}) come from the early 1960s (Procházková and Blažka 1999). This survey already indicated the first effects of atmospheric acidification (**Fig. 7**) on the lake water composition, predominantly lowered pH (5.4–6.2) and increased nitrate concentrations (30–40 µmol l^{-1}) compared to the 1930s. The lake water pH decreased to ~4.5 in the late 1970s, and acidification progressed until 1986–1988, when nitrate and sulphate concentrations reached their maxima of 80–100 and 67–76 µmol l^{-1}, respectively (Veselý et al. 1998a). Reversal of lake water chemistry has occurred since the late 1980s due to the reduction in S and N emissions and decreasing acidic deposition. Long-term trends in water chemistry have been successfully reconstructed by a dynamic, process-based model, MAGIC 7. The model was calibrated for a set of records on lake water composition over the 1984–2001 period and produced hindcast concentrations that corresponded well to even older irregular determinations of nitrate, sulphate, and pH (Majer et al. 2003). Modelled sulphate concentrations were predicted to decrease by 2050 to the levels found at the beginning of the 20th century (**Fig. 6**). Similar steep changes in water chemistry also occurred in Plešné and Čertovo lakes (Majer et al. 2003).

Rapid changes in lake water chemistry, accompanied by steep trends in pH and concentrations of total and ionic aluminium forms (**Fig. 6**), enabled studies on effects of water acidification on in-lake nutrient cycling. In contrast to the well-known nutrient transformations in circumneutral lakes, the acidified Bohemian Forest lakes are rich in aluminium, which can precipitate as colloidal aluminium hydroxide after an increase in water pH by in-lake microbial processes. Aluminium hydroxide has a large surface area and can strongly bind phosphorus (P) from the liquid to the particulate phase, immobilise orthophosphate in the water column, and prevent its release from sediments (Kopáček et al. 2000, 2004).

Historical biodiversity of the Bohemian Forest lakes

Zooplankton were the first component of aquatic biota documented in historical records. The pioneering survey of crustacean zooplankton in all Bohemian Forest lakes was performed in the end of 19th century by Frič (1872, 1874) and has been considered as representative of the pre-acidification status. The

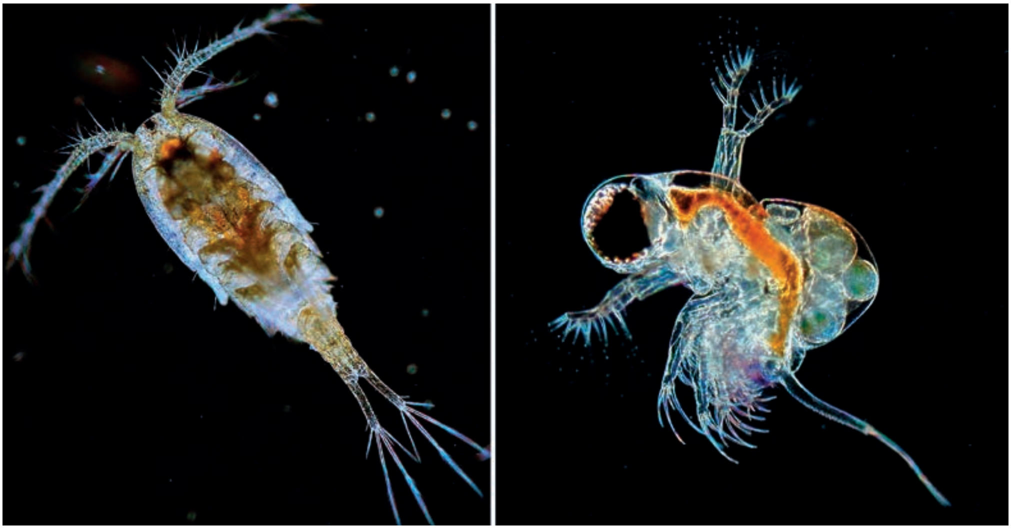

Fig. 8: Crustacean zooplankton – *Cyclops abyssorum* (on the left) and *Polyphemus pediculus* (on the right). Photos by Jan Fott.

past occurrence of cladoceran species in the lakes was also independently verified by the palaeolimnological analyses of sediment cores taken from the lakes. Altogether, seven open-water species (four cladocerans and three copepods) occurred in some (or most) of the Bohemian Forest lakes in the pre-acidification period, but both fish stocking and acidification-driven changes in lake water quality caused their drastic reduction during the 20th century (Vrba et al. 2000, 2003a). As a result, crustacean zooplankton diminished in most of the lakes till the 1980s, and two species became entirely extinct in the Bohemian Forest. Two species (*Daphnia longispina* and *Cyclops abyssorum,* **Fig. 8**) survived exceptionally in Prášilské Lake, the latter also in Großer Arbersee, and another species (*Heterocope saliens,* **Fig. 9**) in Plešné Lake. So far, the only crustacean species responding to overall lake water amelioration is *Ceriodaphnia quadrangula* (**Fig. 9**); however, its return lagged behind the beginning of chemical recovery by more than a decade (Vrba et al. 2003a).

Fig. 9: Crustacean zooplankton – *Ceriodaphnia qudrangula* (above), *Acroperus harpae* (in the centre) and *Heterocope saliens* (below). Photos by Jan Fott.

Besides this general retreat of the crustacean zooplankton in all the lakes, one can expect a similar reduction of other invertebrate species. Our knowledge of such a retreat in rotifers is only fragmentary. In Großer Arbersee and Plešné Lake, Frič (1872, 1874) observed large conspicuous colonies of *Conochilus* sp. during his early expeditions; later on, no *Conochilus* were found in any Bohemian Forest lake. Černy (1910) found non-acidophilic rotifer species, which have not been observed in Plešné Lake after the acidification period either (Vrba et al. 2003a).

Soldán et al. (2012) summarised all published and unpublished data on the occurrence of aquatic insects found in the Bohemian Forest lakes since the middle of 19th century. Due to fragmentary information on pre-acidification biota (or reference conditions) of the lakes and no information on total species richness of original assemblages, it was difficult to determine the target assemblages in which successful recovery may result. Since the 1950s, however, the Ephemeroptera, Plecoptera, and Trichoptera assemblages of the studied lakes have been continuously composed of highly tolerant and tolerant species, or resistant and very resistant species. Hence, Soldán et al. (2012) concluded that original assemblages of the Bohemian Forest lakes were very likely composed of the species able to tolerate natural levels of acidity.

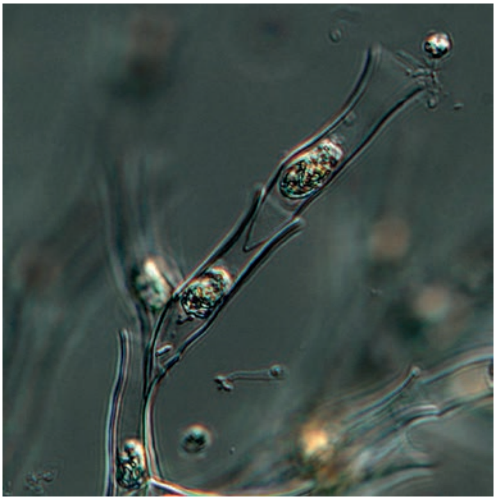

Fig. 10: Colonial chrysophyte flagellate *Dinobryon* sp. Cells are surrounded by cellulose loricae.

Similarly, the comparison of recent phytoplankton composition with the old records suggested that many species of acid-sensitive oligotrophic lakes were able to survive when the lakes became acidic (Fott et al. 1994). Most of the recently present species in the Bohemian Forest lakes, such as acid-tolerant dinoflagellates (*Peridinium umbonatum*, *Gymnodinium* spp., *Katodinium* spp.) or chrysophytes (*Bitrichia ollula*, *Dinobryon* spp.; **Fig. 10**), were observed in Černé Lake as early as in 1936; the only taxon of that time that has not been found until now is a centric diatom, *Cyclotella* sp. (Vrba et al. 2000).

The historical presence or absence of fish in the Bohemian Forest lakes remains a puzzle. As far as we can infer from both archive records and early literature, some lakes (in particular Rachelsee, Čertovo, Plešné and Prášilské) were naturally fishless (Vrba et al. 2000). Among other reasons, difficulty of access might have prevented fish from invading the lakes via outflow; an artificial stocking of brown trout (*Salmo trutta*) could change this situation. Large lake forms of brown trout were documented from Černé, Čertovo and Plešné lakes (Frič and Vávra 1897, Černy 1910). Historical data indicate that Großer Arbersee and Kleiner Arbersee had been fished since the 16th century. Original populations of brown trout were later replaced by introducing alien rainbow trout (*Oncorhynchus mykiss*). As a consequence of atmospheric acidification the fish populations began to disappear from the both lakes in the late 1950s or the early 1960s, and stocking attempts in 1965 failed. Large-scale introduction of alien brook trout (*Salvelinus fontinalis*) into Černé Lake after 1890 led to a significant fall in the population of brown trout. The growth of brook trout was extremely good after it was introduced to the lake and it was still good in 1950. The successful acclimatisation of brook trout to the lake, its higher fitness, even resistance to parasites, and more efficient competition for food resulted in a miserable existence for the indigenous species. The more efficient predation by the newcomer upon zooplankton may explain at least some changes in zooplankton mentioned already by Frič and Vávra (1897). The exact time the brown trout went extinct in the lakes is not known but it certainly could not have survived the onset of acidification in the 1960's. The acid-tolerant brook trout, in contrast, survived in Černé Lake until the mid-1970s **(Fig. 11**; Vrba et al. 2000, 2003a).

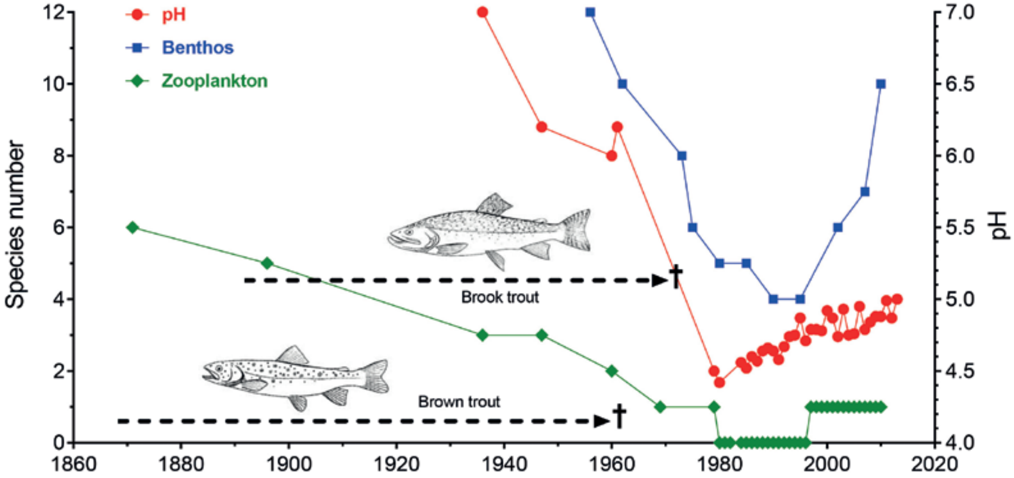

Fig. 11: Acidification and recovery of Černé Lake: the number of zooplankton (distinct crustaceans caught in plankton using plankton nets) and benthos species (larvae of mayflies and stoneflies – left axis) and lake pH (right axis). The occurrence of fish species is indicated via a crossed-out line (†: the year of last observation).

Biological recovery of the lakes

Acidification of the Bohemian Forest lakes caused significant changes in their biodiversity (Fott et al. 1994, Vrba et al. 2003a, Soldán et al. 2012). The lakes had 'simplified' food webs during atmospheric acidification due to the extinction of fish and largely reduced zooplankton (Vrba et al. 1996, 2000, 2003a). Consequently, microbial interactions dominated the pelagic food webs and bacterial filaments formed a significant portion of the plankton biomass. The absence of higher trophic levels in the lakes prevented the biological recycling of phosphorus, typical for non-acidified water bodies (Vrba et al. 2003a,b, 2006, Nedbalová et al. 2006).

Fig. 12: Aerial view of Černé Lake.

The acidification history of Černé Lake (**Fig. 12**) provides an insight into the extent and rate of biological changes, reflecting changes in water chemistry in strongly acidified lakes during the acidification and recovery phases. Since the 1871 survey, zooplankton status has been monitored more or less regularly down to the present (**Fig. 11**). The pH decline from >6 to ~4.5 and rapid increase in aluminium (Al) concentrations between the 1930s and middle 1980s (**Fig. 6**) was accompanied by the disappearance of cladoceran species and fish (Vrba et al. 2003a). While most of the planktonic species apparently died off, one of them (*Ceriodaphnia quadrangula*) survived the period of highest acidity in the littoral zone, although in very low numbers (Fott et al. 1994). Due to the recent pH increase and Al decrease (**Fig. 6**), *C. quadrangula* has reached its pre-acidification abundance in the shore zone and has even been found in the open water since 1997 (**Fig. 11**, Vrba et al. 2003a, 2016; Nedbalová et al. 2006). Similar trends could be documented for aquatic insects that have recovered well in Černé Lake recently (**Fig. 11**, Soldán et al. 2012). The prognosis for potential fish reintroduction into Černé Lake remains, however, poor, because the carbonate buffering system is not predicted to be re-established before 2050 (Majer et al. 2003). Until this time, Al toxicity will limit fish survival (**Fig. 6**).

To disentangle possible environmental and/or biological constraints on the biological recovery of the lakes from acidic stress, we studied the response of planktonic (phytoplankton, ciliates, rotifers, and crustaceans) and littoral (Ephemeroptera, Plecoptera, Trichoptera, and Heteroptera: Nepomorpha) assemblages to chemical recovery over a twelve-year period (1999–2011). Despite the rapid improvement in water chemistry of all studied lakes, only four have partly recovered so far. These lakes have low (<200 µg l^{-1}) Al concentrations (low-Al lakes: Großer Arbersee, Kleiner Arbersee, Laka and Prášilské). In contrast, the other four lakes still remain strongly acidic and have high (>200 µg l^{-1}) Al concentrations (high-Al lakes: Čertovo, Černé, Plešné and Rachelsee; Vrba et al. 2016). Multivariate analyses have revealed that the Al concentrations were the most influential driver structuring the assemblages of phytoplankton, rotifers, and Nepomorpha and also affected crustaceans through the seston C:P ratio. Both direct (toxicity) and indirect (P availability) effects of Al control biological recovery in the Bohemian Forest lakes (Vrba et al. 2006, 2016). The actual Al concentrations influence both primary and secondary producers in particular lakes (Vrba et al. 2003b, 2006, 2014, 2016, Novotná et al. 2010), and apparently control timing of biological recovery by forming the bottleneck that delays the recovery of the high-Al lakes (Vrba et al. 2016). For instance, *Ceriodaphnia quadrangula* first appeared in Černé Lake in 1997, but in closely adjacent (yet more acidic and Al-richer) Čertovo Lake not until a decade later, and in Rachelsee in 2009, only after the same threshold of Al concentrations (as in Černé Lake) was reached there (Vrba et al. 2014, 2016, cf. Stockdale et

Fig. 13: Aerial view of Plešné Lake surrounded by spruce forests infested with bark beetle, 2009.

al. 2014). The harmful Al effect was also recognised as the critical bottleneck preventing reproduction of quillwort populations – *Isoëtes echinospora* in Plešné Lake (**Fig. 13**) until 2004 (Čtvrtlíková et al. 2009, 2012, 2016) and *I. lacustris* (**Fig. 14**) in Černé Lake until the present (Čtvrtlíková et al. 2014).

Although biotic responses (especially in the low-Al lakes) showed important signs of recovery, such as re-appearance of indigenous species, decline in eurytopic acid-tolerant species and colonisation of vagile species, the assemblages of all the lakes still suffer from acidic stress. Our results also indicate the increasing role of biotic interactions between colonisers and residents, leading to the reconstruction of aquatic food webs in the low-Al lakes (Vrba et al. 2016). Fish predation may relax the possible community closure in the low-Al fishless lakes. Since 2010, a population of brook trout (*Salvelinus fontinalis*) has established itself in Kleiner Arbersee, spawning near its main inflow, and the same species recently has been seen in Großer Arbersee. Sympatric occurrence of brook trout and brown trout (*Salmo trutta*) has been observed in both lake outflows (Vrba et al. 2016). Another vital population of brown trout has also been confirmed in the outflow of Laka Lake (Matěna et al., in press), yet not in the lake itself. However, any spontaneous fish return into the other lakes is impossible, due (apart from high water acidity) to stream barriers at the outflows of Čertovo, Černé, Rachelsee, Plešné, and Prášilské lakes.

Fig. 14: *Isoëtes lacustris* growing on the bottom of Černé Lake at the depths of 1–4 m. Photo by Martina Čtvrtlíková.

Soil chemistry, microbial activity and vegetation in lake catchments

Physical and biogeochemical soil parameters have been studied mainly in the Čertovo and Plešné catchments (**Fig. 15**), which differ in bedrock composition, since 2002 (**Table 1**; Kopáček et al. 2002b,c, Kaňa et al. 2014). The soils are acidic, with pH values of 3.1–4.5; their current base saturation is in general significantly lower than the modelled pre-industrial values (Majer et al. 2003). From 55 to 80 percent of the current S pools was accumulated between 1930 and 2000 (Kopáček et al. 2001b). At the current rate of S leaching from soils, a new steady state condition between S input and export will be established around the middle of the 21st century (Kopáček et al. 2001b, Majer et al. 2003).

Despite strong acidification and N saturation of the Bohemian Forest soils, their biochemical and microbial activity is substantial, and they still maintain relatively high N retention capacity

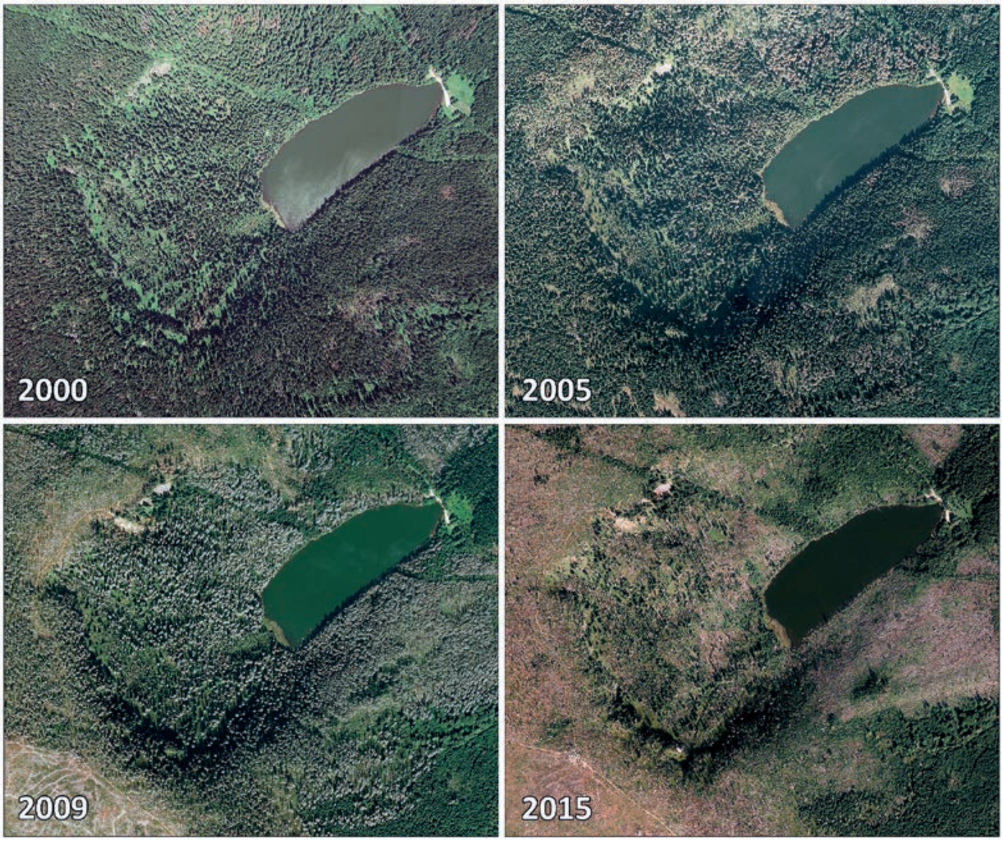

Figure 15: Temporal changes in the Plešné catchment. Note massive forest dieback due to the bark beetle outbreak followed by subsequent deforestation. Pictures were provided by Argus Geo System Hradec Králové and Georeal Plzeň (2000, 2005) and by the Šumava National Park Authority, Vimperk; Geodis Brno and Primis Brno (2009, 2015).

apart from persistent nitrate leaching (Oulehle et al. 2013). The most active upper soil horizons comprise a majority of total soil N (~70 percent; Šantrůčková et al. 2009, Kaňa et al. 2014). It is highly probable that any disturbance of the large microbial N pool can lead to an increased risk of N leaching from these soils. Our studies further show that the tight relationship between microbial N immobilisation and C availability is a mechanism controlling nitrate leaching in N saturated Plešné and Čertovo soils (Tahovská et al. 2013, Kaňa et al. 2015).

Systematic differences between both catchments have been found for soil P pools and mobility. While the granitic Plešné catchment has been releasing P for a long time, the Čertovo catchment situated on mica-schist is accumulating P in soils permanently (Kopáček et al. 2011a). This difference can be explained by: (i) lower ability of mica-schist than granite to release P under acidic conditions and by higher sorption capacity related to high Al and Fe concentrations in the Čertovo soils (Kaňa and Kopáček 2006); and (ii) higher P flux mediated by microbes in the Plešné soils. Microbial activity is certainly important in the P cycling in organic soils in both catchments (Šantrůčková et al. 2004). Mobility of phosphorus is much higher in the Plešné soils than in the Čertovo soils (Tahovská et al. 2016), which accords with the observed highest terrestrial export of P and the highest trophic status of Plešné Lake among the Bohemian Forest lakes (Vrba et al. 2000).

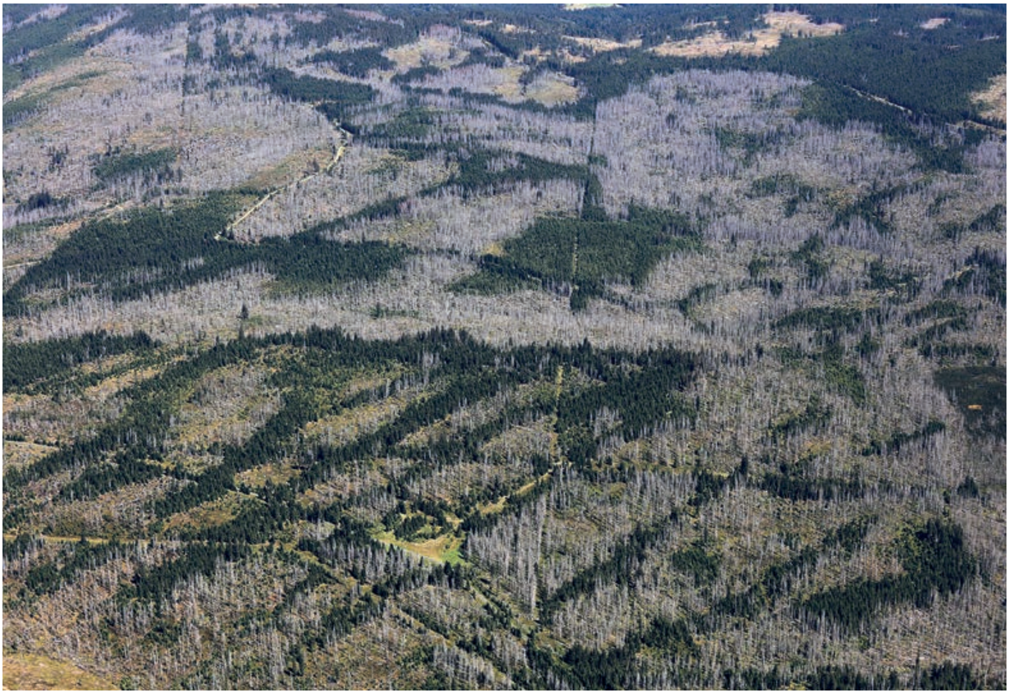

Fig. 16: Forest dieback in the central part of the Bohemian Forest.

Studies on forest biochemistry that evaluated the standing biomass and the associated nutrients in the tree and understorey vegetation biomass (Svoboda et al. 2006a–c, Seedre et al. 2015) have extended our knowledge of element pools in the terrestrial part of the catchment–lake ecosystems. The spruce trees were adversely affected by atmospheric pollution, i.e. by soil acidification, lowered base cation availability, and increased aluminium toxicity in soil solutions. Additionally, trees most probably also suffered from insufficient intrinsic water use efficiency from the 1950s–1980s (Šantrůčková et al. 2007).

Effect of forest dieback on water and soil chemistry in the lake catchments

After the bark beetle infestation and dieback of spruce forest (**Fig. 16**) in the Plešné catchment in 2004–2008, the litter fall dramatically increased from 5.4 to 42 t ha^{-1} yr^{-1} and remained relatively high until 2013 even though >52 percent of the dead trees were already fallen. The chemical composition of spruce litter changed after infestation, with the most pronounced trends being in concentrations of C (decrease) and calcium (increase). Moreover, magnesium, potassium, and P concentrations increased in the Plešné litter compared to the Čertovo litter due to an increasing proportion of litter from rowan, which partly replaced the dead spruce forest (Kopáček et al. 2015). These changes significantly affected water and soil composition in the disturbed Plešné catchment.

Prior to the bark beetle infestation, the average throughfall fluxes of elements were significantly higher than their precipitation fluxes in the Plešné catchment. After the forest infestation, throughfall deposition of ions and nutrients started to decrease due to defoliation, resulting in decreased horizontal deposition and lower element leaching from canopies (Kopáček et al. 2009b, 2013b).

Important changes in water chemistry, associated with the bark beetle outbreak in the Bohemian Forest, occurred in all lakes and streams with affected catchments (Rachelsee, Laka, Černé and Čertovo lakes; Kopáček et al. 2013a, Oulehle et al. 2013, Vrba et al. 2014). Prior to the forest damage, water chemistry in lakes and streams exhibited trends typical for areas recovering from atmospheric acidification, such as decreasing concentrations of strong acid anions, base cations, ionic aluminium, and increasing pH, similar to the 1989–2006 trends in **Fig. 6**. After the forest dieback, however, nitrate leaching increased. Nitrate became the dominant anion and its leaching was accompanied by elevated terrestrial export of ionic aluminium, base cations, total organic N, total P, and decrease in pH (**Fig. 17**). Concentrations of nitrate and base cations started to decline ~6 years after the forest dieback, but the elevated leaching of total organic N and total P have continued until the present (**Fig. 17**). Even in catchments with only a relatively small proportion of damaged forests (such as the Černé Lake catchment), the elevated leaching of nitrate, base cations, and aluminium occurred (Oulehle et al. 2013) and levelled off, in contrast to the water chemistry predicted by forecasts based on anticipated trends in acidic deposition (**Fig. 6**). Our results show that changes in ionic composition of surface waters, following the natural forest dieback, are of only a relatively short duration, of less than about a decade (**Fig. 17**).

Decreased N immobilisation by terrestrial vegetation after the forest dieback was identified as the primary cause of elevated N leaching in the Plešné catchment after the bark beetle outbreak (Tahovská et al. 2010). However, the observed excess of mineral N release to soil water was undoubtedly also related to the soil microbial activity that resulted from the decomposition of the increased litter fall to the forest floor. We observed a rapid increase in net ammonification, concentrations of water-soluble ammonium and organic C and N forms, C and N concentrations in microbial biomass, and after a short (~3 years) delay also an elevated nitrification rate and soil water concentrations of nitrate (Kaňa et al. 2015).

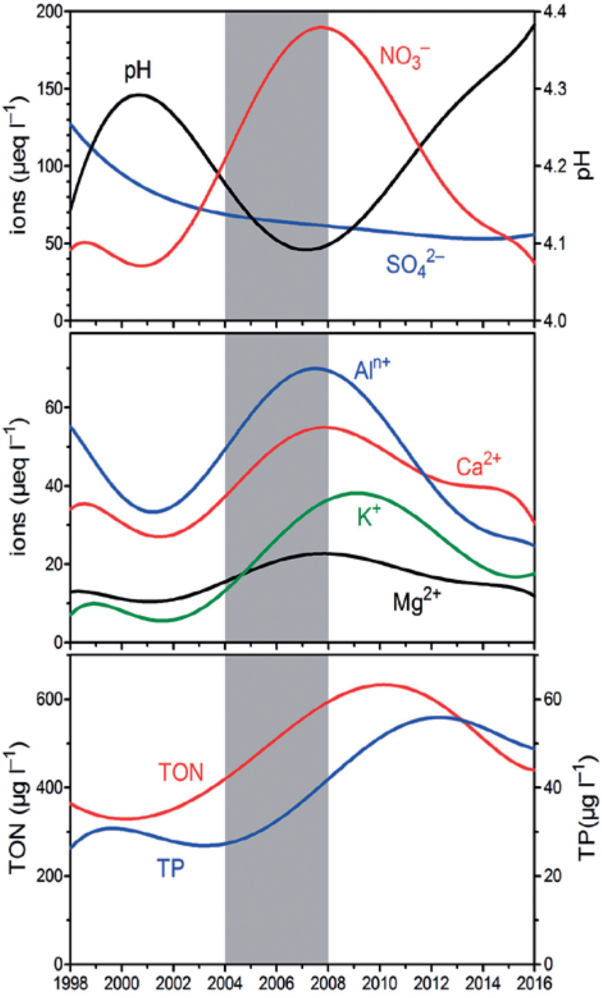

Fig. 17: Temporal trends of pH and concentrations of SO_4^{2-}, NO_3^-, Ca^{2+}, Mg^{2+}, K^+, ionic aluminium (Al^{n+}), total organic nitrogen (TON) and total phosphorus (TP) in the major surface inlet to Plešné Lake. Shaded area represents the period of massive forest dieback due to bark beetle infestation that started already around 2000 and have persisted to a lesser extend till presence.

Distinct population recovery of two aquatic quillworts in acidified lakes

Černé and Plešné lakes are the only sites in the Czech Republic inhabited by submerged aquatic quillworts, *Isoëtes lacustris* (**Fig. 14**) and *I. echinospora*, respectively. These quillworts are rare glacial relicts and critically endangered plant species of the Czech flora. *I. lacustris* inhabits the depths of 1–4 m in Černé Lake, while *I. echinospora* occupies shallow littoral habitats at the depth of 0.3–1 m in Plešné Lake. Both quillwort populations survived a forty-year period of severe acidification, but failed to reproduce until the 2000s. The most sensitive life-history stages affected by lake water acidification were probably the juveniles that were absent in both lake populations until the improvement of lake water chemistry.

Since 2004, sporeling survival and age structure of the deep *I. lacustris* and the shallow *I. echinospora* population in the lakes have been surveyed by scuba diving (**Fig. 18**) and snorkeling, respectively (Čtvrtlíková et al. 2011). We found that the recruitment success, namely the annual increment in the adult quillwort population, is highly responsive to the effects of seasonal extremes in lake water acidity and aluminium toxicity, and is lagged by age at early ontogeny. This has allowed for a water-quality-based reconstruction of population growth since the beginning of lake recovery a few decades ago (Čtvrtlíková et al. 2016).

Our laboratory experiments, conducted to simulate the effects of various pH (4–8) and aluminium concentration (0–1000 µg l^{-1} Al) in the lake water, clearly documented harmful effects of both high aluminium (>300 µg l^{-1} Al) and acidity on sporeling ontogenesis in both quillwort species

Fig. 18: Scuba diver inspecting quillwort population in Černé Lake, 2015.

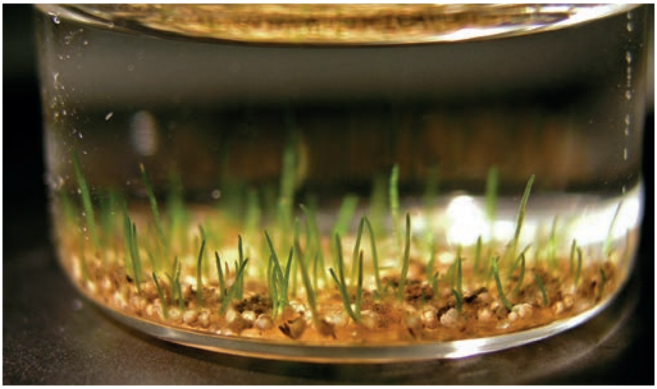

Figure 19: Sporelings of *Isoëtes lacustris* grown under laboratory conditions. Photo by Martina Čtvrtlíková.

(**Fig. 19**, Čtvrtlíková et al. 2009). These effects cause a pronounced reduction of the fine absorptive organs (macrogametophyte rhizoids, roots and root hairs) of the sporelings developing at the sediment surface and in contact with the acidic, aluminium-rich lake water, which, however, is not detrimental to the deep-rooted adults. Moreover, a surprisingly long life span of those undisturbed adult plants allowed for the survival of both quillwort populations over the several decades of the acidification period. The survival of the population that lost sporelings due to the harsh conditions depends entirely on the adult perennials, since quillworts cannot reproduce clonally. Their vitality may be supported by the incidence of mycorrhizal fungi found in the roots of both species (Sudová et al. 2011).

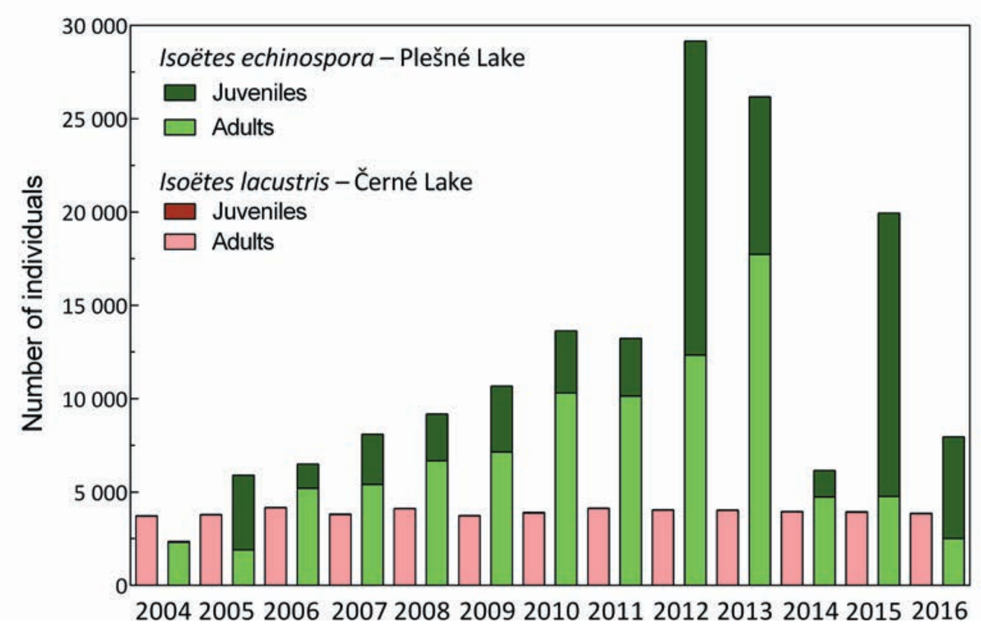

Fig. 20: Plant abundance of *Isoëtes echinospora* in Plešné Lake and *I. lacustris* in Černé Lake observed in July between 2004 and 2016. The former species was largely grazed out in autumn 2013 and 2015 resulting in substantial reduction of its population in 2014 and 2016, respectively.

Despite the recent improvements of water chemistry in both lakes, we discovered essential differences in the population recovery of both quillwort species (**Fig. 20**). While the reproduction boom of the *I. echinospora* in Plešné Lake has been observed since 2005, no renewal of the *I. lacustris* in Černé Lake has yet started. Both laboratory and field studies revealed similar limits of lake water acidity and aluminium toxicity damaging roots of sporelings. The above difference in recovery remained, however, unexplained, until our research into germination phenology revealed another novel finding of the substantially distinct germination length (Čtvrtlíková et al. 2012, 2014). *I. echinospora* germinates in late spring, when Al toxicity is already below the critical limit, whereas the long germination period of *I. lacustris* always includes winter, when extreme Al toxicity prevents any survival of sporelings. While *I. echinospora* shows a progressive recovery, *I. lacustris* is more vulnerable due to a bottleneck in its reproductive phenology that cannot be overcome under the conditions predicted for the next 20 years (**Fig. 6**).

Recently, however, we have observed large natural disturbances negatively affecting the population of *I. echinospora* in Plešné Lake. Dense stands of the recovering quillwort population were suddenly grazed by mallards (*Anas platyrhynchos*), which damaged 76 and 60 percent of all plants in the population between August and October in 2013 and 2015, respectively (**Fig. 20**). The field observations showed a strong consumptive grazing of several mallards on stunted stems of adult plants, which contain nutritional starch tissue in autumn. Nevertheless, given the responsiveness of *I. echinospora* (**Fig. 21**) recruitment to the present lake water chemistry, the current growth rate of the resting population is anticipated to continue or even increase.

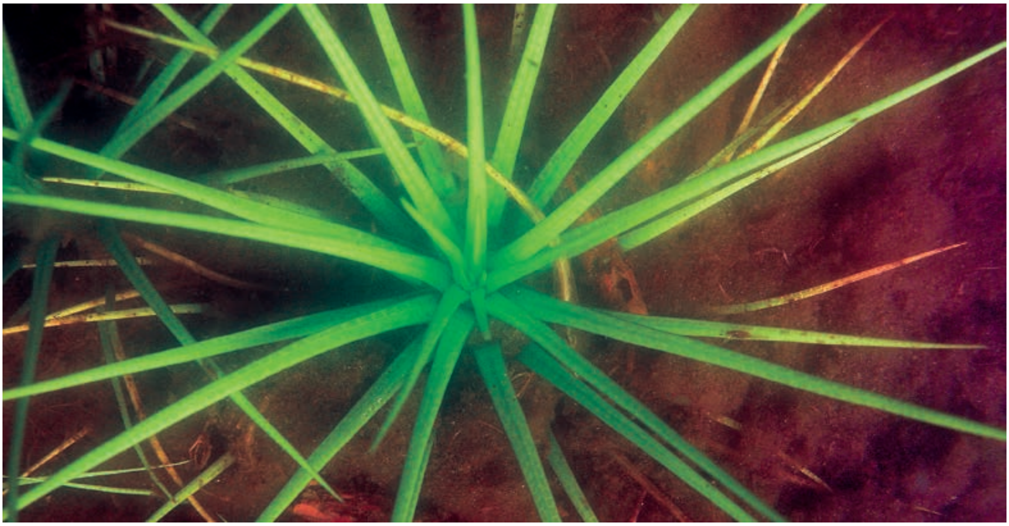

Fig. 21: *Isoëtes echinospora* inhabiting the littoral zone of Plešné Lake. Photo by Martina Čtvrtlíková.

Summary

The Bohemian Forest catchment–lake ecosystems represent valuable central European LTER sites that document the rapidly changing world. They are sensitive indicators of environmental changes, such as long-distance transboundary pollution, large-scale forest dieback, and ongoing climate change. Differences in the lake chemistry and biota enable biological processes and biodiversity to be studied along a gradient of various limiting conditions, such as pH, aluminium concentration, nutrient status, and food webs. Whole-ecosystem studies involving atmospheric deposition, soil, water and sediment compositions enable the present and historical status of nutrient availability to be investigated for both terrestrial and aquatic biota and their future development to be predicted. Ongoing biological recovery is a process of amazing complexity, driven by a synergistic interplay of environmental factors, resource stoichiometry, and complex biotic interactions, which results in the reconstruction of aquatic food webs, though not necessarily in the same way as in the pre-acidification period. Further research into these unique ecosystems may help both understand the mechanisms and verify the conceptual frameworks of biological recovery from acidic stress.

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Černé Lake, August 2016

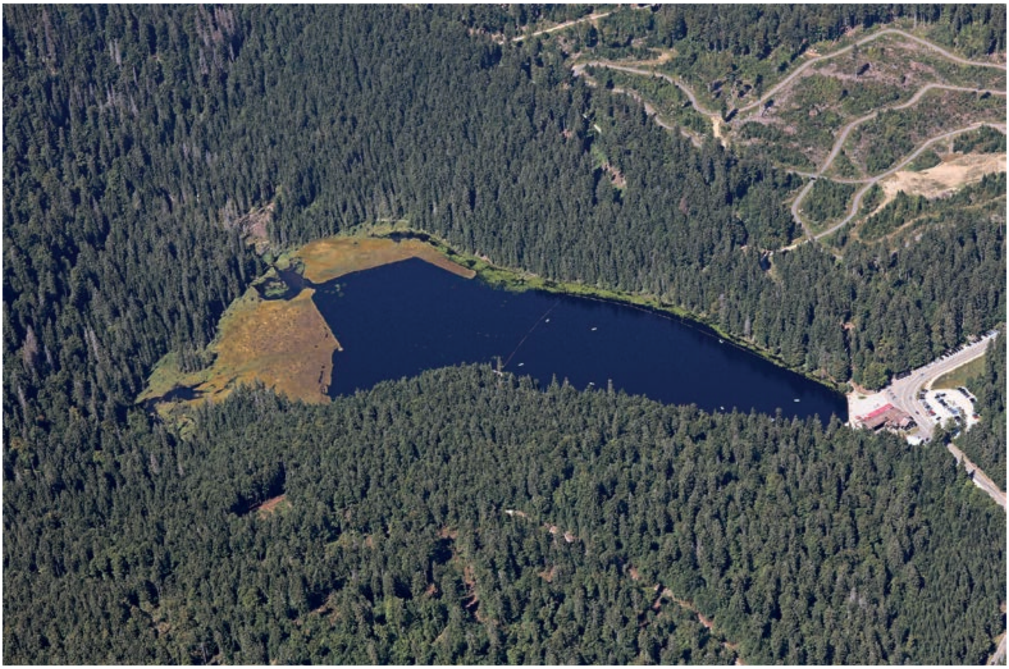
Čertovo Lake, August 2016

Plešné Lake, August 2016

Prášilské Lake, November 2015

Laka Lake, August 2016

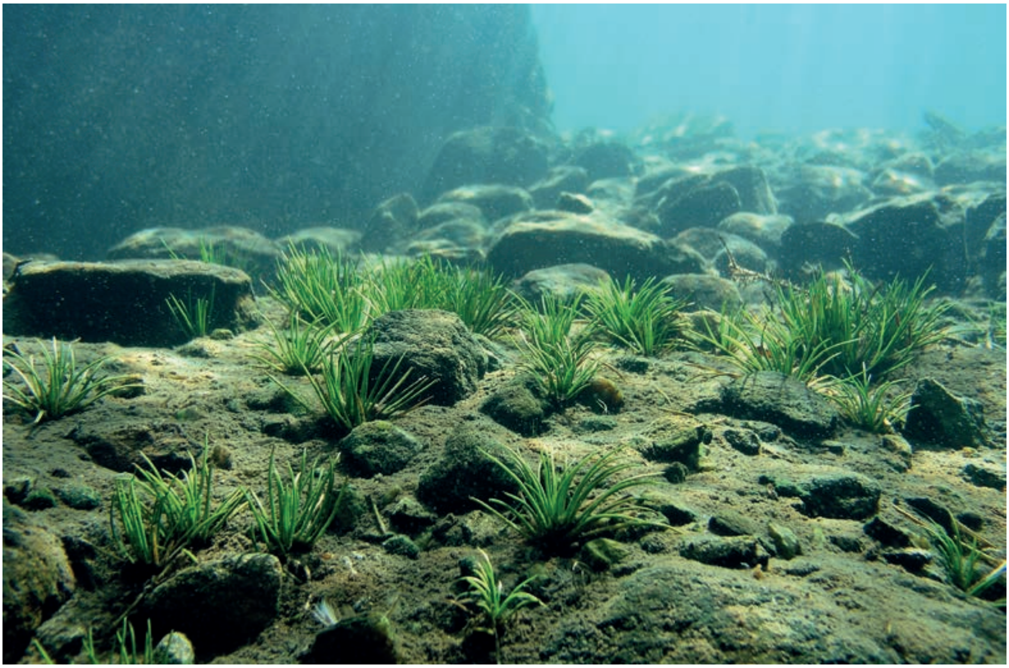
Rachelsee, August 2016



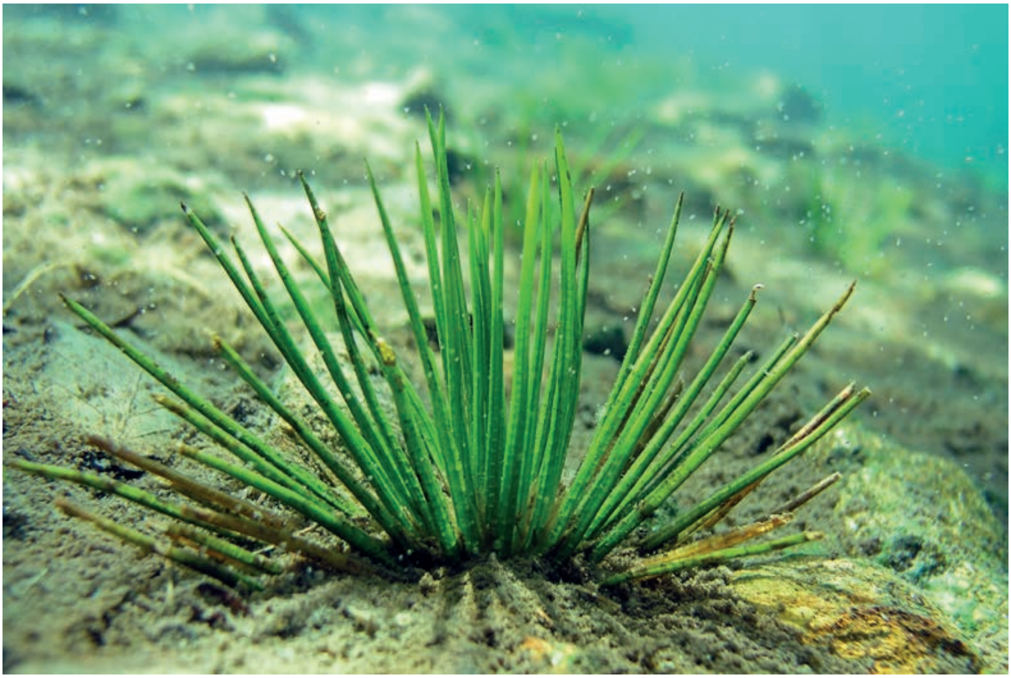
Großer Arbersee, August 2016

Kleiner Arbersee, August 2016

Population of *Isoëtes lacustris,* Černé Lake. Photo by Martina Čtvrtlíková.



Population of *Isoëtes lacustris,* Černé Lake. Photo by Martina Čtvrtlíková.



Isoëtes lacustris, Černé Lake. Photo by Martina Čtvrtlíková.

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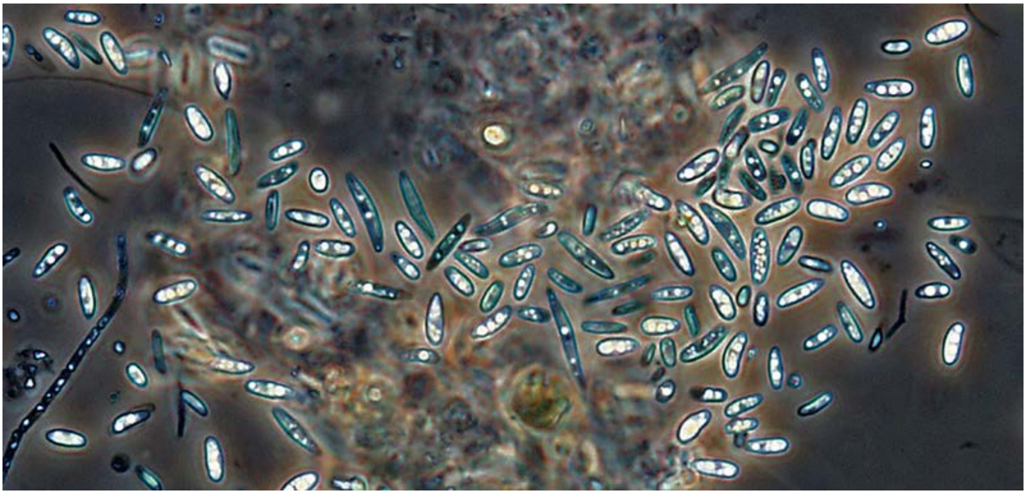

Small planktonic unicellular green alga *Coccomyxa* sp. (~3–8 µm long) from Plešné Lake (below).

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