Biogeomorphological domination of forest landscapes: An example from the Šumava Mountains, Czech Republic

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ARTICLE INFO

ABSTRACT

Biogeomorphological and ecological succession following a disturbance or the exposure of new ground often proceeds in stages, from domination by abiotic, geophysical factors through stages characterized by increasing effects of biota, biotic-abiotic feedbacks, and eventual domination by ecological processes. However, some studies in forest settings have found more varied development patterns, including persistence of states dominated by biogeomorphic feedbacks. In this study we investigated this phenomenon In Norway spruce (*Picea abies* (L.) Karst.) dominated forests on the main ridge of the Šumava Mountains in the Czech Republic along the German and Austrian borders. Throughout most of the Holocene, *Picea* has strongly influenced microtopography and soil/regolith characteristics so as to inhibit hydrological connectivity and development of surface drainage, and maintain hydromorphic soil conditions. These strongly historically and geographically contingent ecosystem engineering effects create and maintain habitat that favors spruce over other trees. These interactions have maintained a landscape dominated by biogeomorphic feedbacks.

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1. Introduction

After a disturbance or the exposure of new substrate, landscape evolution often follows a general trend. At the outset, abiotic phenomena and geochemical and geophysical processes are dominant. Biota soon colonize, and begin influencing the abiotic environment via processes such as biotic weathering of exposed rock, stabilization of substrates, sediment trapping, and production of organic matter. The biotic/abiotic reciprocal interactions and feedbacks typically intensify, with increasing domination by ecological interactions. In later stages, unless or until a large disturbance or change in boundary conditions occurs, ecological processes dominate and abiotic processes are diminished in importance. However, in some cases more variable and complex developmental trends occur, and landscape states dominated by biogeomorphic interactions may persist. This paper examines one such case, in spruce dominated forests of the main ridge of the Šumava mountains in central Europe, to assess the persistence of biogeomorphic domination, and the extent to which biogeomorphic ecosystem engineering in this environment benefits the engineer species.

This general sequence above is explicit in the biogeomorphic succession concept developed by Corenblit et al. (2009, 2014), who focused on

fluvial and riparian environments. The concept was later applied to coastal, wetland, and other water-terrestrial interfaces in general (Corenblit et al., 2015), glacial moraine slope development (Eichel et al., 2016), subalpine alluvial fans (Lane et al., 2016), and recently deglaciated areas (Miller and Lane, 2019). The sequence is implicit in primary ecological succession in general, where sequences lead from newly exposed abiotic surfaces to mature ecosystems (Walker and del Moral, 2011). This is particularly evident in bare-rock succession, where the biogenic weathering that initiates soil formation and facilitates subsequent biological colonization is strongly controlled by the mineral composition of the material and its initial porosity and other physical properties (Chizhikova et al., 2016; Ciccazzo et al., 2016). In some mature communities, however, vegetation and other biota may have no direct dependence on properties of underlying rocks.

As widely recognized by studies of biogeomorphic or ecological succession in recent decades, there are often multiple possible succession pathways, and biogeomorphic changes may take the form of state transitions that do not conform to a linear successional model. In some coastal salt marshes, for example, Wang and Temmerman (2013) found that biogeomorphic feedbacks result in oscillation between alternative stable states. In Mojave Desert landscapes, Pietrasiak et al. (2014) showed that biotically or abiotically-dominated evolutionary trajectories may occur, depending on bioturbation. Complex patterns of geomorphological/ecological state transitions were found in coastal landscape responses to sea-level rise by Phillips (2018a).

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In the abiotic domination phase (Fig. 1), organisms and biological effects may be present, but are minimal compared to geophysical and geochemical processes and are overwhelmed by the latter. In the abiotic/biotic feedbacks stage, biological effects are still secondary, but have begun to have important impacts on landforms and surface processes. The word reversal in the biotic/abiotic feedbacks phase indicates the biological processes are at least co-dominant—this is the stage where biogeomorphological domination may occur. Finally, in the biotic phase, geophysical and geochemical processes are secondary to biological factors, or at least manifested chiefly through ecological effects.

1.1. Studies in old-growth forests

In a beech-dominated old-growth forest in the flysch Outer Western Carpathians in the Czech Republic, Phillips et al. (2017) found that hillslope processes at the Razula forest preserve are dominated by tree uprooting. Regolith disturbed by uprooting is the major form of mass wasting at the site, and secondary forms (soil and rock creep, ravel, and small avalanches) occur mainly on slopes of the resulting pit-and-

Fig. 1. A: General pattern of biogeomorphic succession proposed by Corenblit et al. (2009).
B: Biogeomorphic state transition model for old-growth forests.
Adapted from Figs. 9 and 10 of Phillips et al. (2017).

mound pairs. Surface runoff is dominated by the pit-mound topography created by uprooting, with short, unconnected overland flow paths delivering flow to tree throw depressions. Based on these results, Phillips et al. (2017) produced an alternative state-and-transition type model to the biogeomorphic succession sequence (Fig. 1). The key points of the alternative scheme are that a progression from abiotic to biotic domination is not inevitable, other transitions are possible; and that, at least in a forest with minimal direct human interventions, a biogeomorphic domination state may persist for long periods.

In another Czech old-growth forest, Žofínský Primeval Forest (hereafter Zofin) on granite, Šamonil et al. (2020a) examined the role of tree uprooting in soil erosion and deposition on both millennial and decadal time scales using meteoric and *in situ* ^{10}Be and $^{239+240}$Pu, respectively, combined with 43 years of monitoring of tree layer changes, including uprooting. They found that tree uprooting is the main driver of denudation over the last several millennia in this fir-spruce-beech (*Abies alba-Picea abies-Fagus sylvatica*) forest. At a third site (Boubínský Primeval Forest on gneiss and migmatite) dominated by spruce and beech, Šamonil et al. (2018) evaluated biomechanical geomorphic effects of 4000 standing and lying trees in a 10.2 ha area. Such effects were recorded for 59% of standing and 51% of lying dead trees (not counting effects associated with nearly all trees such as soil displacement by thickening trunks and roots and the infilling of decayed stumps). Active bioprotection (sediment trapping and promoting deposition, vs. the ubiquitous passive bioprotection of nearly all living plants) was the most frequent phenomenon observed, while uprooting prevailed in terms of areas and soil volumes affected. The other eight studied biomechanical effects of trees were not so frequently observed, but still geomorphologically significant.

A key issue is the extent to which the biogeomorphic ecosystem engineering (BEE) effects favor the engineer species. At Razula, tree throw mounds are favorable sites for establishment of new trees, which (like the uprooted trees) are mostly European beech (*Fagus sylvatica*); similar results have been found in other central European beech forests (Šebkova et al., 2012). However, It is difficult to prove positive ecosystem engineering effects, as the seed and propagule source is overwhelmingly beech, and the habitat conditions on the mounds, which include good drainage and increased sunlight, are favorable for many plants. If propagules of other trees were present, they might fare equally well on the mounds. Kern et al. (2019), for example, found that mounds in mixed hemlock and hardwood forest favored light-seeded tree species sensitive to browsing. The limited overland flow and increased infiltration associated with uprooting effects (Phillips et al., 2017) also create favorable soil drainage conditions for *Fagus*, which prefers moist but not saturated sites, but has not been demonstrated to preferentially facilitate beech vs. other trees.

Similarly, results at the other old-growth sites (Šamonil et al., 2018, 2020a) are consistent with BEE effects that help maintain forest cover and are generally favorable to the engineer species. However, largely because of the paucity of propagule sources for potential competitor or alternative species, and ecosystem engineering effects that do not uniquely or preferentially favor the engineer species, it is difficult at present to demonstrate that these effects preferentially favor the BEE trees.

1.2. Other forests

In Eucalypt forests of Australia, Verboom and Pate (2006a, 2006b, 2013); Pate and Verboom (2009) developed the phytotarium concept, whereby specific plant layers and associated microbes create niches to maximize access to limiting resources of water and nutrients. The ecosystem engineering they describe occurs largely due to impacts on soil and regolith development, and includes lateritic imprints of cluster-root plants and clay pavements from lateral root catchments of eucalypts. They also present evidence of tree-driven biogenic formation of silcretes and ferricretes, hydrophobic surface layers, low-permeability
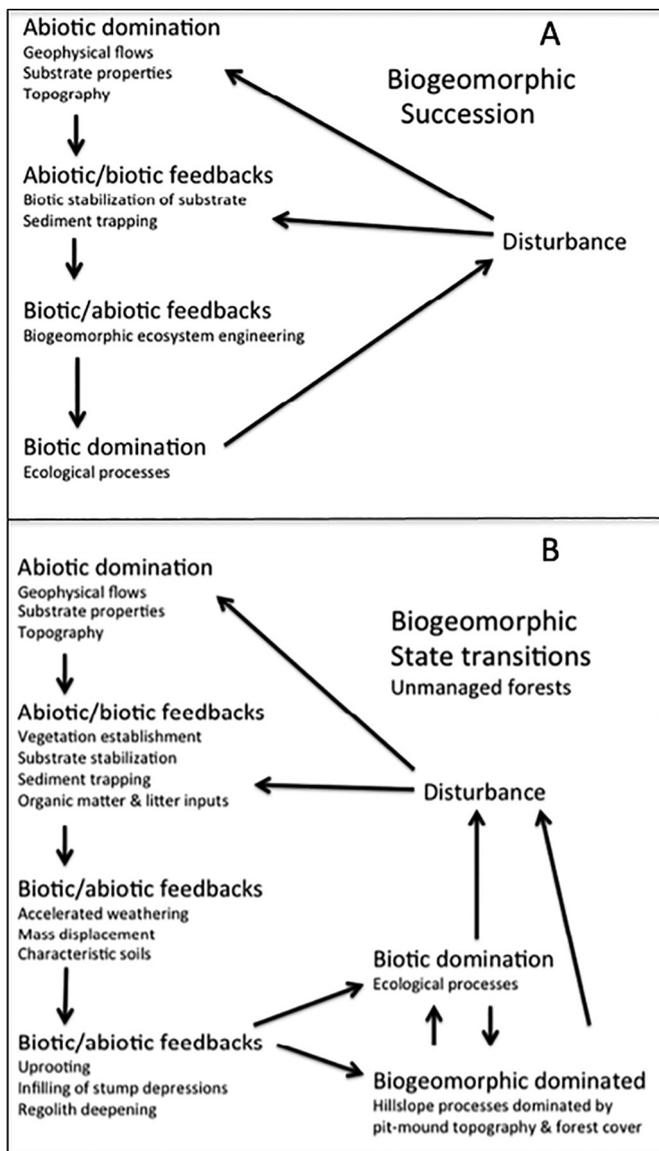
subsoil layers, clay translocation, Si translocation, water conduits, sand binding, and root channels lined with ferricrete and silcrete. In these forests the ecosystem engineering does seem to preferentially favor the Eucalypts.

In karst landscapes of central Kentucky, *Quercus muehlenbergii* (chinkapin oak) is a biogeomorphic ecosystem engineer. The species is able to penetrate limestone joints and fissures, where it facilitates weathering and soil formation, resulting in soil-filled rock partings and thicker soils that are favorable for future establishment of trees in general and *Quercus muehlenbergii* in particular (Phillips, 2016). However, this form of ecosystem engineering by chinkapin oak and other trees is self-limited, once a sufficiently thick substrate has developed (Phillips, 2018b). Further, there is no evidence that *Q. muehlenbergii* is a bigeomorphic keystone species in this setting. Jerin and Phillips (2020) defined biogeomorphic keystones are species whose removal from, or introduction into, a landscape would result in major geomorphic changes.

Ecological succession on deglaciated plots in Glacier Bay, Alaska monitored for 100 years show the woody plant community "stuck" in a *Salix* dominated state, despite expectations that *Salix*, a successional pioneer on the plots, would give way to other species (Buma et al., 2017). The mechanisms allowing *Salix* to maintain dominance are not yet understood, but the results raise the possibility that positive ecosystem engineering, biogeomorphic or otherwise, could play a role.

1.3. Longer time scales

Over longer time scales of biological and Earth system evolution, there exists evidence of positive ecosystem engineering and niche construction by trees and forests on very broad spatial and temporal scales. The Devonian plant hypothesis (DPH) seeks to explain climate changes and mass extinctions in the Late Devonian period, where one of the most dramatic losses of diversity in the Earth history occurred. Originally proposed by Algeo et al. (1995) as the Devonian plant-weathering hypothesis, the DPH links minerals that indicate low oxygen availability to the expansion of plants (and especially forests). The increase in vegetation is thought to have contributed to eutrophication in shallow seas and accelerated silicate weathering, reducing CO_2 globally due to chemical weathering reactions that derive CO_2 from the atmosphere. This, according to the DPH, reduced global temperatures, potentially causing short but intense glacial periods (Berner, 2006; Algeo and Scheckler, 2012).

Pawlik et al. (2020) evaluated the DPH and other hypotheses of the extensive global changes that occurred in the Devonian in light of the biogeomorphic engineering effects of trees, particularly on weathering. They found that trees can be considered biogeomorphic ecosystem engineers in the Devonian, but that the scope of forest and tree influences on weathering and soil formation is still unclear. While many aspects of BEE by trees in the Devonian are still uncertain, Pawlik et al.'s (2020) synthesis indicates that, at least, trees and early tree-like plants coevolved with certain soil types, and with meandering (or other non-braided) river systems. These effects alone resulted in landscape metamorphoses that favored woody plants and forests, though information is insufficient to determine whether certain taxa were favored by BEE effects relative to others.

The goal of this paper is to explore the possibility of an extended period of landscape evolution dominated by biogeomorphic feedbacks, and that these ecosystem engineering effects benefit the engineer species.

2. Study area

The Šumava Mountains are part of the Bohemian Forest region of the Czech Republic, Germany, and Austria (Fig. 2). The Šumavas are the highest uplands of the Bohemian Massif. They create a natural border between the Czech Republic on one side and Germany and Austria on the other. The range is the largest forested area in central Europe. The
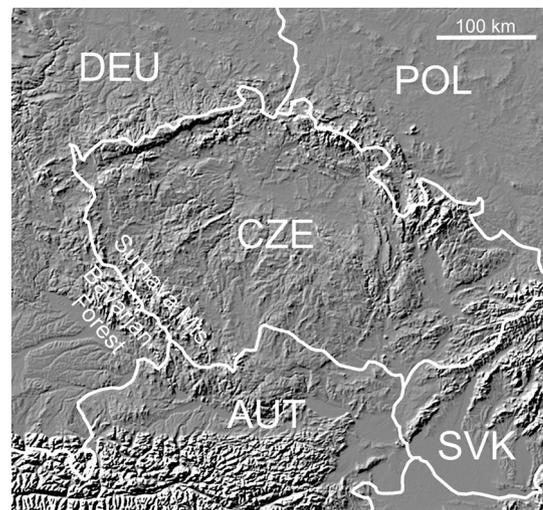
Fig. 2. Study area. The Sumava Mountains and Bavarian Forest are contiguous Czech and German national Parks.

climate is humid temperate. Mean annual precipitation along the main ridge ranges from 800 to 1600 mm yr^{-1}. Minimum monthly precipitation occurs in early spring (April); the maximum in July.

The main ridge and summits range from about 800–1400 masl. The underlying geology is comprised of crystalline igneous rocks—gneiss, granites, and mica schist. Peat bogs occur in valleys. Soils at higher elevations are highly acidic and organic, and often are informally described as peaty. However, they typically do not have organic matter thick enough to qualify as Histosols in the World Reference Base classification system (>10 cm thick histic horizon on solid rock or >40 cm elsewhere). In the 1:50,000 soil map of the Czech Republic (https://mapy.geology.cz/pudy/) and in Daněk et al. (2016) the soils are classified as Dystric Cambisols, Entic or Albic Podzols, Haplic Histosols, and Histic or Haplic Gleysols. Leptosols are also present.

This research was initiated to explain field observations in the Šumava Mountains of very low drainage density and limited evidence of channelized surface drainage at higher elevations (Fig. 3). This occurs even though the climate is moist, hydromorphic soils are present, and high water tables were frequently observed. Further, fluvial dissection is present at lower elevations nearby and in valley bottoms.

2.1. Setting the stage

Though continental ice sheets did not reach it, the Šumava region experienced mountain glaciation in the late Pleistocene (Nývlt et al., 2011;

Fig. 3. View of a portion of the Šumava main ridge from the Boubin observation tower (1362 masl). Note the lack of evident fluvial dissection.

Mentlik et al., 2013; Krause and Margold, 2019). Glaciers were confined to high elevations (generally above 1200 masl) and valleys, and lower elevations experienced periglacial conditions. [10]Be exposure ages from moraine boulders obtained by Mentlik et al. (2013) cluster into three groups. The oldest moraines of the late Weichselian glaciation in the Bohemian Forest formed ~19.5 ka. Later advances of local glaciers occurred around 15.7 ± 0.6 ka and 16.2 ± 1.4 ka. The youngest moraines have exposure ages of 13.7 ± 1.3 ka and 14.1 ± 1.1 ka.

Glacial debris, and rock fragments produced by periglacial hydrofracturing, thus produced a substrate of thin, rocky soils on the main ridge at the altitudinal range 800–1400 masl on the main ridge of the Šumava Mountains (Hartvich and Mentlík, 2010; Mentlik et al., 2010; Rypl, 2010; Rypl et al., 2014). Lower altitudes have never been glaciated (Krause and Margold, 2019) and are frequently occupied by deeper soils and thicker weathering profiles (Šamonil et al., 2020b).

A postglacial spread of woody vegetation occurred in the region, associated with changes in hillslope dynamics and disturbance regimes. In the earliest Holocene mountain forests were dominated by *Pinus sylvestris*, with *Picea abies* following. European beech (*Fagus sylvatica*) began increasing around the mid-Holocene. The disturbance regime was modified, with decreased fire associated with beech. The spread of spruce led to more vulnerability to uprooting by wind, and to spruce bark beetles (Willis and van Andel, 2004; Carter et al., 2018; Bobek et al., 2019). More temperate trees such as beech and fir (*Abies alba*) migrated from areas further south, while spruce and boreal woody species apparently survived the glacial maximum and late ice age within the Šumavas (e.g. Tollefsrud et al., 2008; Mandák et al., 2016).

Paleobotanical studies at higher elevations in the Šumava region found broadly similar trends, but with differing details. Svobodová et al.'s (2001) palynological studies indicated that open, park-like plant cover existed in the Oldest Dryas/Bøling. *Pinus* and *Betula* woodland developed in the Allerød. The Younger Dryas featured steppe tundra, followed in the Pre-boreal by woodland tundra. During the Boreal (8.8–7.5 ka BP) *Corylus* (hazel) spread, and a major expansion of *Picea* began in the early Boreal. Spruce expansion continued during the Atlantic (7.5–5 ka). *Fagus* had its major expansion in the early, and *Abies* in the late Atlantic.

Humans were present by 3.3 ka (Kozáková et al., 2021). Later, plantation of *Picea* during the historical period interrupted the natural (non-human) vegetation development. From the 1700s to establishment of the national parks, spruce-based forestry was the main human impact at higher elevations. Kozáková et al. (2021) recently used pollen and charcoal indicators to determine the prehistoric human impacts in the Šumava mountains. They detected secondary pollen indicators of anthropic vegetation change from 3.3 ka. These varied in intensity at different sites, but were stronger at sites dated to the late Bronze and Iron ages, some of which are located on trade routes known since Medieval times but which are likely much older. Pollen data reveal no specific prehistoric human activities such as farming or grazing, but reflect small-scale disturbances. These human impacts could be linked primarily to activities along trade routes and to hunting, but Kozáková et al. (2021) indicated that other factors cannot be excluded. In general, palynological studies have concluded that while prehistoric human interventions may have affected local vegetation composition, they likely had minimal effects at the regional scale (Svobodová et al., 2001, 2002; Bobek et al., 2019; Kozáková et al., 2021).

In the study region a typical sequence saw *Picea* dominating from about 6 ka, then *Picea/Fagus*, and later *Abies* from about 4 ka (Svobodová et al., 2002), though fir was probably never dominant at the highest elevations. In the 18th century spruce monoculture was established by the forest industry, although some primeval forests survived up to the present. Vočadlova et al. (2015) developed multi-proxy records for the Bohemian Forest, which indicate domination by *Betula* in the latest glacial period, and stabilization and domination of *Picea* (and expansion of *Fagus*) at 8.2 Ka. Macrofossils and pollen from spruce appeared in the record by 10.1 ka. Vočadlova et al. (2015)

also found that around 10.5 ka, tree line descended to about 1000 m elevation, consistent with periglacial conditions above treeline.

The glacial and periglacial Pleistocene regime at higher elevations, mostly absent at lower elevations, was important in creating conditions of thin soils and abundant rock debris when spruce became established.

3. Methods

Based on initial field observations in 2016, we developed the hypothesis that biogeomorphic effects of *Picea abies* (Norway spruce), which dominates forest composition, are primarily responsible for the limited development of surface drainage channels. We postulated that irregular, hummocky topography associated with basal and root mounding of spruce trees, tree uprooting and resulting pit-mound systems, and (to a lesser extent) stump depressions limit the length of overland flow, inhibiting incision and channel formation. Further, we hypothesized that the root architecture of the trees and the nature of the root zone, soil, and regolith (critical zone) also inhibit concentrated subsurface flow paths that might promote channel incision through exhumation or seeps and springs. To test this hypothesis we relied on:

- Recently completed and ongoing studies of biogeomorphic impacts of trees at several Czech old-growth forest sites, including one within and one just outside the Šumava region. Methods are described by Šamonil et al. (2017, 2018, 2020a).
- Additional field observations to confirm the presence of the proposed mechanisms by which *Picea abies* affects soil and hillslope hydrology.
- An extensive literature review of hydrological, ecological, pedological, and geomorphological studies in the Šumava region.
- Analysis of digital elevation models (DEM), described in more detail below.

If the ecosystem engineering effects of trees act to reduce surface channels and drainage density as we hypothesize, then the drainage density should be less than that expected by usual topographic convergence and flow accumulation. To compute the latter, we analyzed a 30 m resolution DEM obtained from ALOS (Advanced Land Observing Satellite) World 3D, a digital surface model captured by the Japan Aerospace Exploration Agency and known as AW3D30 (https://www.eorc.jaxa.jp/ALOS/en/aw3d30/). Boulton and Stokes (2018) compared three 30 m resolution DEMs and one 12 m resolution DEM with respect to analysis of fluvial landscape development in mountainous terrains. They concluded that the AW3D30 data performed better than the other data sets and currently offers the best choice for regional mountain geomorphological analyses. The same three 30 m DEMs were compared by González-Moradas and Viveen (2020) in the Peruvian Andes. An analysis of drainage networks showed that all three 30-m DEMs (AW3D30, ASTER, and SRTM3) were capable of producing a similar number of Strahler orders, total number of channels, minimum and maximum channel length and accumulative channel length. All produced accurate networks in the upper reaches of the catchments (the main interest in this study), though they did less well in wide fluvial valleys.

High-resolution LiDAR DEM data are available for portions of the study area. However, the 30 m data were used to allow coverage of the entire main ridge area, and to facilitate computations. Further, higher-resolution DEMs will generally result in the extraction of more channels and lead to higher drainage density estimates. A 25 to 30 m resolution typically offers good agreement with channels extracted using aerial photography and consistent with field observations (Ariza- Villaverde et al., 2015; Boulton and Stokes, 2018; González-Moradas and Viveen, 2020). In any case the 30 m DEM provides a more conservative estimate of drainage density than higher-resolution datasets.

A flow grid was extracted using a standard D8 flow direction algorithm from a depression-filled version of the DEM. A treefile network

was extracted, pruned at a threshold Strahler order of 3; an effective threshold drainage area of 4370 m^2 (4.37 ha). Analysis was conducted using RiverTools™ software (Rivix, Inc.).

Field observations were in the form of a regional reconnaissance survey. In 2016 these were focused on higher elevations (>800 m) between the road connecting the Czech towns of Prasily, Modrava, and Kvilda and the German border. In 2018 we examined the national park area along the Czech-German border near Brezik (CZ), Waldhauser (DEU), and the Upper Vydra River, the main ridge near Horni Vltace, and the ridges near Jezero Laka, a glacial lake.

With the exception of detailed measurements at Boubínský Primeval Forest reserve (reported in other studies, cited below), our observations were based on visual assessments of (1) biogeomorphic impacts of trees (basal mounding, root mounding, stump depressions, and uprooting; see Šamonil et al., 2018, Fig. S1); (2) thickness and rock fragment content of rootwads of uprooted trees; (3) forest composition (extent of domination by Norway spruce); (4) evidence of surface runoff and channelized drainage; and (5) presence of hummocky topography.

4. Results

4.1. Field observations

We hypothesized that *Picea abies* influences local topography and drainage patterns primarily via the biogeomorphic effects of basal mounding at the trunk, and effects of uprooting. Some trees, including Norway spruce, displace soil at the base of the trunk and root crown, producing pronounced mounds. These were observed ubiquitously in the region, typically resulting in mounds 20 to 40 cm higher at their peak than the surrounding ground surface outside the mounded area. The ubiquity of such mounds in summit and flat areas implicates displacement by tree growth rather than trapping and deflection of transported sediment as the major mechanism. We also observed mounding associated with soil displacement by large near-surface roots, and with fallen trunks (Fig. 4).

Essentially all mature spruce trees were observed to have visibly evident basal mounding (Fig. 5). Root mounding by lateral roots away from the root crown at the base of the tree was less common. In addition to lower, apparently undisturbed, ground between spruce mounds, we frequently observed depressions associated with decomposition of stumps of dead trees (Fig. 4). These were recognized by a size commensurate with the basal diameters of mature spruce and undecomposed stumps, and remnants of partially decomposed wood. While all trees that die in standing position (as opposed to uprooting) would presumably leave voids within the soil as decay proceeds, a far smaller number of visibly evident holes or depressions were observed. At the Boubínský Primeval Forest reserve, an old-growth forest at elevations of 925–1050 m nearby, such holes were recorded for only about 1% of non-uprooted dead trees and were less common for spruce than for beech and fir (Šamonil et al., 2018).

Microtopographic highs were also observed associated with lying trunks of deceased trees. These were due to the local accumulation of decomposing wood, and additional organic matter produced by vegetation growing on the decomposing trunks. Living, standing dead and downed trees also often trapped slope sediment on steeper slopes. This was observed for about 50% of all trees at Boubínský (Šamonil et al., 2018), but is less relevant for the less steep summit areas.

Tree uprooting is a major source of topographic change (Šamonil et al., 2015, 2017, 2018, 2020a). The uprooting of trees in strong windstorms displaces substrate held within the roots. As this material sloughs off the rootwad and the roots decompose, a mound is formed adjacent to the pit formed by the soil removal. A major regional windthrow event occurred with the Kyrill storm of 2007, and a more localized but intense blowdown event in 2017 (Herwart storm). However, at least one strong windstorm was historically recorded in the Šumava region each century. Huge areas of the Šumava forested

Fig. 4. Top: root mound associated with large lateral root (soil probe for scale). Bottom: Fern growing in stump rot depression.

landscape were strongly affected by strong storms and subsequent bark beetle outbreaks in 1612, 1740, 1840s, 1868, and 1870 (Dobrovolný and Brázdil, 2003; Brázdil et al., 2004).

The root wads of uprooted trees also show the shallow, laterally oriented root systems of *Picea abies*. While spruce has some phenotypic plasticity in root adaptations to environmental conditions (see Puhe, 2003), and variations certainly occur within the study area, the spruce we observed overwhelmingly exhibited shallow, laterally oriented root systems. There is also the chance that shallow-rooted individuals

Fig. 5. Examples of hummocky microtopography on the Šumava main ridge. In both areas shown spruce trees killed by the spruce bark beetle (*Ips typographus*) have been removed. In the lower photograph natural regrowth of spruce is evident. The mounds are mainly due to basal mounding.

Fig. 6. Root wads of uprooted trees at higher elevations in the Šumava Mountains. These show that the trees are rooted in rock debris produced by periglacial and glacial processes.

are preferentially uprooted, potentially biasing our observations. However, our assessments included several locations (e.g., Polednik Mountain) where nearly all mature trees were uprooted in the 2007 Kyrill storm, greatly reducing this potential source of bias. Most in the summit area also show that the trees were rooted in gravel to boulder size rock debris derived from periglacial and glacial processes as described earlier. Fig. 6 shows some examples. In some cases roots could penetrate joints or fractures in underlying bedrock, and pluck fragments from this underlying rock as they uproot. However, the shallow rooting depth of the trees, and the highly variable orientation and weathering

of the displaced rock fragments suggest that most were part of a rubble layer in the regolith.

The shallow, laterally oriented root systems (Fig. 7) have several implications. Their concentration in the upper regolith, and lack of a central taproot, limit spruce's ability to deepen the soil beneath them, as is common in tap-root type species (see, e.g., Shouse and Phillips, 2016). This root architecture also contributes to a greater propensity to uproot than other trees common in the region, and contributes to a higher propensity for basal mounding in spruce (Šamonil et al., 2017). Moisture flux along roots and root channels is also, accordingly, shallow

Fig. 7. Root wads of uprooted *Picea abies* showing the typical shallow, laterally oriented root systems.

Table 1

Summary of biogeomorphic impacts of *Picea abies* relevant to drainage development on Šumava Mountains main ridge.

Biogeomorphic effect	Process or mechanism
Basal mounding	Soil/regolith displacement by growth of trunk & root crown
Root mounding	Soil/regolith displacement by growth of large lateral roots
Downed trunk mounding	Accumulation of partially decomposed wood & organic matter derived from vegetation growing on decomposing trunk
Tree uproot mounding	Accumulation of soil/regolith displaced by root wads of trees uprooted by wind
Tree uproot pits	Removal of soil/regolith displaced by root wads of trees uprooted by wind
Root channels	Hydrological fluxes along roots & root channels dominated by lateral flow
Bedrock weathering	Limited facilitation of weathering by tree roots due to lateral root architecture
Stump depressions	Decomposition of tree stumps and roots

and laterally oriented, with less concentration of flow than with tap or cluster root architectures.

The observed biogeomorphic impacts of *Picea abies* potentially relevant to microtopography formation and change and development of drainage in the higher elevations of the Šumava Mountains are summarized in Table 1. A detailed and comprehensive examination of biogeomorphic impacts of spruce and other trees at the Boubínský site is given by Šamonil et al. (2018).

In our field observations we did not observe surface runoff in the form of sheet, rill, or channel flow, except on unpaved roads and artificially constructed ditches to channel road runoff. A key issue in surface runoff connectivity is whether depressions are filled. We did not observed any intermound lows, tree uproot pits, or large stump depressions even holding water, much less filled (some smaller stump depressions did show high water tables), even though some of the fieldwork was conducted in rainy weather. We also did not note wrack indicating any previous filling of depressions, or evidence of surface runoff such as rills, bare soil, or organic debris micro-dams. Potential flow lengths (possible gravity-driven paths from local highs to lows) were generally <2 m.

4.2. Terrain analysis

A 5475 km^2 area of the Šumava Mountains was selected for terrain analysis (Fig. 8). The nearly 6.3 million 30 m pixels in the area have drainage areas ranging from 0.06 to 160,000 ha, with a median of 0.189 (Fig. 9). This indicates that in terms of macro-topographically driven flow accumulation, there exists more than adequate support for the formation of stream channels.
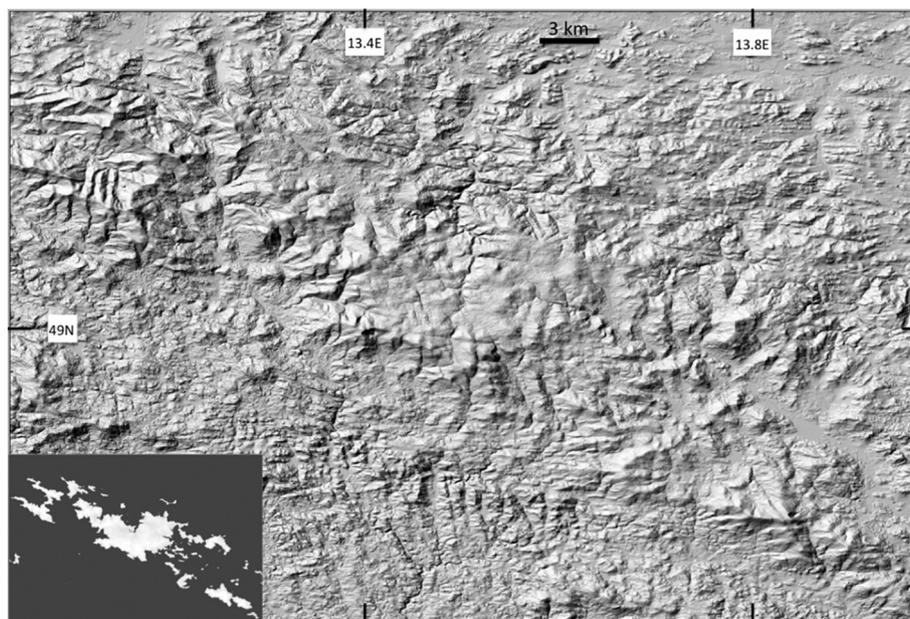
Fig. 10 shows the channel network extracted from the DEM. This shows drainage channels extending well into the main ridge area, and high drainage densities there—if all the macro-topographically defined channels actually existed. Drainage density for the 3rd order network is 6.39 km^{-1}. Fig. 11 shows samples of the much sparser drainage network mapped as blue lines on 1:25,000 topographic maps. Even allowing for the fact that "blue" line analyses typically show fewer channels that those extracted from DEMs, the differences are striking.

The terrain analysis shows that the limited fluvial dissection and channelized surface drainage observed on the Šumava main ridge is *not* due to any lack of flow convergence driven by (macro) topography.

5. Interpretation and discussion

5.1. Supporting evidence

The presence of perennial streams in valleys and at lower elevations indicates that overall excess precipitation is sufficient to support fluvial channels.

The topographic analysis based on the DEM indicates that, in the absence of some mechanism to limit hydrological connectivity, topographically driven flow convergence (in concert with the humid climate) should result in a dense channel network. Field observations indicate mechanisms by which *Picea abies* influences microtopography and surface and near-surface hydrological flows in such a way as to inhibit the development of fluvial channels by reducing hydrological connectivity.

Several hydrological studies support the proposed influences of spruce on drainage and soil hydrology. Šípek et al.'s (2020) studies of

Fig. 8. Area examined in the terrain analysis. Inset shows the same area, with all elevations below 1000 masl shaded out.
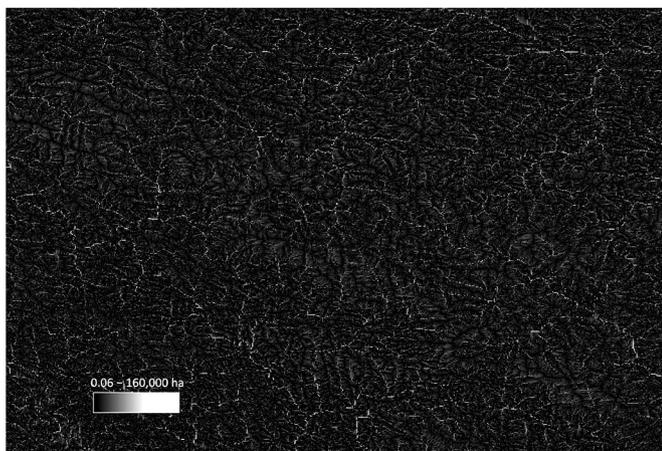
Fig. 9. Drainage area per 30 m × 30 m pixel for the area shown in Fig. 8.

soil water dynamics under *Picea* and *Fagus* forests and two other vegetation cover types in the Šumavas found differences between spruce and beech in pressure head distributions beneath the trees. Based on visual observations, they attribute the differences mainly to the contrasting root distributions—generally 40 to 50 cm deep and concentrated in topsoil for spruce, and deeper and more uniformly vertically distributed for beech. Hydrology also differed due to differences between the species in interception and transpiration. Hartvich and Mentlík (2010) found that water flow was restricted to sheet flow and subsurface percolation at the Obří Hrad site. They attributed that to the short length
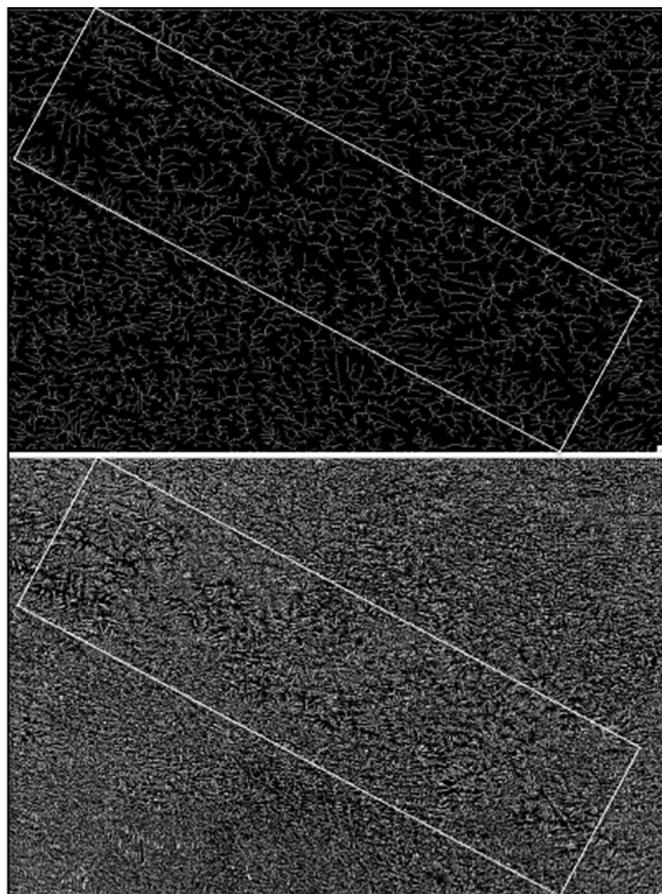
Fig. 10. Extracted drainage network for the Sumava Mountains area shown in Fig. 8 with the main ridge area indicated by the rectangle. The top shows the network with channels of order 3 or greater; the bottom shows the entire extracted network.
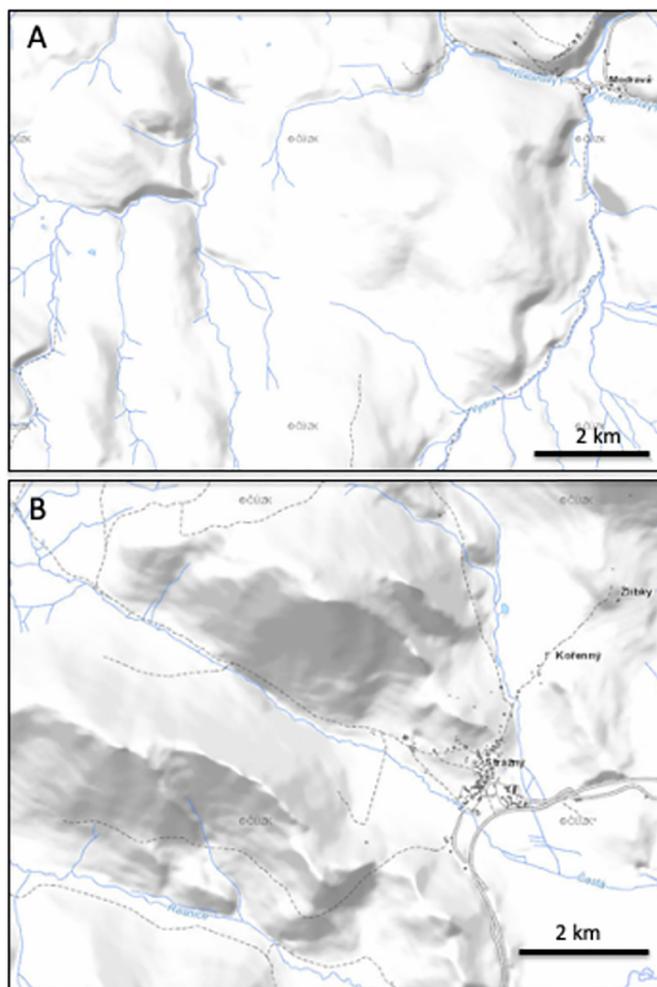
Fig. 11. Two sample areas of the Šumava Mountains, showing streams mapped at 1:25,000 scale by the Czech Geological Survey. Note the near absence of stream lines at higher elevations and on upper slopes. A: Area near Modrava; peak elevations are 1150 to 1200 m. B: Area near Strážný; peak elevations 1025 to 1100 m. Blue lines are streams; other lines are roads. Source: Czech Geological survey, http://mapy.geology.cz/geocr_25/. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the studied slope, consistent with our arguments about limited hydrological connectivity due to restricted overland flow lengths.

In the Modravský stream watershed, tree mortality from spruce bark beetles and clear-cut logging did not change the precipitation-runoff ratio (Bílá, 2016), suggesting that terrain and soil characteristics exert more control over the hydrology than short-term vegetation changes that do not greatly modify the microtopographic and soil characteristics. Vlcek et al. (2017) used dye tracing to identify runoff processes and flow paths on adjacent hillslopes in the Rokytka headwater area. One slope featured relatively shallow (<0.5 m) Histosols; the other was dominated by Podzols. At both sites shallow subsurface flow in the organic topsoil layer occurred; but at the shallow groundwater peat bog hillslope it was significantly more prominent. Dye solutions infiltrated and continued either as lateral subsurface pipe flow in the case of the peat bog, or percolated vertically downwards in the Podzol. Subsurface pipe flow and lateral preferential flow along decomposed tree roots or logs in the unsaturated zone was a major runoff process at the peat bog hillslope. Peat soils in headwater areas of the Vydra River were found store more water during dry and normal conditions, but to produce more runoff during very wet, flood-producing conditions (Vlcek et al., 2016).

In the Vltava River headwaters, Kocum et al. (2016) used geochemical evidence to determine peat bog contributions to stream discharge.

Their results indicate that peatlands within the study area are not well connected hydraulically to surface streams, and that the peat bogs do not have a significant hydrological function with respect to the stream network. Water storage in the peat is probably not a factor, as excess moisture is plentiful, and studies in the region have shown that water storage in peat is not a major influence on stream discharge (Jansky and Kocum, 2008). However, these studies focus on true peat bogs and Histosols in valley settings, rather than the shallower soils at higher elevations classified characteristically as Haplic and Histic Gleysols.

Geomorphic studies at multiple sites in the Šumavas have shown that slope processes are dominated by mass movement operating on debris produced by Pleistocene periglacial and glacial processes, and tree uprooting, as opposed to fluvial processes (Hartvich and Vilímek, 2008; Hartvich and Mentlík, 2010). Site-specific studies also show that hillslope geomorphic and hydrologic processes can be dominated by tree uprooting. At Zofin, on granite, near the Šumava Mountains with abundant spruce, Šamonil et al. (2020a) found that over the past few millennia denudation has been driven by tree uprooting dynamics. Soil and regolith volume associated with mass movement on slopes due to tree uprooting significantly exceeded the total volume of erosion.

Forest disturbances resulting in uprooting and/or numerous tree deaths may be important for forest stand, hillslope, and landscape-scale hydrogeomorphic modifications. The role of disturbance in Norway spruce stand dynamics on upper elevations in the Šumavas, particularly windstorms and bark beetle outbreaks, was highlighted by Dobrovolný and Brázdil (2003) and Brázdil et al. (2018). This is relevant because it results in synchronous biogeomorphic impacts both in the effects of dead trees and contemporaneous regrowth. Kašpar et al. (2020) explored this further, finding that spruce and beech express different disturbance histories and phenotypic strategies in the Šumava region, and that the spontaneous development of mountain forests may temporarily simplify forest spatial structure. By analyzing dendrochronological records from Boubínský and 30 other sites, they found that the disturbance history of nearly all study areas showed clear evidence of severe disturbances in the nineteenth century. Kašpar et al. (2020) also found that regeneration of spruce was more dependent on severe disturbances than that of beech. This suggests that biogeomorphic effects of spruce may influence entire landscapes within the same time frame.

Other supporting evidence relates to the affinity of Norway spruce for wetter soils. Daněk et al. (2019) compared two dominant overstory trees in the region, P. abies and Fagus sylvatica, showing a clear association between spruce and the wetter soils classified particularly as Gleysols, Stagnosols, and Histosols. The biogeography of the two species reflects a gradient of soil hydromorphism, with spruce dominating wetter sites and beech on drier soils (Podzols, Cambisols). Fagus has been spreading in recent years, but Daněk et al. (2019) predicted that expansion will be minimal on wetter soils, where spruce will continue to prevail. They also emphasized the greater importance of coarse scale disturbance on the more poorly drained soils. Particularly important is the fact that trees in wet environments are often more vulnerable to uprooting by wind because of shallow root systems. Dyderski and Pawlik (2020) analyzed the relative importance of geomorphic and climate variables on distributions of P. abies, F. sylvatica and three other trees in southern Poland. Their results indicated that P. abies does not tolerate dry or droughty sites or waterlogged soils, but does prefer wet, acidic soils a high water table. In mountain peatlands, they found that spruce is the dominant tree, where it not only prefers, but helps create peaty soils.

Spruce monoculture in the Šumavas is a result of human agency, but this practice has prevailed since the 1700s, and Picea has been a major component of the mountain forests on granitic rocks throughout most of the Holocene. Along the Šumava main ridge, and on wetter sites, it can be assumed that Picea has always been dominant over Fagus. Silver fir became dominant in some settings around 4 ka, but it was likely not dominant on the main ridge due to temperature limitations, and from the 18th century its prevalence was further reduced by the preference

of the forest industry for spruce. Abies alba also has a greater vulnerability to damage by air pollution, which reached its peak severity in the 1980s, and to browsing by deer. Fir is not quite as well adapted as spruce to the wetter soils, but it does occur on hydromorphic soils in many of the same settings where spruce is found. It is often found with stagnic soil properties (associated with slowly percolating water), but seldom with soils with gleyic properties due to a consistently high water table with limited drainage, whereas spruce is found in the latter setting. Abies typically has a deeper, more vertically oriented root system than Picea, and its fallen trunks decompose more slowly. At Boubínský an inventory of biomechanical impacts of trees showed that, proportionally, fir and spruce are similar with respect to root mounding and creation of stump hole depressions, but spruce is much more susceptible to uprooting (Šamonil et al., 2018).

Forests in the study area have been protected from logging and other anthropic disturbances in recent decades and are mostly left to function with minimal human interference. Much of this area is within the zone of the National Park designated as natural, where only spontaneous dynamics are allowed. One exception is stands damaged by spruce bark beetle outbreaks, where some removal of dead trees sometimes occurs (outside the natural zone). Replanting has occurred on both the Czech and German sides.

Managed P. abies forests in similar settings experienced reduced uprooting, due to harvesting. Surface processes are also more strongly influenced by road building, site preparation, and harvesting activities. Thus, landscape evolution in these managed forests likely differs substantially, though this has not been examined directly.

5.2. Spruce, hydrology, and topography

Fig. 12 summarizes the way biomechanical effects of Picea abies reduce hydrological connectivity and inhibit the development of channelized surface drainage and fluvial dissection. Mounding effects at tree bases—and to a lesser extent around some large lateral roots and downed trunks—create topographic highs, with inter-mound areas in dense stands forming shallow depressions. Root mounding and mounds associated with downed trunks generate generally smaller but more linear microtopographic highs, while cavities or depressions associated with decayed stumps create local pits. Tree throw (uprooting), which may involve scattered individuals or entire forest stands, results in pit-and-mound topography.

The hummocky microtopography leads to low connectivity of surface runoff, due to the spatial mosaic of water-shedding mounds and
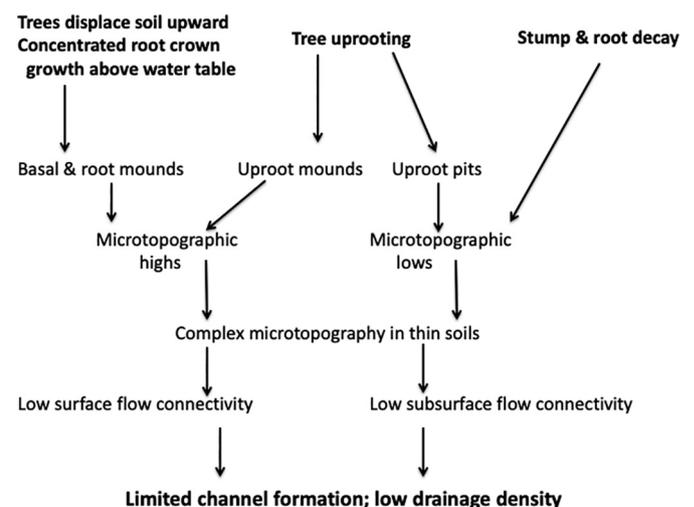
Fig. 12. Biogeomorphic effects of Picea abies limiting the development of fluvial dissection and channelized surface drainage.

water-collecting pits. The microtopography limits local-scale drainage areas and slope lengths, inhibiting the ability for concentrated flows to develop enough discharge or depth to generate shear stresses sufficient for channel formation. The distance or length of overland flow paths is critical in development of concentrated flow and sufficient shear stress to incise the surface, as indicated by the inclusion of slope length in soil erosion and sediment transport models (Merritt et al., 2003). Connectivity of surface runoff depends on the filling of surface depressions (Antoine et al., 2009; Peñuela et al., 2015). The depressions associated with tree uproot pits, intermound areas, and larger stump depressions do not fill, and thus inhibit connectivity.

Because this local topographic variability occurs in thin soils, and typically on a base of rock debris, there is also limited opportunity for subsurface flow concentration, and low below-ground hydrological connectivity.

Spruce also intensifies podzolization of soils in these environments (e.g. Sauer et al., 2007; Nikodem et al., 2013), which in turn decreases the rate of decomposition of litter and downed trunks. Moss layers on downed trunks also slow decay (e.g. Gottschall et al., 2019; Stursova et al., 2020). The woody debris and thick litter layers increase the moisture storage capacity and the amount of readily available water for spruce, and saturation also slows decay of organic matter.

In many cases trees growing in shallow soils are able to deepen the soil and regolith. Roots penetrate joints and fractures in underlying rock, facilitating weathering by promoting moisture flux, microbial activity, and formation of organic acids. Roots may also encircle rock fragments, causing them to be "mined" if the tree uproots (Phillips, 2008; Shouse and Phillips, 2016; Pawlik et al., 2016). However, these effects are most pronounced in trees with a tap-root architecture (a large, dominant, deep root descending directly below the trunk), and least pronounced in species (such as *Picea abies*) with a lateral root architecture. The ability of spruce to survive and thrive in a thin solum and rocky layer limits its deepening or soil and regolith. This is also facilitated by the frequent regeneration of spruce on decaying lying trunks, reducing root penetration of the ground. Further, water flow along roots and root channels is spread laterally, rather than concentrated vertically as in tap root species. This appears to be a case of bidirectional feedback, whereby the thin soil is conducive to shallow, lateral root morphologies, and the latter inhibits soils thickening by biomechanical effects of trees.

Together, these effects suggest positive ecosystem engineering and niche construction for spruce in the Šumava Mountains, as shown in Fig. 13. *Picea* has decided advantages over other common trees in the

region in terms of adaptations to wet soils and high water tables. The limited hydrological connectivity and flow concentration slow rates of drainage. Generation and slow decay of litter layers and woody debris, along with microtopgraphic depressions, increase near-surface moisture storage. Meanwhile, limited regolith deepening and laterally-dominated hydrological fluxes concentrate water near the surface. These together create conditions that are favorable for spruce and unfavorable for other woody plants.

We do not wish to leave the impression that *Picea abies* or BEE is solely responsible for the development of drainage in the study area—no single factor is ever in full control. Other geomorphic and ecological processes and human activity have likely played a role, along with climate change.

In their overview on future challenges in the study of ecological succession, Chang and Turner (2019) highlighted the need to consider broader spatial and temporal scales, and to better understand the specific mechanisms involved. With respect to the latter, positive BEE, as shown here, is a key mechanism is some environments and deserves further investigation. The regional reconnaissance approach of this paper, while differing from the plot-style studies common in ecology and forestry (and typical geomorphological research), is an effective way to expand the spatial scope of biogeomorphological and successional studies. And though this research did not present any original historical data, the sources we used to establish the background for landscape evolution since the late Pleistocene highlight the utility of combining Quaternary and historical geomorphology and paleoecology with contemporary geomorphological, hydrological, and ecological studies to expand the temporal framework.

5.3. Future landscape change

In recent decades *Picea abies* forests in the Šumava region have been ravaged by the tree-killing spruce bark beetle (*Ips typographus*). Bark beetle outbreaks cause extensive spruce mortality, often 100% within a stand. While it is native to the study region, the spread of *Ips typographus* has been facilitated by climate change, the extensive spruce monoculture practiced in the area, late 20th century damage and stress from air pollution, and uprooting events caused by windstorms (in the first stages of infestations bark beetles generally attack stressed trees). In many affected areas rapid regeneration of *Picea abies* is occurring, and if spruce remains dominant the present landscape evolution regime will likely continue. However, where bark beetle outbreaks or climate
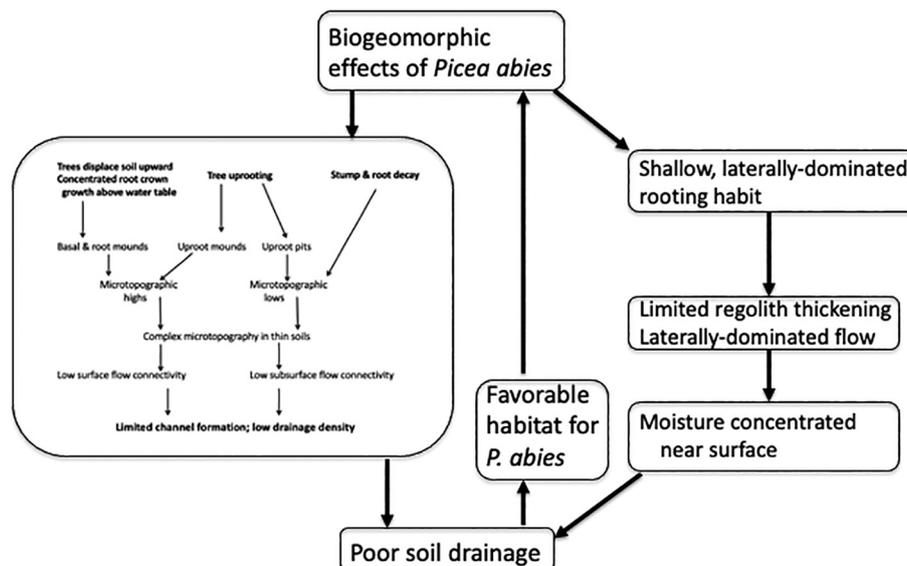
Fig. 13. Summary of how biogeomorphic feedbacks of *Picea abies* maintain favorable habitat for the species. Subsystem at left is the same as Fig. 12.

change stimulate a shift to other species, or cause a decline in forest cover, the regime could break down. Forest composition change could occur due to the spread of beech or other trees, or conceivably due to higher fire risk due to the high fuel loading in outbreak areas. Both of these are themselves influenced by climate change, and by soil hydromorphic properties. Widespread beech expansion onto wetter soils is unlikely, though (Daněk et al., 2019).

Possible indirect biogeomorphic and soil impacts of spruce bark beetles were identified by Šamonil et al. (2020c). Because these are mainly based on reduction of Norway spruce, they are a reasonable guideline for potential changes to the spruce-driven landscape evolution on the Šumava main ridge. Reduced uprooting is a major potential impact that would affect topography, mass movements, regolith and soil formation, and slope hydrology. Fewer uprooted trees would also decrease microtopographic irregularity and the associated hydrological and pedological impacts. Šamonil et al. (2020c) also identified other possible changes in bioprotection, and biochemical and biomechanical effects on soils, regolith, and hillslope morphology. They highlighted five factors that could influence developmental trajectories in bark beetle infected forests. These include whether a site is vulnerable to potential uprooting, or whether an outbreak is prompted by a tree throw event; prevalence of mineral soils or Histosols; and managed vs. unmanaged forests, which strongly influences tree species composition and coarse woody debris and disturbance regimes. Post-outbreak management, and slope gradient thresholds that determine the significance of impacts on mass movements and erosion are the other two key factors. This analysis, combined with the results of the present study, indicate that *P. abies* is a biogeomorphic keystone species along the Šumava main ridge.

Spruce forests in central Europe managed for timber production experience less uprooting, due to harvesting, and reduced bioprotection from downed trees. Trees in these commercial forests also do not grow as large as those in unmanaged forests, resulting in smaller soil volumes affected by biomechanical effects (Roering et al., 2010; Šamonil et al., 2018). Microtopography and surface processes are also typically strongly influenced by road building, site preparation, and harvesting activities in these forests, which may reduce the hummocky, irregular topography that occurs in unmanaged *Picea abies*-dominated forests. Thus the biogeomorphically dominated landscape evolution observed in the national parks on the main ridge may be modified or absent in managed forests. This deserves further research.

6. Conclusions

Landscape and ecosystem changes after a disturbance or exposure of new substrates may follow a sequence from domination by abiotic, geophysical factors, through stages characterized by increasing effects of biota, biotic-abiotic feedbacks, and eventual domination by ecological processes. Research on biogeomorphology in forest settings, however, has found more diverse development patterns, including persistence of states dominated by biogeomorphic feedbacks. This is the case in Norway spruce dominated forests on the main ridge of the Šumava Mountains. Throughout most of the Holocene, *Picea* has strongly influenced microtopography via basal and root mounding, effects of uprooting, and stump depressions, as well as pit-and-mound topography associated with uprooting. The hummocky microtopography limits hydrological connectivity of both surface and subsurface runoffs and inhibits development of channelized surface drainage and fluvial erosion. Spruce also promotes accumulation of moisture-retaining woody debris, litter, and organic matter. Its shallow, laterally dominated root systems also inhibit concentrated downward flows, and biomechanical and biochemical soil and regolith deepening.

Together, these effects result in poorly drained soils that retain most of the water in the root zone. This constitutes positive ecosystem engineering. *Picea abies* has advantages over other common trees in the region with respect to adaptations to wet acidic soils, high water tables and generally low temperature. These interactions have maintained a landscape dominated by biogeomorphic feedbacks.

As in any landscape, particular local conditions strongly influence landscape development. In this case, thin soil overlying rock debris produced by glaciers and periglacial processes is important, along with a biogeographic context generally lacking competitors for hydromorphic soils. However, studies at other forest sites with different geographically and historically contingent factors have also shown persistent biogeomorphic domination, showing that the general phenomenon is not unique to the study area.

While the biogeomorphic domination phase has been persistent, it is by no means permanent. Increases in strong disturbances (e.g., strong convective storms, bark beetle outbreaks, slope failures) are expected in the near future (e.g. Seidl et al., 2014; Spencer et al., 2017; Šamonil et al., 2020c). These can be expected to influence geomorphological and ecological processes and their interactions.

This and the other studies indicating the persistence of a biogeomorphologically dominated state were conducted in unmanaged forests with minimal recent human disturbance. The effects of silviculture, harvesting, and other forestry activities on, e.g., ecological dynamics, soil chemistry, runoff responses, and erosion have been extensively studied. The need now is to extend these to how forest management and disturbance influences highly interrelated and mutually adjusting geomorphological, ecological, hydrological, and pedological processes.

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