

Effects of Bark Beetle Disturbance on Soil Nutrient Retention and Lake Chemistry in Glacial Catchment

Filip Oulehle,^{1,2} Richard F. Wright,³ Miroslav Svoboda,⁴ Radek Bače,⁴ Karel Matějka,⁵ Jiří Kaňa,⁶ Jakub Hruška,^{1,2} Raoul-Marie Couture,^{3,7} and Jiří Kopáček⁶

1 Global Change Research Institute CAS, Bělidla 986/4a, 603 00 Brno, Czech Republic;

2 Czech Geological Survey, Klárov 3, 11821 Prague, Czech Republic;

3 Norwegian Institute for Water Research, Gaustadalléen 21, 0349 Oslo, Norway;

4 Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 129, 16521 Prague, Czech Republic;

5 IDS, Na Komořsku 2175/2a, 14300 Prague, Czech Republic;

6 Biology Centre CAS, Na Šádkách 7, 37005 Ceske Budejovice, Czech Republic;

7 Département de chimie, Université Laval, 1045 Avenue de la Médecine, Québec, QC G1V0A6, Canada

Author Contributions: Filip Oulehle, Miroslav Svoboda, Jiří Kopáček and Richard F. Wright designed study and wrote the paper. Filip Oulehle analysed data and parametrized models. Jiří Kopáček, Jiří Kaňa, Radek Bače and Karel Matějka analysed data, Raoul-Marie Couture and Jakub Hruška analysed data and substantially contributed to new model development.

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ABSTRACT

Forest ecosystems worldwide are subjected to human-induced stressors, including eutrophication and acidification, and to natural disturbances (for example, insect infestation, windstorms, fires). The occurrence of the later is expected to increase due to the ongoing climate change. These multi-stressor forcings modify ecosystem biogeochemistry, including the retention of limiting nutrients, with implications for terrestrial and aquatic biodiversity. Here we present whole ecosystem nutrient (N, Ca, Mg, K) mass balances in the forested catchment of Plešné Lake, CZ, which has undergone transient changes linked to the recovery from anthropogenic acidification and to the forest disturbances caused by severe infestations by the bark beetle (*Ips typographus*). Measured fluxes and storage of nutrients in the lake-catchment ecosystem were used to constrain the process-oriented biogeochemical model MAGIC (Model of Acidification of Groundwater In Catchments). Simulated lake water chemistry and changes in soil nutrient pools fitted observed data and revealed that (1) the ecosystem N retention declined, thus nitrate leaching increased for 10 years following the bark beetle disturbance, with transient adverse effects on the acid–base status of lake water, (2) the kinetics of nutrient mineralisation from decaying biomass coupled with nutrient immobilisation in regrowing vegetation constrained the magnitude and duration of ecosystem losses of N, Ca and Mg, (3) the excess of mineralised base cations from decomposing biomass replenished the soil cation exchange matrix, which led to increased soil base saturation, and (4) the improvement of the catchment soil acid–base status led to an increase of lake water pH and acid neutralising capacity. Forested ecosystems underlain by nutrient-poor soils and bedrock are prone to human-induced damages caused by acidification and eutrophication, and any natural disturbance may further lead to nutrient imbalances. We demonstrated that in this natural forest ecosystem protected from human intervention, disturbances together with natural post-disturbance vegetation recovery have temporally positive effects on the nutrient stores in the soil.

INTRODUCTION

Forest ecosystems in the northern hemisphere are subject to a variety of natural and human-induced stresses, such as insect attacks, fire, windthrows, acid deposition and climate change. Disturbances cause changes in soil and runoff chemistry and affect freshwater ecosystems downstream. Changes in streamwater chemistry provide a sensitive and integrated signal of disturbances in terrestrial ecosystems. In central Europe chronically high deposition of sulphur (S) and nitrogen (N) compounds in the 1900s led to “forest dieback” and acidification of surface waters. Since the mid-1980s, decreases in emissions of acidifying compounds to the atmosphere have resulted in recovery from acidification with improvement in forest growth and declines in surface water acidification (Garmo and others 2014; Helliwell and others 2014).

Current bark beetle outbreaks in the northern hemisphere affect millions of hectares of forested landscape (Harvey and others 2014; Marini and others 2017; Wong and Daniels 2017). Drought conditions and windstorms are main predisposing factors causing insect disturbances to forests (Svoboda and others 2012; Neumann and others 2017; Seidl and Rammer 2017); both are expected to worsen under climate change (Bentz and others 2010; Seidl and others 2017). Changes in canopy cover, interception and evapotranspiration have the potential to significantly alter soil moisture, runoff patterns and ecosystem biogeochemistry (Mikkelsen and others 2013; Beudert and others 2015). Besides the negative economic consequences for the forest industry (Grégoire and others 2015), forest ecosystem disturbances are important drivers (Müller and others 2008) for maintaining biodiversity at different scales (Jonášová and Prach 2004).

One of the most extensive forested landscapes in Europe is situated along the Czech-German-Austrian border of which the central part belongs to two protected areas, the Bavarian Forest National Park in Germany and the Šumava National Park in the Czech Republic. The parks contain several natural lakes, located in cirques formed during the last Pleistocene glaciation. Several of the lakes and their catchments have been sites of intensive environmental monitoring since the 1980s with focus on lake acidification (Veselý and others 1998; Majer and others 2003). The area has received high levels of acid deposition. In recent years an extensive bark beetle (*Ips typographus*) outbreak has attacked the forests (Lausch and others 2011; Čada and others 2016). At Plešné Lake catchment, Czech Republic, most of the forest canopy has been lost since 2004 (Oulehle and others 2013).

Acid deposition and the bark beetle attack at Plešné Lake have separately and together resulted in changes in vegetation, soil, streamwater and lakewater chemistry. Plešné Lake offers the rare opportunity to study the combined effect of these multiple drivers on the coupled terrestrial and aquatic ecosystem. The long-term monitoring of the lake and its catchment provide information on element mass balances, storage of nutrients in various ecosystem pools, and the changes due to declining acid deposition and the bark beetle attack. These data can be systematically combined as input to process-oriented biogeochemical models. Model for acidification of groundwater in catchments (MAGIC) (Cosby and others 1985b, 2001; Oulehle and others 2015) is one such model and has been used to simulate acidification and recovery in lakes in the Šumava National Park and many other sites elsewhere in Europe and North America. Once calibrated, MAGIC can be used to simulate the hypothetical effects of each of the drivers separately, and thus provide insights into the synergistic or antagonistic actions as well as the temporal dynamics over years to decades. At Plešné Lake the combined ecosystem disturbances have been profound and long-lasting, and are unusually well-documented.

Here we leverage long-term datasets from the intensively monitored Plešné Lake catchment to:

1. Calibrate MAGIC to the year 2000, the year prior to the onset of the bark beetle attack, using the long-term monitoring data for atmospheric deposition, vegetation, soil and water for the Plešné Lake catchment and lake;
2. Construct an input scenario to MAGIC for the period 2000–2016 to simulate the effects of changing forest cover on lakewater chemistry using measurements of nutrients and base ca-726 F. Oulehle and others tions in vegetation before, during and after the bark beetle outbreak;
3. Compare the bark beetle scenario with a hypothetical beetle-free “control” scenario 2000–2016 to give an estimate of the effect of the bark beetle outbreak on the long-term recovery of Plešné Lake from acid deposition.

Modelled nutrient dynamics fitted with the measured data were used to clarify the bark beetle disturbance impacts on soil nutrient retention, including N, calcium (Ca), magnesium (Mg) and potassium (K). We hypothesise

1. that over the short term (years) the nitrogen released from decomposing vegetation will result in a peak in nitrate (NO_3^-) concentrations in stream and lakewater, with decreased acid neutralisation capacity (ANC) and pH;
2. that over the intermediate term (decades) NO_3^- concentrations will decrease to levels below predisturbance, whereas base cation concentrations will remain higher than pre-disturbance, and thus ANC and pH will be higher than pre-disturbance;
3. that over the long term (century) lake chemistry will converge to the chemistry simulated for the scenario without bark beetle disturbance.

MATERIALS AND METHODS

Site Description

Plešné Lake is situated at 47.777°N, 13.867°E, and an elevation of 1089 m. The lake is in a Pleistocene glacial cirque, and is dimictic and mesotrophic. Its surface area is 7.5 ha, maximum depth is 17 m, and water residence time is approximately 1 year. At present, the lake is barren of fish, with recovering plankton (Vrba and others 2016). Anoxia occurs regularly in the hypolimnion during both the winter and summer stratification periods (Kopáček and others 2004). The lake has four tributaries.

The Plešné Lake catchment (67 ha including the lake) is steep, with a maximum local relief of 288 m. The catchment lies on a granitic bedrock covered with acidic and shallow soils (leptosol, podsol, and dystic cambisol); wetlands and bare rocks cover about 5 and 1%, respectively. Forest vegetation occupied 90% of the Plešné catchment and was dominated by Norway spruce (*Picea abies*) with a minor contribution of deciduous trees. The average density was about 300 adult trees ha^{-1} and only ~7% of the trees were dead in 2000. Understorey vegetation is dominated by blueberry (*Vaccinium myrtillus*), fern (*Athyrium distentifolium*), and grass (*Calamagrostis villosa*). The Plešné forest was attacked by a bark beetle (*I. typographus*) between 2004 and 2008, and 93% of the forested area lost more than 80% of its mature spruce trees (Kopáček and others 2015, 2017). All dead biomass has been left in the unmanaged catchment. Natural forest regeneration started rapidly within 1–3 years after the tree dieback, and the number of seedlings increased by an order of magnitude between 2005 and 2015, with average densities of 47 and 670 trees ha^{-1} , respectively. Similarly, the biomass of understorey vegetation, especially blueberry, increased after the forest dieback (Matějka 2015).

Catchment Mass Balance and Nutrient Storage

Atmospheric Deposition

Samples of atmospheric deposition have been collected monthly by precipitation bulk and throughfall collectors since 1998 and analysed for sulphur (S), nitrogen (N-NO_3 and N-NH_4), chloride (Cl), Ca, Mg, Na, K and protons (pH) (Supplementary Information; Kopáček and others 2017). Historical (back to 1860) deposition of S and N were estimated by Kopáček and others (2012) and Oulehle and others (2016) and deposition of base

cations by Kopáček and others (2016). S dry deposition to the forest was estimated as the difference between throughfall and bulk precipitation fluxes. These estimates of dry deposition were then scaled based on percent canopy in the forest after the bark beetle attack. Total deposition of base cations for areas covered by Norway spruce was estimated from throughfall chemistry by a canopy budget model using sodium as a tracer. On site meteorological data, including air and soil temperature (at 5 cm depth) have been collected since 2001.

Lake Chemistry and Solute Fluxes

Samples for lake water chemistry (surface to depth profiles) have been taken twice a year (in summer and autumn) since 1984 (Vesely and others 1998) and at the outlet once every three weeks since 1998 (Kopáček and others 2017). Analyses comprised acid anions (SO_4 , NO_3 , Cl), cations (Ca, Mg, Na, K, Al), dissolved organic carbon (DOC), dissolved organic nitrogen (DON) and pH. Fluxes from the lake have been calculated since 2000, when the lake outlet was equipped with a calibrated weir and water level recorder. All lake inlets have been sampled since 1998 at three-week intervals. Equivalent concentrations of ionic aluminium (Al_i) were obtained from molar concentration and the average charge of the respective hydroxy-Al, estimated for the sample pH. Concentrations of organic acid anions were estimated from concentrations of DOC, organically bound Al and Fe (Al_o and Fe_o , respectively) and pH (Kopáček and others 2000).

Soil Chemistry and Nutrient Pools

Samples for soil chemistry were collected in 14 soil pits excavated between 1997 and 2001. Sampling points were chosen to represent the major soil types and topographical features within the Plešné Lake catchment. Soil samples were taken from 0.25 m² pits (50 x 50 cm), excavated to the bedrock. Additional details on sampling procedures and chemical analyses are given in Kopáček and others (2002). Both in 2010 (Kaňa and others 2012) and 2015, soils were resampled from 20 pits and analysed following the procedure from 2000.

Biomass Nutrient Pools

Two components of catchment vegetation biomass were assessed—trees and understory. Understory vegetation species composition, biomass and associated nutrient pools (C, N, Ca, Mg, K) in aboveand below-ground components were measured in 2004 on 23 plant sample plots distributed across the catchment (circle plot area of 200 m²), representing the main types of understory vegetation plant communities (Svoboda and others 2006a). Biomass development in selected plots was then monitored annually through 2015 (Matějka 2015). The whole-catchment biomass of a species was estimated by multiplying the whole-catchment average coverage by the average biomass of the species under optimal growth conditions.

In 2015, we sampled forty 500-m² circular plots located in catchments. Plots were established using a stratified-random design. At each plot, we sampled all trees with diameter at breast height (DBH) at least 7 cm, recorded their species, DBH, and their live/dead status. All regeneration of trees within forest plots was identified to the species level, and densities were recorded in particular height classes by 50 cm. Biomass in 2000 was calculated using allometric equations (Wirth and others 2004) based on the assumption that all measured snags in 2015 were alive in 2000. The rate of tree mortality between 2000 and 2015 was derived using the percentage of dead adult trees estimated from aerial photographs. The future (up to year 2100) prediction of new forest biomass increment was built on a linear model that related the amount of biomass over time since the stand-replacing disturbance. To develop the model, data from an extensive database of mountain spruce forests covering a wide area of Central Europe were used (for more information about the database, see <https://www.remoteforests.org>). The dependence of the biomass on time since the stand-replacing disturbance was modelled using 110 permanent research plots (1000 m²) that were affected by a disturbance with a severity greater than 80% of the removed canopy over a period of 30 years. Disturbance history reconstructions were based on a dendroecological study reconstructing disturbance histories. All living trees (≥ 7 cm) were measured and 25 living dominant trees per plot were randomly selected and cored. Variables characterising the disturbance history covering the last 200 years—the maximum disturbance severity and time since the maximum disturbance were used. For more information on the construction of disturbance years and severities, see Bače and others (2017). For the reconstruction of the amount of biomass in 1860, four sub-regions covering the lake catchment represented by one dominant age group (mean age of canopy trees) were identified. The size of the age group and its mean age were derived from the dendrochronological study on canopy trees of the catchment by Čada and others (2016) and historical maps (Brůna and others 2013). The amount of biomass for the four sub-regions was calculated using the same model for the prediction of future development and summarized for whole catchment.

The tissue nutrient concentrations were measured in samples taken from trees chosen to reflect the spatial heterogeneity within the catchment (Svoboda and others 2006b) (for more details see Supplementary Information; Table S1).

Description of the Model and Calibration Procedure

The MAGIC model is described by Cosby and others (1985a, 1985b, 2001) and the most recent formulation of N processes by Oulehle and others (2012). MAGIC is a lumped-parameter model of intermediate complexity which calculates the concentration of major ions at a monthly timestep under the assumption that the reactions involving SO_4 adsorption, cation exchange, dissolution–precipitation–speciation of aluminium and dissolution speciation of inorganic and organic C are at equilibrium. MAGIC accounts for the mass balance of major ions in the soil by bookkeeping the fluxes from atmospheric inputs, chemical weathering, net uptake in biomass and loss to runoff. In the model, retention of C and N are driven by the decomposer activity. Decomposers process the C and N content of soil organic matter (SOM), using part of the organic matter for energy and part

to generate new biomass. The turnover of SOM results in the release of CO₂, NH₄, DOC and DON to soil solution as the result of decomposition and solubilisation, and the removal of inorganic N from soil solution as the result of decomposer growth.

The plant litter flux provides input of organic C and N to the soil pool. Several assumptions were applied in this application of MAGIC, following Oulehle and others (2015)—seasonal litter decomposition, N mineralisation and plant N uptake were assumed to be a function of soil temperature (Q₁₀); denitrification and N fixation were assumed to be either constant or negligible; only a single active SOM pool was used, and DOC in runoff was set as a fixed fraction of organic matter decomposition. Furthermore, plant litter flux was set proportional to the standing tree biomass in the catchment, and the seasonal uptake of inorganic N by plants from soil solution was set equal to the amount necessary to replace the annual plant N losses through litter, with a small additional increment to represent the annual storage of N in biomass. Similarly, the C/N ratio in the annual litter flux was assumed to be constant over time, and the annual decomposition rate of SOM was set equivalent to the annual litter C flux, such that there was no change in the soil C pool over time. The gross N mineralisation rate was calculated from the soil C decomposition rate based on soil C/N. The seasonal pattern of N uptake, together with microbial N mineralisation and immobilisation, determined the balance of N cycle within the ecosystem, and asynchrony of plant demand and N availability was a major cause of N leaching.

A small additional increment was introduced to allow for the annual storage of N and base cations in woody tissue. Net accumulation of N (22 meq m⁻² y⁻¹) and base cations (14.9 meq m⁻² y⁻¹) in vegetation between 1860 and 2000 was assumed to mimic the increase of forest biomass over this period. MAGIC was calibrated to the observed volume-weighted monthly concentrations and fluxes (pre-disturbance year 2000) of SO₄, Cl, NO₃, NH₄, Ca, Mg, K, Na, Al and protons (pH) in lake water, and to the observed C/N ratio and base saturation (BS) in the soil (Table 1).

The calibration started from an assumed initial steady-state condition (here the year 1860). The model simulated pools of base cations, C and N in the soil, and concentrations of strong acid anions (SAA = SO₄ + Cl + NO₃), base cations (BC = Ca + Mg + Na + K), organic acids, acid neutralising capacity (ANC = BC-SAA), Al and pH in lakewater for each month through to the end of the simulation period (here 2000). A trial-and-error procedure was used to obtain the best match between simulated and observed pools of soil base cations, C and N as well as observed monthly concentrations and fluxes of solutes in lakewater in the calibration year 2000 (for detailed calibration procedure see Supplementary Information).

Estimated and measured total deposition (see “Atmospheric deposition” section) constrain the model simulation. To predict hypothetical lake and soil chemistry without bark beetle disturbance (**Control simulation**, until the year 2100) all model parameters were fixed to the year 2000, and atmospheric deposition fluxes held constant to those in year 2004. MAGIC does not explicitly model plant dynamics and base cation mineralisation. To account for and predict the effects of the bark beetle disturbance (**Disturbance simulation**, until 2100), catchment scale inputs of nutrients from decaying biomass and catchment scale nutrient immobilisation in regrown vegetation were entered as external inputs to the model.

Carbon Decomposition, Nutrient Mineralisation and Vegetation Uptake Kinetics

In 2000, the unmanaged mature spruce forest was healthy, with a biomass stock of 420 t ha⁻¹. Between 2004 and 2008 most of the forest in the catchment was infested by the bark beetle, resulting in 89% reduction of live standing biomass. Standing dead trees lost most of their needles during the first several months after infestation, and subsequently they have been continuously losing twigs, bark, and branches (Figure 1).

Biomass Decomposition and Nutrient Mineralisation

The decomposition of dead tree biomass was calculated according to:

$$AML_t = 1 - e^{-kt} \quad (1)$$

where AML_t is the accumulated mass loss at time *t* (years) and the parameter *k* represents the decomposition rate. We assumed complete decomposition, thus neglecting the recalcitrant fraction of the organic matter (Berg and Laskowski 2006). Each tree compartment differs in decomposition rate and tissue chemical composition (see Supplementary information; Figure S1, S2). Mineralisation of nutrients followed the same kinetics as decomposition of dead tree biomass, and started with the initial nutrient pools in tree biomass (C = 193 t ha⁻¹; N = 1.17 t ha⁻¹; Ca = 0.66 t ha⁻¹; Mg = 0.11 t ha⁻¹; K = 0.53 t ha⁻¹). With the assumed decomposition rate by 2100, 93% of tree biomass killed by the bark beetle will be decomposed and 96% of nutrients formerly stored in tree biomass will be mineralised (Figure 2). To assess the uncertainty of nutrient mineralisation associated with different decomposition rates (*k* values) we simulated decomposition rates under *k* values within range of 0.091 and 0.023 (see Supplementary Information; Figure S3).

Vegetation Uptake in Regrown Biomass

The repeated surveys at selected relevés (Matějka 2015) indicated that the understory herbaceous biomass expanded by about 70% after the opening of the canopy (increase from 6.2 t ha⁻¹ in 2004 to 10.7 t ha⁻¹ in 2014). Understory vegetation had relatively low C/nutrient ratios compared to tree biomass (Table S2). Understory vegetation accumulated 102 kg N ha⁻¹, 33kg Ca ha⁻¹, 7.3 kg Mg ha⁻¹ and 31 kg K ha⁻¹ over the period 2004–2014. By 2100, tree biomass is estimated to reach 73% of that measured in 2000. This estimate gives immobilisation of nutrients in regrown trees in the year 2100 of 89, 77, 81 and 85% (N, Ca, Mg and K, respectively) of the amount measured in 2000 (see Supplementary Information; Figure 2). Nutrient uptake was time dependent and reflected dynamics of forest regrowth. In the control scenario, BC net tree uptake was assumed negligible, as the scenario assumed no change in total forest biomass through to year 2100 (compared to year 2000).

Neglecting alteration of SOM heterotrophic respiration (no net soil C release) by forest disturbance, mass-balance calculations indicate that the decaying biomass in the ecosystem was a net source of C to the atmosphere (averaging 4 t C ha⁻¹ y⁻¹ in years 5–8 since start of the disturbance). This

declines as new forest regrows in years 10–15 following disturbance. The steady-state C balance is predicted to be established roughly 50 years after the disturbance (Figure 2).

RESULTS

Lake Chemistry

Peak concentrations of SO_4 and Cl in lakewater were observed during the 1980s, with SO_4 concentration of $\approx 180 \mu\text{eq l}^{-1}$ and Cl concentration of $\approx 23 \mu\text{eq l}^{-1}$. Since then a steady decrease of SO_4 and Cl to 46 and $11 \mu\text{eq l}^{-1}$, respectively, in 2016 was observed. These trends were closely simulated by the MAGIC model. The simulated monthly $\text{SO}_4 + \text{Cl}$ concentrations reflect observed values ($R^2 = 0.83$). Measured fluxes of both SO_4 and Cl were well simulated by MAGIC ($R^2 = 0.94$). The bark beetle disturbance had only minor influence on the concentrations of SO_4 and Cl, with predicted higher concentrations of both ions in the future due to the higher total deposition in control simulation due to greater scavenging of dry deposition by the forest canopy (Figure 3). Over the period 2001–2016, the average net SO_4 release from soil pools contributed $38 \text{ meq m}^{-2} \text{ y}^{-1}$ to the total SO_4 leaching of $69 \text{ meq m}^{-2} \text{ y}^{-1}$. Simulated SO_4 leaching was 10% higher than observed leaching between 2001 and 2016. Simulated and observed Cl fluxes were, on average, in balance with deposition (Table 2).

A peak of NO_3 concentration was observed in the 1980s followed by decline to 2003 (Figure 4). A new increase in NO_3 concentration began in 2004 and elevated NO_3 concentrations lasted until 2016 when NO_3 had again declined to pre-disturbance levels. Monthly NO_3 concentrations and fluxes were well simulated by the model ($R_2 = 0.64$ and $R_2 = 0.87$, respectively). For the future from 2016, simulated NO_3 concentrations were lower for the bark beetle scenario relative to the control scenario. In the period 2001–2016, the simulated ecosystem NO_3 leaching overestimated the observed values by only 9% (73 vs. $67 \text{ meq m}^{-2} \text{ y}^{-1}$). Over this period, 65% of mineralised N from decaying tree biomass was assumed to be taken up by regrown vegetation (Table 2).

Lake water concentrations of the sum of base cations followed the strong acid anions with a first peak during the acidification period, driven by SO_4 , and a second peak during the bark beetle disturbance, driven by NO_3 . Monthly SBC fluxes were simulated well ($R^2 = 0.92$) but with a lower coefficient of determination for SBC monthly concentrations ($R^2 = 0.39$) (Figure 5). Over the period 2001–2016, simulated leaching of both Ca and Mg agreed with observed values (difference by 4 and 2%, respectively). The model indicated that a significant part of available Ca (from weathering, deposition and mineralisation of dead biomass) ended up in soil and in vegetation, and part was lost from the ecosystem by leaching ($49 \text{ meq m}^{-2} \text{ y}^{-1}$). Average annual mineralisation of Ca from dead biomass accounted for $80 \text{ meq m}^{-2} \text{ y}^{-1}$, and thus increased the Ca input by about 140%. Net uptake of Ca in vegetation was estimated to be $37 \text{ meq m}^{-2} \text{ yr}^{-1}$ (Table 2). Similarly, within the disturbance period simulated Mg leaching fitted the observed data (both $19 \text{ meq m}^{-2} \text{ y}^{-1}$). Mineralisation of Mg from dead biomass accounted for $21 \text{ meq m}^{-2} \text{ y}^{-1}$, an increase of Mg input of 110%. Net uptake in vegetation accounted for $12 \text{ meq Mg m}^{-2} \text{ y}^{-1}$, which corresponded to 57% of available Mg from mineralisation (Table 2). Whereas the model simulated Ca and Mg concentrations and fluxes well, for K the observed and simulated values differed significantly. The simulated flux of K between 2001 and 2016 was 25% lower than the observed. Estimated mineralisation of K from dead biomass increased the K input by 292%. Uptake by vegetation was estimated to $19 \text{ meq m}^{-2} \text{ y}^{-1}$ (Table 2).

Sensitivity analysis revealed the important role of decomposition kinetics on N and base cation dynamics. If mineralisation was doubled, leaching of N, Ca, Mg was overestimated, whereas K leaching fitted well measured data. Decrease of k values by 50% resulted in underestimation of all nutrients leaching (Figure S4).

Long-term simulated annual pH and ANC fitted the observed data (1984–2016). The increase of water acidity, following soil acidification by S deposition, peaked in the 1980s with lake water pH below 4.5 and ANC below $100 \mu\text{eq l}^{-1}$ (Figure 6). Concentrations of ionic Al reached levels $\approx 100 \mu\text{eq l}^{-1}$ (Figure S5). The ongoing recovery of lakewater chemistry was temporarily interrupted with the onset of bark beetle disturbance, when NO_3 started to increase. For future years the control scenario suggested only slow additional recovery of water pH and ANC, while the bark beetle scenario indicated that the change in water composition after year 2015 was followed by rapid increase of lake water pH and ANC (Figure 6).

Soil Chemistry

In 2000, measured soil chemistry reflected relatively high N status, demonstrated by the low soil C/N ratio of 24. Soil C/N was almost unchanged in repeated surveys in 2010 and 2015 (C/N = 24.5). The estimated soil C/N ratio in 1860 was 26 and had been gradually decreasing until the 1980s. The simulated effect of bark beetle disturbance on soil C/N was negligible, and similar to the control simulation (Figure 7).

The measured pool of exchangeable Ca increased from 1053 meq m^{-2} in 2000 to 1792 and 1526 meq m^{-2} in 2010 and 2015, respectively. Similarly, the exchangeable pool of Mg increased from 270 meq m^{-2} in 2000 to 346 and 340 meq m^{-2} in 2010 and 2015, respectively. In contrast the measured pool of soil exchangeable K was highest in 2010 (311 meq m^{-2}), with lower values in 2000 and 2015 (224 and 230 meq m^{-2} , respectively). MAGIC simulations fitted the soil base saturation in 2000 (BS of 15%), and thus indicated an ongoing depletion of the soil pool of exchangeable base cations since 1860 (initial BS estimated to 33%). The control simulation without bark beetle disturbance resulted in only limited recovery of the soil base saturation (Figure 7). With the bark beetle disturbance, the MAGIC model predicted accumulation of Ca and Mg in the soil pool, at a rate similar to that measured. The simulation suggested an accumulation of K in the soil pool by 2016; this was not observed (Table 2; Figure S6). Overall the simulated effects of the bark beetle disturbance on soil base saturation agreed well with measured data, showing an increase of base saturation from 15 to 20% by 2015 (Figure 7).

DISCUSSION

The forest catchment of Plešné Lake has been impacted by multi-stressors over the last century. Deposition of acidifying compounds from the atmosphere depleted the soil pool of base cations, decreased the ANC and mobilised Al_i in soil solution. Peak levels of acid deposition were reached in the 1980s. As a consequence, lakewater pH and ANC fell below the level suitable for maintenance of a diverse trophic structure of the lake ecosystem (Vrba and others 2016). Only acid tolerant species of plankton survived the peak of acidification period (Vrba and others 2003). Chemical recovery of soil and water began in the 1990s when acid deposition began to decrease due to implementation of national and international emission abatement policies (Majer and others 2003). The exceptionally hot and dry year of 2003 (Ciais and others 2005) most likely triggered the bark beetle infestation of the spruce trees and resulted in the 90% reduction of standing tree biomass over the next 7 years.

Modelling nutrient balances at the catchment scale revealed the importance of vegetation dynamics and its role in nutrient retention after large-scale disturbance. Despite the temporally elevated NO_3 leaching, accompanied by terrestrial BC losses, the base cations released from dead biomass increased their soil pools. Forest disturbance thus accelerated chemical recovery of this chronically acidified unmanaged ecosystem.

Modelling the Catchment Response to Acidification Stress

This application of MAGIC to the Plešné Lake ecosystem includes, for the first time, C turnover and decomposition processes. The results indicated that chronic excess N deposition caused a gradual enrichment of the soil N pool, led to a surplus of available N in the soil, and beginning in the 1950s an elevated leaching of NO_3 to surface waters. Since then, leaching of inorganic N has been tightly linked to the atmospheric N inputs. The model simulated the key role of N deposition in determining losses of inorganic N to surface waters at N-rich sites, similar to those observed in field experiments (Wright and others 1990; Boxman and others 1998). The reduction in N deposition from the late 1980s was followed by reduced N leaching until 2004. Overall, nitrate leaching played a moderate role in causing soil and lake water acidification. Rather SO_4 played the major role in base cation leaching and depletion of soil base cation pools. The MAGIC simulations here indicated significant depletion of soil base cations, from an estimated base saturation of 33% in 1860 to 15% in 2000. The projected recovery, under the control scenario, with acid deposition assumed unchanged from the levels of 2004, revealed only minor improvements of soil base saturation, indicating balanced BC inputs (weathering + deposition) and outputs (uptake + leaching). Our results are consistent with previous estimates of soil acidification and subsequent recovery by Majer and others (2003).

Modelling of the Catchment Response to the Bark Beetle Disturbance

The unprecedented extent of forest dieback caused by the bark beetle infestation influenced the catchment biogeochemistry. In a timeframe of few years a substantial amount of dead tree biomass started to decompose. Biomass decomposition rates used in our decomposition model agree well with published data, which consider decomposition rates of coarse woody debris according to a decay class system (Zielonka 2006; Lombardi and others 2008; Šamonil and others 2009; Krüger and others 2014; Russell and others 2015; Přivětivý and others 2016). We assumed the average turnover rate of whole dead spruce trees to be 76 years, accounting for 90% progress in decomposition which is considered to be proportional to the “late-stage” decomposition using the decay class system. We assumed that nutrient release from decaying trees (mineralisation of N, Ca, Mg and K) was proportional to the decomposition (release of CO_2), thus leaving the SOM pool unchanged. The amounts of nutrients in decaying wood may either decrease by preferential mineralisation and leaching, remain stable or even increase, due to the atmospheric deposition and nutrient translocation from soil to organic matter by fungi (Holub and others 2001; Palviainen and others 2010; Bade and others 2015). In the synthesis made by Laiho and Prescott (2004), wood debris was considered of minor importance in the nutrient retention in coniferous forests. Furthermore, nutrient-rich needles decompose much faster compared to more nutrient-poor woody fractions; needles lose on average 50% of their mass within 2 years. As such, approximately 40–60% of mineralised nutrients were derived from needle decomposition during the first 7 years following forest dieback. This implies that fresh fallen photosynthetic tissue played an important role in the transient enhancement of nutrient availability.

Whereas the rate of mineralisation of nutrients from dead tree biomass was estimated from other studies, the uptake of nutrients by growing vegetation was based on site surveys of vegetation plots (Matějka 2015) and well-established models of natural forest development in the study area (Svoboda and others 2010; Bače and others 2012; Janda and others 2014; Macek and others 2017). Microhabitat conditions, including substrate quality, increased soil moisture, nutrient and light availability after forest disturbance became important drivers for vegetation recovery (Nováková and Edwards-Jonášová 2015; Pec and others 2015). Modelled nutrient immobilisation in new trees reflected the distinct allometry of young trees (seedlings) compared to mature trees; the later are relatively richer in structural, low nutrient, woody tissues compared to young trees where needles account for approximately 30% of whole-tree biomass. Modelled uptake of nutrients into new forest biomass dominated (70%) over the nutrient immobilisation into the understory vegetation (30%) between 2001 and 2016.

The simplified ecosystem net C balance calculated as the difference between biomass decomposition and vegetation regrowth, and the assumption of no net change in soil C storage (Figure 2), are consistent with the conceptual framework proposed by Edburg and others (2012), where recovery of steady-state net ecosystem productivity is proposed to be achieved within several decades following bark beetle disturbance. In our study we did not attempt to assess whole ecosystem C balance, but used the C dynamics of decomposition and vegetation regrowth to constrain the balance of nutrients.

Forest ecosystems in the Bohemian Forest areas glaciated during the Pleistocene are considered N-saturated (Kopáček and others 2001), as manifest by elevated NO_3 concentrations in streams and lakes. Any disturbance will potentially have adverse effects on catchment N retention and increase the threat of elevated NO_3 leaching from these ecosystems. Over last several decades, regional scale surface water monitoring indicated a potential for NO_3 leaching following bark beetle disturbance, however the magnitude (maximum of 25 mg NO_3 l⁻¹) and duration (several years) did

not induce large-scale deterioration of surface water quality in drinking water supplies in the area (Huber 2005; Oulehle and others 2013; Beudert and others 2015). Elevated NO_3 leaching may have ecological consequences for surface water biodiversity through both eutrophication and acidification impacts. The MAGIC model correctly simulated long-term NO_3 lake water concentrations as well as the seasonal variations. Surplus of available inorganic N from mineralisation, especially from decomposing needles in the early stages of forest decay, was partly immobilised in regrowing vegetation and partly leached from the catchment soils. Our simulation highlighted the pivotal role of vegetation in nutrient immobilisation, as suggested by Rhoades and others (2013). It has been proposed (Edburg and others 2012) and observed (Kaňá and others 2015) that the immediate increase of available labile C after forest disturbance may stimulate mineral N consumption by microbes, thus delaying NO_3 leaching. Because the bark beetle propagation across the whole catchment took several years, these fine-scale dynamics will be largely smoothed by surface water NO_3 concentrations which integrate leaching from the whole catchment.

The model simulated somewhat higher NO_3 concentrations compared to measured data between 2004 and 2007 (Figure 4). The mismatch is consistent with DOC-mediated NO_3 immobilisation, which is not included in the model (Goodale and others 2005). Modelling nitrogen cycling is notoriously difficult as is measuring N fluxes such as N fixation and gaseous losses (N_2 , N_2O) and soil processes (for example, nitrification) at the catchment scale. We demonstrated that a relatively simple mass-balance approach is able to constrain N leaching, and provides a plausible mechanism of N retention on the catchment scale.

Further evidence of the pivotal role of forest regeneration dynamics after the bark-beetle disturbance came from mass-balance modelling of the base cations. Pre-disturbance model calibration constrained the weathering rates of BC and concentrations of base cations in lakewater. Mineralisation of dead biomass significantly increased the BC inputs into the soil. The model suggested that about 46 and 57% of Ca and Mg released from decaying trees was immobilised in regrowing vegetation during the period 2001–2016. As there are no BC sinks in the catchment other than uptake by vegetation and storage in the soil, the model predicted an increase of the soil BC pool and elevated BC leaching proportional to the NO_3 increases. Simulated Ca and Mg leaching and increases of the soil Ca and Mg pools matched the observations. Changing N, Ca, Mg mineralisation kinetics resulted either in underestimation of nutrient leaching (by halving the original k values) or in overestimation when k values were doubled. This further indicated that mineralisation and uptake nutrient kinetics were reasonably well constrained.

For K, on the other hand, these same assumptions on mineralisation and uptake gave a poor match between simulated and observed K mass balance. The MAGIC model underestimated the K leaching by 25% and predicted an increase of soil K pool. The measured data revealed only a temporary increase of soil K pool in 2010 compared to 2000 with no difference between the 2000 and 2015 estimates. It has been hypothesised, that in contrast to Ca and Mg, which are structurally bound in tissues, K is present in plant tissues as water soluble salts, thus prone to immediate leaching (Holub and others 2001). Preferential K leaching from canopy over other base cations was observed in Plešné Lake throughfall after forest infestation by the bark beetle (Kopáček and others 2011, 2017), consistent with the higher K mobility hypothesis. The high mobility of K may also partly explain the only transient increase of the measured soil K pool in 2010 and the higher measured vs simulated leaching rates. It is likely that the optimised K exchange selectivity coefficient in the MAGIC model represents conditions maintaining long-term weathering supply, thus overestimates the ability of K to adsorb to the soil exchange matrix. Contrary to N, Ca and Mg, K mineralisation is most likely not proportional to the decomposition of tree tissues, but progresses at rates higher than assumed in our modelling exercise. This was highlighted by sensitivity analysis where doubling the k values of K mineralisation resulted in well fitted modelled K leaching with observations. However, increased soil K availability immediately after tree death was likely a result of foliar leaching and subsequent failure of plant demand, besides than preferential K mineralisation of litter.

Implications for Long-Term Ecosystem Nutrient Dynamics and Surface Water Chemistry

In the control scenario with no bark beetle disturbance, only slow recovery from acidification of catchment soils and surface waters was predicted. Leaching rates of SO_4 and Cl reflected atmospheric inputs, and NO_3 leaching was constrained by the soil N mineralisation and atmospheric inputs on the one hand and N demands by decomposers and vegetation on the other hand. Similarly, concentrations of BC in lakewater balanced the acid anions as counter-ions such that lakewater pH and ANC were predicted to increase only slightly after 2004. In the bark beetle scenario, the excess of BC from mineralisation, which accelerated recovery of soil base saturation, coupled with only a temporary increase in NO_3 leaching from soil resulted in an unprecedented pH increase and, conversely, a decrease of Al_i in lakewater. As biological recovery in the lake is constrained by acidity and Al_i concentrations (Vrba and others 2016), any increase of lakewater alkalinity will have profound positive impacts on biodiversity in Plešné Lake.

Long-term ecological research in the Plešné Lake ecosystem (LTER site; https://data.lter-europe.net/deims/site/lter_eu_cz_003) provides science-based insights into the altered lake-catchment biogeochemistry affected by multiple stressors, starting with acidification in twentieth century, followed by biotic disturbances over the last two decades. Synthesis of monitoring data back to the 1980s was used to constrain nutrient budgets of the catchment. Measured data combined with well parametrised processes in the biogeochemical model MAGIC elucidated the role of tree mortality in unmanaged catchments in long-term nutrient dynamics. We demonstrated unexpected improvement of lake water quality following disturbance. Measured catchment characteristics together with modelled soil and lakewater chemistry emphasize the positive role of natural regeneration and provide evidence that exclusion of human intervention is an adequate practise in protected areas.

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Table 1. Fixed and Calibrated Parameters Used for the MAGIC Simulation at Plešné Lake Catchment

		Units	Values
Fixed parameters			
Average soil depth	Measured	m	0.33
Bulk density (< 2 mm fine fraction)	Measured	kg m ⁻³	281
Cation exchange capacity (CEC)	Measured	meq kg ⁻¹	130
Lake water retention time	Measured	year	0.92
CO ₂ partial pressure	Estimated	atm	0.48 (0.033)
Organic acids	Measured	mmol m ⁻³	50 (15)
pK ₁ (organic acids)	Measured	– log	3.5 (4.4)
pK ₂ (organic acids)	Measured	– log	4.4 (5.5)
pK ₃ (organic acids)	Measured	– log	5.5 (6.6)
Plant net base cations uptake*	Estimated	meq m ⁻² yr ⁻¹	14.9
Plant gross uptake N (2000)*	Estimated	mmol m ⁻² yr ⁻¹	638
Denitrification	Estimated	mmol m ⁻² yr ⁻¹	7.2
Litter C flux*	Measured	mmol m ⁻² yr ⁻¹	32,934
Litter C/N	Measured	mol mol ⁻¹	53
Organic C decomposition*	Estimated	mmol m ⁻² yr ⁻¹	32,292
Soil base saturation (2000)	Measured	%	15.7
Soil C/N (2000)	Measured	mol mol ⁻¹	24
Calibrated parameters			
SO ₄ adsorption half saturation		meq m ⁻³	95
SO ₄ maximum adsorption capacity		meq kg ⁻¹	35
Solubility Al(OH) ₃		log	8.5 (8.8)
Base cations (Ca + Mg + Na + K) weathering		meq m ⁻² yr ⁻¹	75.5
Initial (1860) base saturation		%	33.5
Initial (1860) soil C pool		mol m ⁻²	936
Initial (1860) soil N pool		mol m ⁻²	36
Microbial biomass C/N		mol mol ⁻¹	10
In-lake base cations sedimentation		meq m ⁻² yr ⁻¹	36
In-lake N retention		% of input	48

Values are for soil; lake values in brackets. Parameters marked by asterisk are time dependent; all others are held constant.

Table 2. Annual Calibrated Nutrient Fluxes (Weathering, Decomposition, Uptake— $\text{meq m}^{-2} \text{y}^{-1}$), Measured Nutrient Fluxes (Deposition, Soil Change— Δ , Leaching— $\text{meq m}^{-2} \text{y}^{-1}$) and Simulated Nutrient Fluxes (Soil Change— Δ and Leaching— $\text{meq m}^{-2} \text{y}^{-1}$) Over the Period 2001–2016 in the Catchment Plus Lake at Plešné Lake

Period	Weathering $\text{meq m}^{-2} \text{yr}^{-1}$	Mineralization	Uptake	Deposition	Δ Soil measured	Leaching measured	Δ Soil simulated	Leaching simulated	Leaching (Sim – Obs)/Obs %
2001–2016									
S	0	0	0	30	N.D.	63	- 38	69	10
Cl	0	0	0	14	N.D.	15	0	13	- 12
N	0	223	144	99	N.D.	67	- 1	73	9
Ca	20	80	37	16	30	51	23	49	- 4
Mg	14	21	12	5	4	19	6	19	- 2
K	7	35	19	5	0	18	13	13	- 25

Differences of elemental leaching between simulated and measured values in %. Soil base cations changes reflected exchangeable pools. Leaching of N represented as NO_3 .

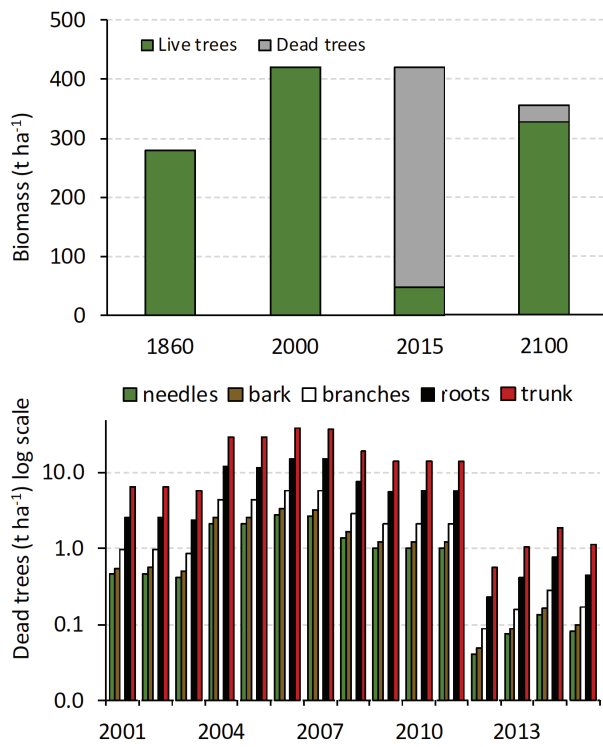


Figure 1. Biomass of live and dead trees in 1860 (estimated), 2000 (measured), 2015 (measured) and 2100 (estimated) (upper panel), and temporal development of the bark beetle dieback between 2001 and 2015 (lower panel), with depiction of each tree compartment.

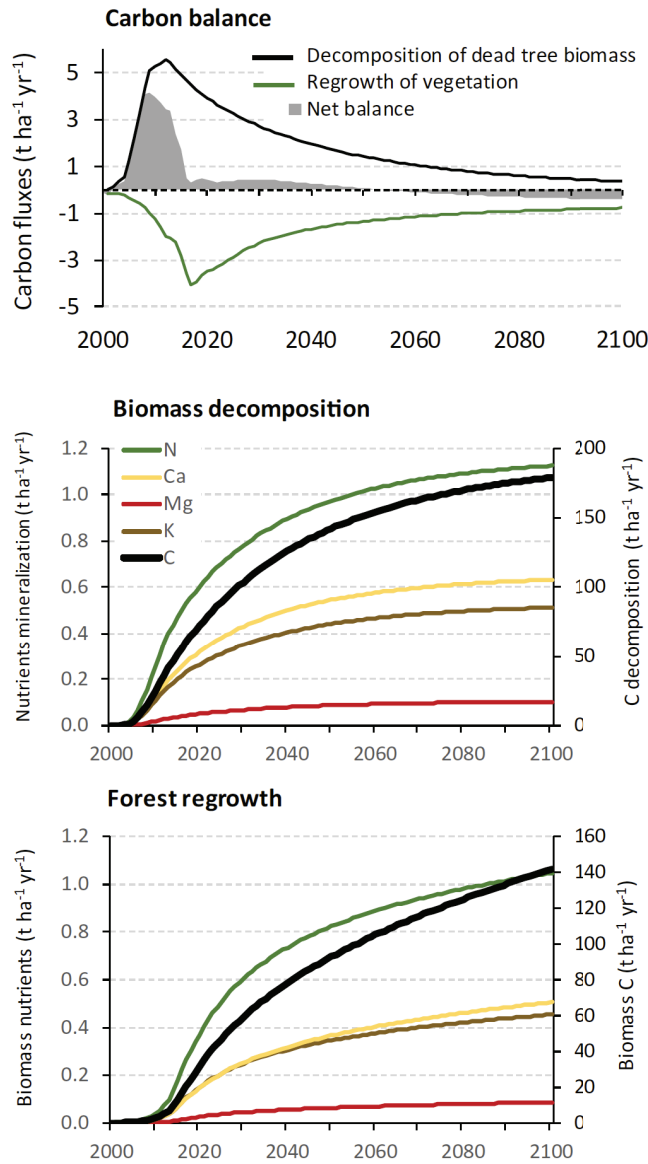


Figure 2. Dynamics of biomass decomposition, forest regrowth and calculated net carbon balance (upper panel), associated mineralisation of nutrients from decomposing tree biomass (middle panel), and rate of immobilisation of nutrients in regrown tree biomass in the Plešné Lake ecosystem (lower panel).

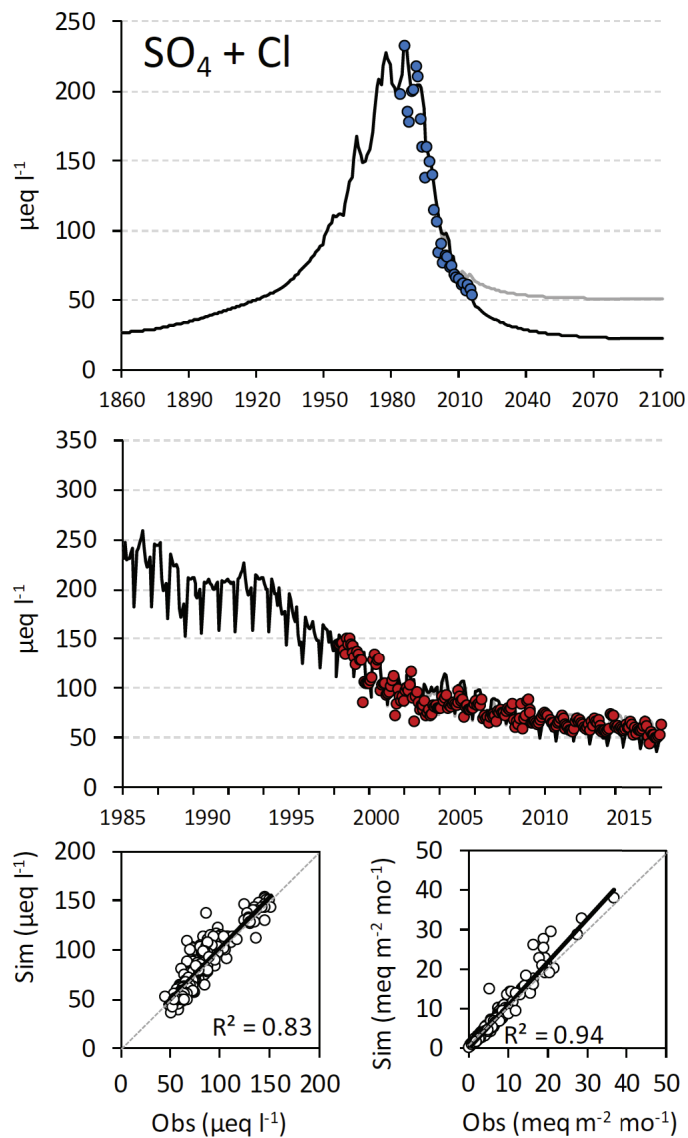


Figure 3. Concentrations of the sum of SO_4 and Cl in lakewater observed annually (blue dots) and monthly (red dots) and simulated (lines) for the period 1860–2100 (upper panel) and 1985–2015 (middle panel). The grey line is the control scenario (without bark beetle disturbance) and the black line is the bark beetle scenario. Observed (Obs) and simulated (Sim) monthly concentrations and fluxes are also shown with coefficient of determination (R^2) and linear regression line (lower panels) (Color figure online).

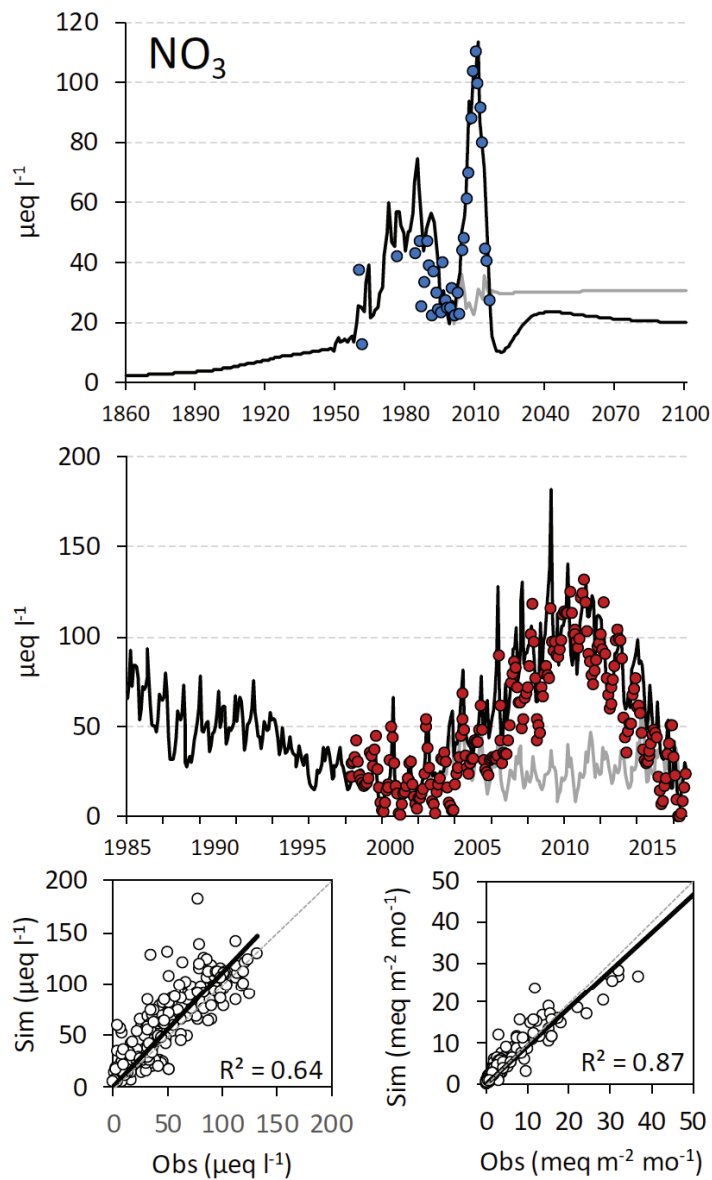


Figure 4. Concentrations of NO_3 in lakewater observed annually (blue dots) and monthly (red dots) and simulated (lines) for the period 1860–2100 (upper panel) and 1985–2015 (middle panel). The grey line is the control scenario (without bark beetle disturbance) and the black line is the bark beetle scenario. Observed (Obs) and simulated (Sim) monthly concentrations and fluxes are also shown with coefficient of determination (R^2) and linear regression line (lower panels) (Color figure online).

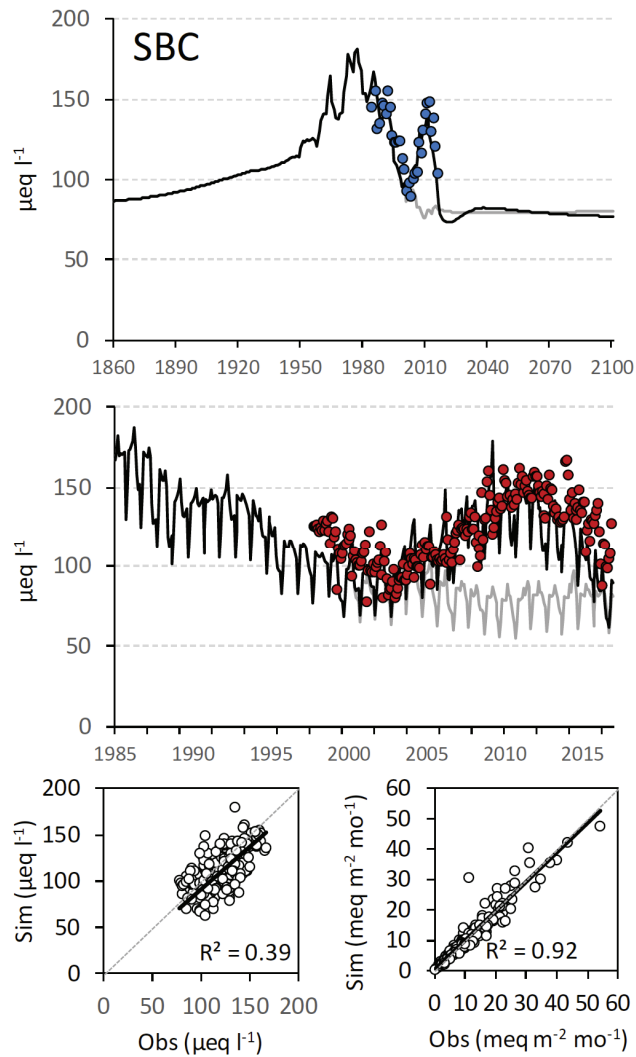


Figure 5. Concentrations of the sum base cations (SBC = Ca + Mg + Na + K) in lakewater observed annually (blue dots) and monthly (red dots) and simulated (lines) for the period 1860–2100 (upper panel) and 1985–2015 (middle panel). The grey line is the control scenario (without bark beetle disturbance) and the black line is the bark beetle scenario. Observed (Obs) and simulated (Sim) monthly concentrations and fluxes are also shown with coefficient of determination (R^2) and linear regression line (lower panels) (Color figure online).

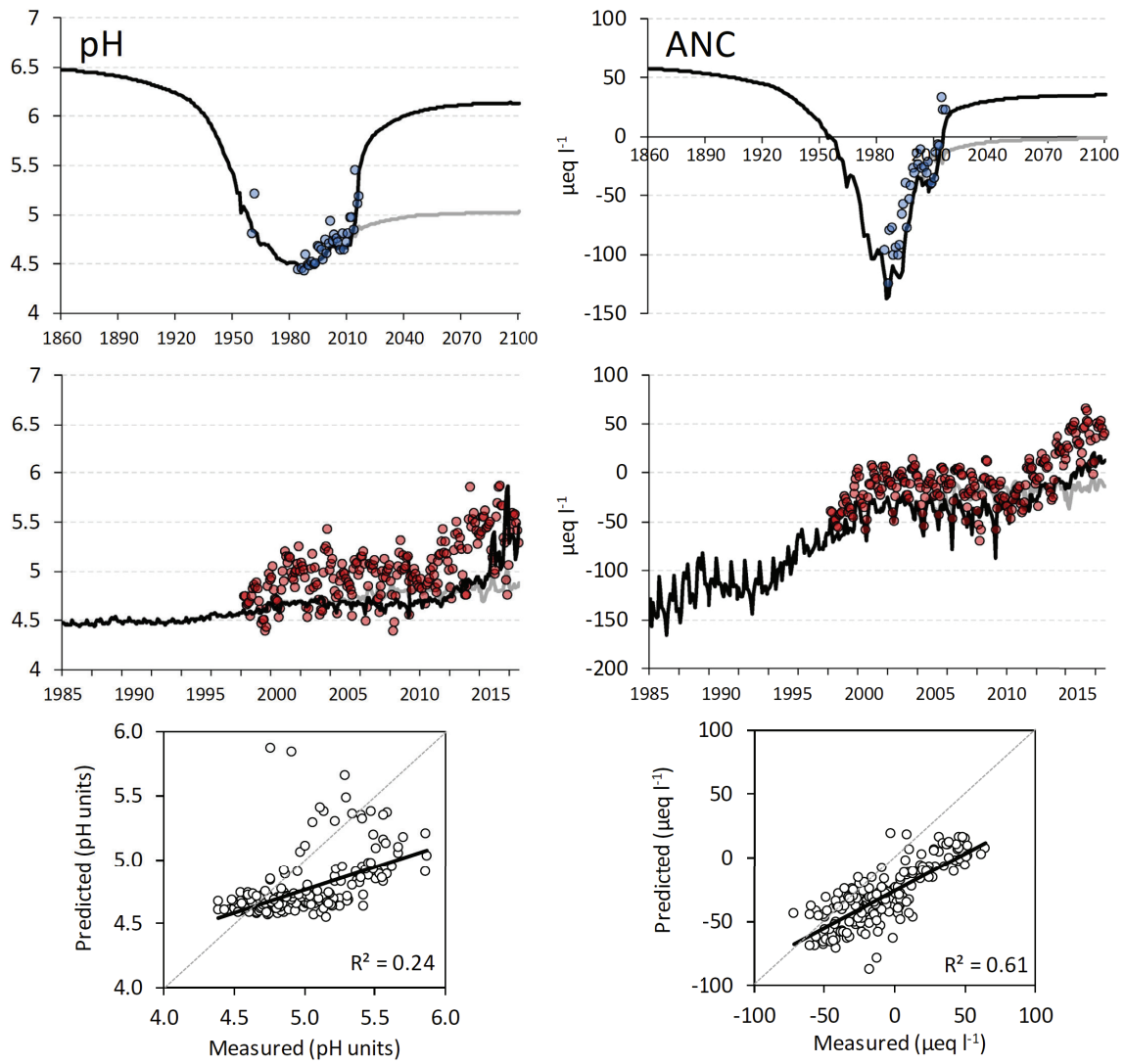


Figure 6. Acid neutralising capacity (ANC) and pH in lakewater observed annually (blue dots) and monthly (red dots) and simulated (lines) for the period 1860–2100 (upper panel) and 1985–2015 (middle panel). The grey line is the control scenario (without bark beetle disturbance) and the black line is the bark beetle scenario. Observed (Obs) and simulated (Sim) monthly concentrations and fluxes are also shown with coefficient of determination (R^2) and linear regression line (lower panels) (Color figure online).

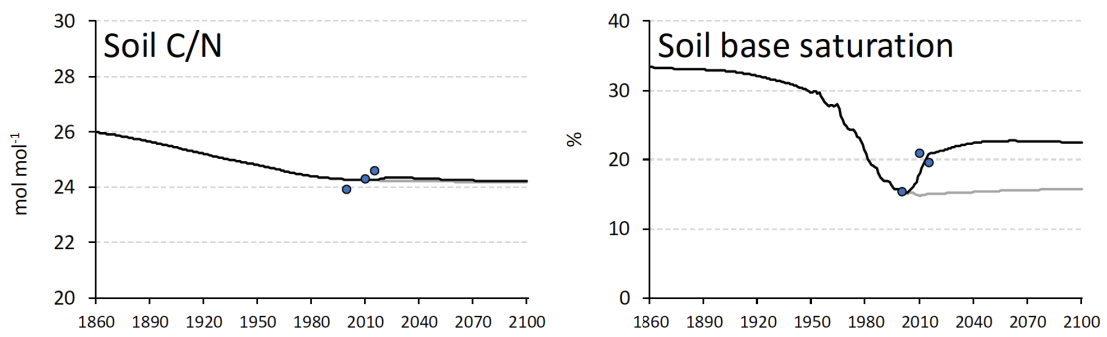


Figure 7. Observed (blue dots) and simulated (grey line—control, black line—bark beetle disturbance) soil C/N (mol mol⁻¹) and soil base saturation (%) over the period 1860–2100 (Color figure online).