On the hydrological relationship between Petrifying-springs, Alkaline-fens, and Calcareous-spring-mires in the lowlands of North-West and Central Europe; consequences for restoration

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SUMMARY

(1) Petrifying-springs and Calcareous-spring-mires are threatened ecosystems in Europe and are protected under the Natura 2000 Habitats Directive. In European and national legislations Petrifying-springs and associated tufa cascades, small streams and flushes (7220) are treated as separate entities from Alkaline-fens and Calcareous-spring-mires (7230), each with their own protection and restoration measures. This may, however, create conflicts if the two habitats are physically connected or adjacent to one another: restoration measures aimed at one of the two may have negative effects on the other.

(2) The present study focuses on the spatial and temporal relationships between Petrifying-springs and Alkaline-fens with tufa deposition, and discusses consequences of this relationship for restoration of degraded sites. When a Petrifying-spring co-occurs with an Alkaline-fen or Calcareous-spring-mire, restoration measures should take account of the needs of both habitat types.

KEY WORDS: Caricion davallianae, *Cratoneurion*, drainage, hydrology, restoration, tufa

INTRODUCTION

Petrifying-springs are rare and threatened ecosystems throughout Europe (Toivonen 2016). In densely populated areas these unique habitats are threatened by drainage, excavations, and contamination by intensive agriculture (de Mars *et al*. 2016). This is particularly true for European lowland areas (see Figure 1). Historical climate change can also cause changes in the hydrological cycle, leading to shifting in groundwater flows, and consequently to spring degradation (Hartmann *et al*. 2014).

Petrifying-springs that can precipitate calcium carbonate on the soil surface have a global distribution (Cantonati *et al*. 2016). These deposits are commonly named ‘tufa’ or ‘tufa limestone’ (Sanders *et al*. 2011), and this term is frequently applied to cool water deposits of highly porous or 'spongy' freshwater carbonates, often incorporating leaves and woody tissue (Pedley 1990). The term ‘travertine’ is often used to indicate the harder, more resilient deposits (Pentecost 2005). In the present study we will also use the term tufa for rather soft deposits that fall in the category 'meteogene (paludal) travertine', defined by Pentecost (2005), later called ‘moss tufa’ by Sanders *et al*. (2011).

Alkaline-fens and Calcareous-spring-mires are nutrient poor mires with peat deposits of various depths, which, just like Petrifying-springs, are usually hotspots of biodiversity and are refugia for many rare and threatened species (Hájková *et al.* 2020). This habitat type is also rapidly declining in most European countries (Bita-Nicolae *et al*. 2016, Wołejko *et al*. 2019a, Figure 1).

In Europe the following habitat types are protected under European law (Natura 2000 Habitats Directive; EC 2013): 1) 7210*: Calcareous-fens with *Cladium mariscus* and *Carex buxbaumi*, 2) 7220*: Petrifying-springs with tufa formation (*Cratoneurion*), 3) 7230: Alkaline-fens and Calcareous-spring-mires that include base-rich to very alkaline fen habitats and 4): Alkaline-spring alder wood (91EO). The asterisk in each of the first two habitat types indicates that the habitat is a priority habitat where the highest degree of conservation is required. The four habitat types usually have many characteristic species of the alliance *Caricion davallianae* in common (Joosten *et al.* 2017).

Nowadays Petrifying-springs (7220) and Alkaline-fens (7230) are the most widespread wet

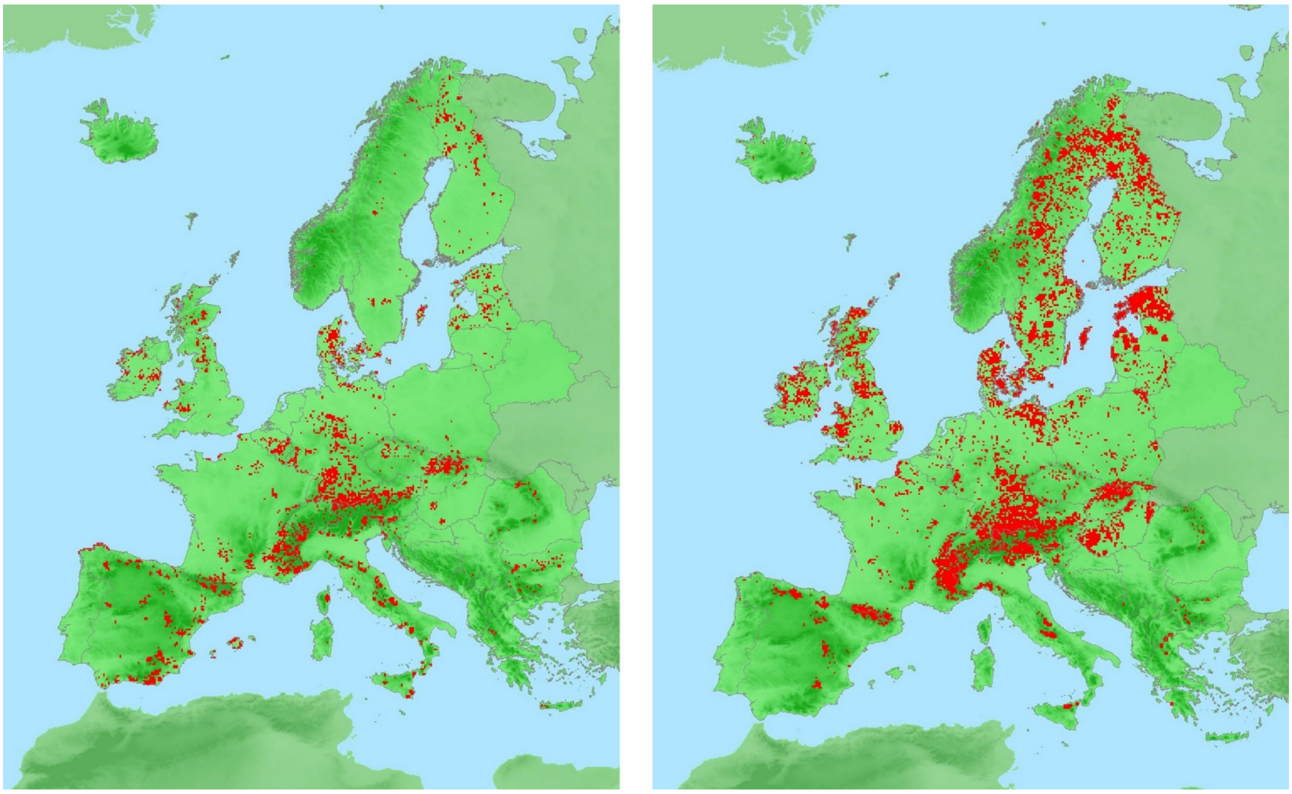

Figure 1. Occurrence across Europe of (left) Petrifying-springs, associated tufa cascades, small streams and flushes; and (right) of Alkaline-fens and Calcareous-spring-mires. Data originate from Toivonen 2016 (left) and Bita-Nicolae *et al*. 2016 (right). Information on Norway, Iceland, Portugal and former Yugoslavian countries may be incomplete.

calcareous habitats in NW- and Central Europe and they occur both in lowlands and in mountainous areas (Figure 1; Bita-Nicolae *et al*. 2016, Toivonen 2016, Wołejko *et al*. 2018a,b, Dobrowolski *et al*. 2019, Wołejko *et al*. 2019b).

Under the Natura 2000 documentation and subsequent policy documents (Natura 2000 Habitats Directive, EU-HD 1992) the two habitat types are treated as separate entities. In practice, however, measures proposed to conserve or restore Petrifying-springs or Alkaline-fens may potentially create conflicts between the two if connected or adjacent to one another. In that case (restoration) measures aimed at one of these two habitat types may not be beneficial for both, and may even negatively affect one of the habitat types. Measures to improve the quality of the Petrifying-spring habitat could end in further deterioration of the Spring-fen complex. Petrifying-springs and Alkaline-fens are most threatened in the European Lowlands (Toivonen 2016), where the two habitat types usually occur together in the landscape, or did co-occur at one time (Grube & Usinger 2017).

In the present study we focus on the two habitat types in the Central European lowlands (Figure 2); (1) Petrifying-springs (7220) and (2) Alkaline-fens (7230), and on evaluating the relationships between them. Using knowledge available in the literature and some private observations we investigate developments in time and possible anthropogenic impacts, and describe consequences for future (restoration) measures in these ecosystems.

PETRIFYING-SPRINGS

Active tufa forming springs occur throughout Europe where the annual mean air temperature is > 5 ºC . Pentecost (1995) has briefly reviewed 320 published travertine sites in Europe, 156 of which are still active in some form. The remaining ones are inactive - fossil travertines - and range in area from 650 km^2 to just a few square metres and in thickness from a few cm to more than 300 m (Pentecost 2005). Fossil travertines are often quarried.

Petrifying-springs derive their name from their petrifying nature. In a literal sense these objects are not petrified, but rather laminated with calcium carbonate (also called ‘spring-associated-limestone (SAL; Sanders *et al*. 2011); Figure 3). The main

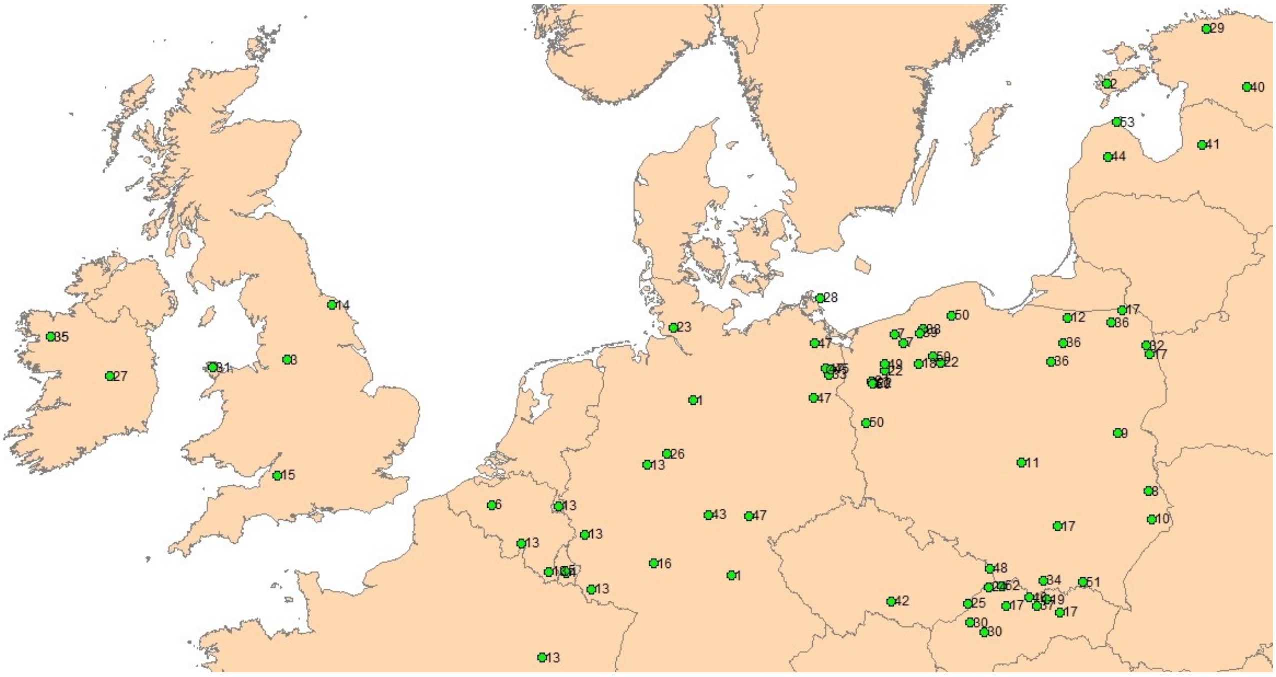

Figure 2. Occurrence and references of Petrifying-springs and Calcareous-spring-mire sites discussed in the current study. 1 - Arp *et al*. 2010; 2 - Blaus *et al*. 2020; 3 - Columbu *et al*. 2013; 4 - Couteaux 1969; 5 - Dabkowski *et al*. 2015; 6 - Denys & Oosterlynck 2015; 7 - Dobrowolski *et al*. 2010; 8 - Dobrowolski *et al*. 2005; 9 - Dobrowolski *et al*. 2012; 10 - Dobrowolski *et al*. 2016; 11 - Dobrowolski *et al*. 2017; 12 - Dobrowolski *et al*. 2019; 13 - de Mars *et al*. 2016; 14 - Eades *et al*. 2012; 15 - Farr *et al*. 2014; 16 - Gregor & Wedra 1991; 17 - Grootjans & Gojdičová 2011; 18 - Grootjans *et al*. 1999; 19 - Grootjans *et al*. 2005; 20 - Grootjans *et al*. 2006b; 21 - Grootjans *et al*. 2007; 22 - Grootjans *et al*. 2015; 23 - Grube & Usinger 2017; 24 - Hajek *et al.* 2002; 25 - Hajkova & Hajek 2003; 26 - Hartkopf-Froeder *et al*. 1989; 27 - Heery 2007; 28 - Holdack 1959; 29 - Ilomets *et al*. 2010; 30 - Jamrichová *et al*. 2018; 31 - Jones *et al*. 2016; 32 - Kopeć *et al*. 2016; 33 - Koska & Stegman 2001; 34 - Krause *et al*. 2015; 35 - Lyons 2015; 36 - Łachacz 2000; 37 - Madaras *et al*. 2012; 38 - Osadowski 2010; 40 - Paal & Leibak 2011; 41 - Pakalne & Čakare 2001; 42 - Peterka *et al*. 2014; 43 - Pietsch 1984; 44 - Priede 2017; 45 - Rowinski 2014; 46 - Smieja & Smieja-Król 2007; 47 - Succow 1988; 48 - Tyc & Jonderko 2017; 49 - Wołejko *et al.* 1994; 50 - Wołejko *et al*. 2018a; 51 - Wołejko *et al.* 2018b; 52 - Wołejko *et al*. 2019b; 53 - Wołejko *et al*. 2019a.

driver of tufa formation is based on supersaturation of dissolved calcium (Ca^{2+}) and bicarbonate (HCO_3^-) in discharging groundwater. When this supersaturated groundwater comes to the surface, CO_2 escapes (de-gases) into the atmosphere. As a result, the water becomes oversaturated with $CaCO_3$, which precipitates as SAL (Sanders *et al.* 2011, Heery 2007). Tufa formation in *Cratoneurion*-springs occurs in a pH range of 6.9 to 9.0 with a mean of about pH 8 (Pentecost & Zhaohui 2002, Columbu *et a*l. 2013, Lyons 2015).

The rate at which tufa precipitates depends on several factors such as Ca^{2+} and HCO_3^- concentrations, the amount of CO_2 de-gassing and water temperature. Due to the deposition of tufa in petrifying springs a significant change in water chemistry occurs in the outflowing groundwater within a zone of 10–100 metres. Due to the de-gassing of CO_2 the (bi)carbonate (alkalinity) and calcium concentrations decrease while the pH increases downstream (Coûteaux 1969, Arp *et al*. 2010, Sanders *et al.* 2011, Farr *et al*. 2014; Figure 4).

A steeper gradient will lead to a shorter residence time and may therefore also lead to less CO_2 de-gassing. A steeper gradient, however, will also lead to more turbulence which concomitantly leads to increased CO_2 de-gassing (Jacobson & Usdowski 1975). This is especially true when the flowing surface water spreads out over the slope. In addition to the inorganic driver of calcium carbonate precipitation, there can also be an active biotic component involved in tufa formation. Spring associated limestone deposition is generally promoted in the presence of cyanobacteria (Pentecost 1978), algae (Freytet & Verrecchia 1998) and bryophytes (Parihar & Pant 1975). Although

Figure 3. Top left: a calcareous mire (Belianske Lúky) at the foot of the Tatra Mountains in Slovakia (photo A.P. Grootjans). Top right: tufa deposition can be observed on the branches of a moss (photo: L. Wołejko). Bottom left: a hill with tufa deposition dominated by spring mosses (Cascade de Bonne Fontaine) Vodeleé, Belgium, photo: H. de Mars). Bottom right: alternating layers of tufa and peat in a in a core from a Calcareous-spring-mire in East Poland, photo: A.P. Grootjans).

Pentecost (1996) estimated the contribution of bryophytes to be only 6–12 %, they may not only remove carbon dioxide from the water during photosynthesis but can also act as an extensive framework providing an increased surface area of nuclei enhancing the precipitation of calcium carbonate in other ways (Emeis *et al*. 1987). Although some bryophyte species are confined to alkaline springs, they may become petrified themselves. The vertical growth rate of such bryophytes must be greater than that of the tufa formation (Lyons & Kelly 2020).

At higher altitudes or in lowland areas with very steep cliffs, petrifying springs may never have been part of larger mires due to unsuitable conditions for peat formation. The current petrifying springs in the lowlands of Western Europe, however, are very often under intensive human influence and may not be part of Alkaline-spring mires any longer; only some small deteriorated relics may be present. In the lowlands of Central Europe, however, the situation is different, and petrifying springs are often part of larger Alkaline-spring mire complexes.

ALKALINE-FENS AND CALACAREOUS-SPRING-MIRES

Fens and petrifying processes

Alkaline-fens are fed by calcareous groundwater and often contain zones with active tufa deposition on the surface of a mire. The precipitation process itself occurs in shallow pools, on the leaves of aquatic plants or on bryophytes (Pentecost 1995, Grootjans *et al*. 2015). Sometimes these alkaline-spring mires form distinctive cupolas of combined peat and tufa formation over 10 m tall (Łachacz 2000, Grootjans & Gojdičová 2011, Osadowski *et al*. 2019). The Sidra

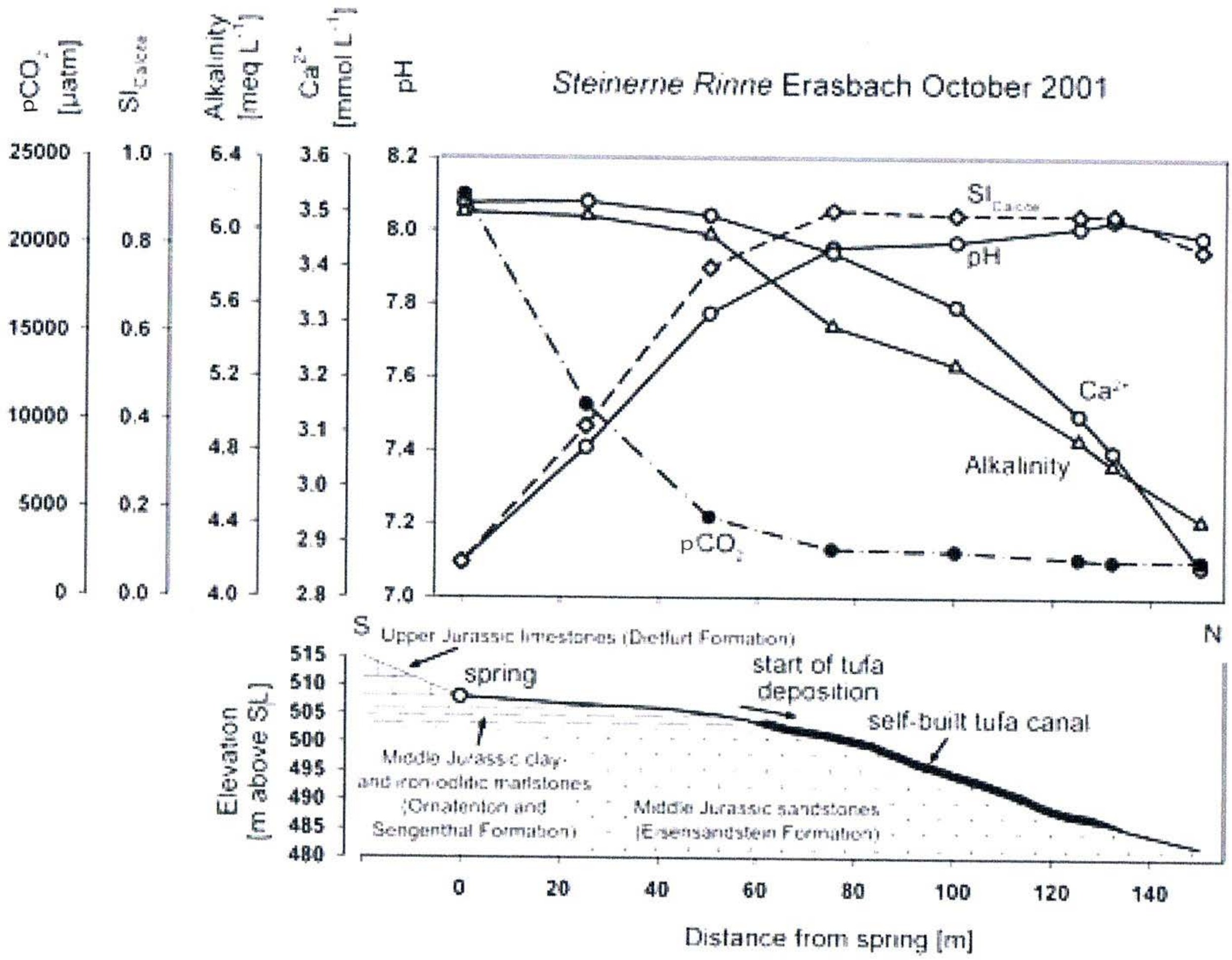

Figure 4. An example of the downstream changes in: CO_2 pressure (pCO_2), calcite saturation ($Si_{calcite}$), alkalinity, calcium concentration and pH along a travertine deposition stream. The outgassing of CO_2 results in an increase of the pH from about 7 up to 8–8.5. As the outgassing takes some time the precipitation of tufa usually starts somewhat downstream of the spring (after Arp *et al.* 2010).

spring fen in Eastern Poland, for instance, reaches up to about 10 m above the valley bottom, and is considered to be the tallest known spring fen cupola in Poland (Bitner 1961). Cupola-shaped Calcareous-spring-mires with alternating peat and tufa deposits are found in various topographical situations, where a long-lasting, continuous supply of groundwater occurs. The groundwater reaching the mire surface is usually under considerable hydraulic pressure (Dobrowolski *et al*. 2005, 2019; Grube & Usinger 2017). Other springs with sustantial tufa deposition, up to ~8 m in depth (Opatówek Mire), occur near Bobolice in northern Poland (Wołejko 2001, Pidek *et al*. 2012). Judging from publications from the end of the nineteenth century and the beginning of the 20th century, such tufa forming mires were much more common then, for example in north Germany (Schleswig Holstein; Grube & Usinger 2017) and Poland (Łachacz 2000, Dobrowolski *et al*. 2002, 2016, 2017, 2019). The cupola near Sidra mainly consists of tufa, alternating with thin layers of peat (Figure 3, bottom right) and with a ‘coating’ of small-sedge peat that covers the tufa core (Pawlikowski in Grootjans & Gojdičová 2011). The mechanism of the alternating periods of tufa deposition and peat formation in Alkaline-fens is not very well known. Madaras *et al.* (2012) noticed a pattern in the alternating periods of tufa and peat formation: “*a very compacted and highly decomposed peat layer is present above the calcareous layered horizon. The deepest layers were more decomposed than the upper ones. The peat was, without exception, non-calcareous and contained remnants of wood, pointing to presence of forest vegetation.* He concluded that these changes in the vegetation “*can only be explained by a considerable drop in groundwater pressure at the site. Groundwater levels were still high enough to permit peat formation, but* *not high enough for tufa formation at the surface of the mire*". At a later stage brown moss peat without deposition of tufa has been formed, pointing to wetter conditions again and the retreat of the forest. Madaras *et al*. (2012) further wrote that "*tufa is presently found at the surface of the central part of the mire, which points to intensive precipitation of $CaCO_3$. Strong discharge of calcareous groundwater hampered by the compacted impermeable peat layer (forest phase) and restricted outflow in flat areas has led to very high water levels and long residence times in the soil profile, leading to very anoxic conditions. This stimulates sulphate reduction and formation of pyrite in the profile. The slow flow of discharging supersaturated groundwater will than come in contact with the atmosphere and tufa will be deposited at the surface* (see also Figure 4, and Kemmers *et al*. 2004).

So, we can conclude that changes in groundwater fluctuation patterns most probably triggered the alternating periods of tufa deposition and peat formation through time. Dobrowolski *et al*. (2016, 2017, 2019) gave convincing evidence that these changes in groundwater supply were mainly caused by changes in climate conditions in the past.

Spring-fen development in time

In the NW-European lowlands the Alkaline-fens have almost all been affected and severely degraded by hydrological changes. Pristine spring fens, untouched by humans, probably do not exist here any more. Lyons & Kelly (2016, 2017) described two types of unshaded, weakly and strongly tufaceous petrifying springs in Ireland, which seemed to be still embedded in well-developed *Caricion davallianae* fen communities. Lyons (2015) mentions several vegetation studies from Scotland, England and Ireland which were published between 1955 and 1980, which also showed co-occurrence of *Cratoneurion* and *Caricion davallianae* vegetation, but many of these 'turfy marshes' may not be real mires, since the organic layer appears to be absent or very thin (much less than 30 cm thick). Farr *et al*. (2014) report an example of a slightly drained, but rather well-preserved Calcareous-spring-fen complex named "Cors Erddreiniog" in Wales (UK). This mire is situated at the foot of a limestone ridge where various active petrifying springs and seepages occu;, whereas adjacent in the mire, peat alternates with tufa layers, indicating changing hydrological conditions: more or less than the average discharge of groundwater or a change in groundwater composition (Grootjans *et al*. 2015).

In Eastern Europe alkaline spring-fed fens are still quite common, but active tufa deposition at the surface is rare. Wołejko (2001) studied about 100 stratigraphic profiles in groundwater-fed mires in NE Poland, situated in 13 small river valleys. The profiles provided information about the co-existence of so-called percolating mires and spring fens: percolating mires were relatively frequent in the past while typical tufa-accumulating spring mires have always been rare. The most common development started with an alder wood, developed directly upon a paludified mineral soil around a spring or, in the case of a terrestrialising lake, with tall sedge communities. Further successional stages commonly include the development of tall sedge and small sedge-moss communities, but the return of forest communities has also been observed. The continuous existence of mesotrophic sedge-moss communities up to the present time has been found in only 2 % of the profiles studied. This points to rather dynamic hydrological conditions, induced either by climate or by human impact (see also Hájková *et al*. 2012b, 2020, Jamrichová *et al*. 2018). Similar dynamic alternating sequences are known from Germany (Succow 1988) and from headwater valleys in The Netherlands and in Belgian Limburg (Jansen 1960, Diriken 1982).

To our knowledge the best-preserved Alkaline-spring-fen in NW and Central Europe is the Brezové mire in the foothills of the Tatra Mountains in Slovakia. Peat layer thickness in this small dome-shaped and sloping mire (about 2 hectares) varies between 60 and 150 cm and the mire has a spring cupola on top (Madaras *et al*. 2012). Several peat and tufa layers alternate in the soil profile. Tufa deposition is occurring on the surface of the mire and in small pools. The exact origin of the calcareous groundwater is unknown, but it is most likely artesian water, forced to the surface by a geological fault (Madaras *et al*. 2012). The hydrological system of Brezové mire itself has been described by Grootjans *et al*. (2006a) using summer temperature measurement to indicate groundwater flow (Figure 5). The coldest groundwater (less than 10 °C) discharges from one of the two springs. Warmer water is present at the surface in between the two springs. In more detail (Figure 5) we see that the system of small pools attracts groundwater at one side, then this surface water is warmed up and infiltrates again on the other side of the pools. In this way relatively warm water is present at the lower end of the system and also between the cold springs. The basal parts of the deepest profiles consist almost exclusively of tufa, but higher in the profile alternating layers of tufa and peat are present. Madaras *et al.* (2012) relate these dynamic changes to hydrological or climate changes. Under relatively dry climate conditions, the

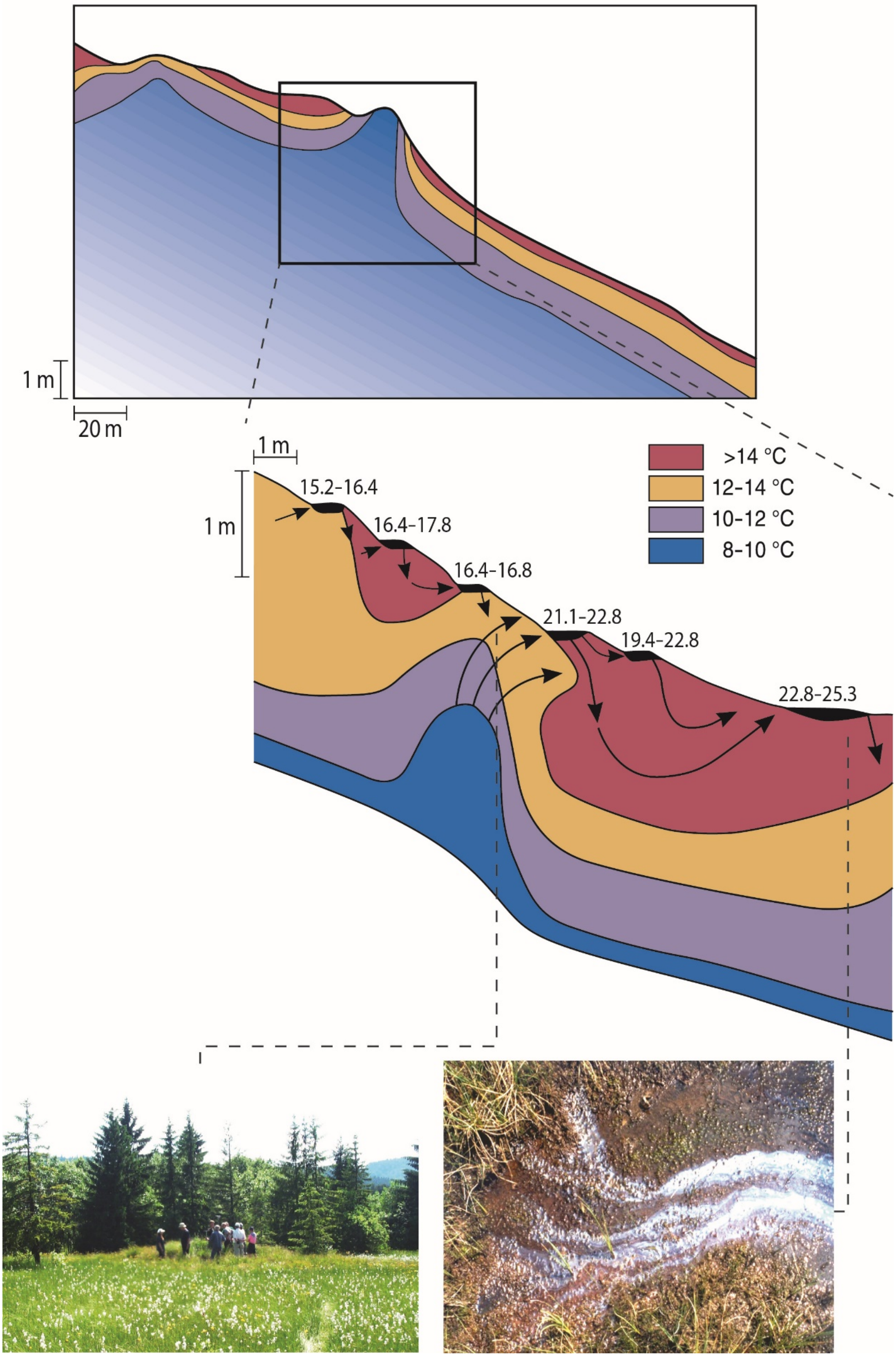

Figure 5. Temperature profiles in the Brezové mire (Slovakia), indicating the groundwater flow from a spring to a cascade of small pools (black) in which precipitation of tufa occurs. The left-hand photo shows people standing on the main spring cupola with *Eriophorum latifolium* in the foreground on the sloping mire. The right-hand photo shows that iron rich seepage water (with an iridescent surface bacterial film) is flowing through a small pool (after Grootjans *et al*. 2006a).

groundwater may not reach the topsoil and then peat formation is predominantly influenced by rainwater (Almendinger & Leete 1998, Hájková *et al*. 2012a).

A remarkable development in time was reported by Hájková *et al*. (2012a). They studied the largest, but slightly affected, European Alkaline-mire "Belianske Lúky" north of the city of Poprad in the foothills of the Slovak Tatra Mountains. The mire started forming ca. 11,000 cal BP as a minerotrophic fen woodland influenced by alkaline groundwater. However, after 10,700 cal BP the mire changed into an ombrotrophic *Sphagnum fuscum* bog. Such bog development can occur only under a very stable groundwater level and in the absence of regular flooding with alkaline water, which allows continuous *Sphagnum* growth (Vicherová *et al*. 2015, Koks *et al*. 2019, Figure 6).

Between 9000 and 8600 cal BP the conditions for bog growth deteriorated substantially. The mire complex dried out and large sections were destroyed by fire. During several millennia after this event hydrological conditions were not favourable for mire development and peat accumulation rates remained extremely low. The peat started to grow again during the last 1000 years cal BP, but now tufa formation occurred quite intensively. Most probably human

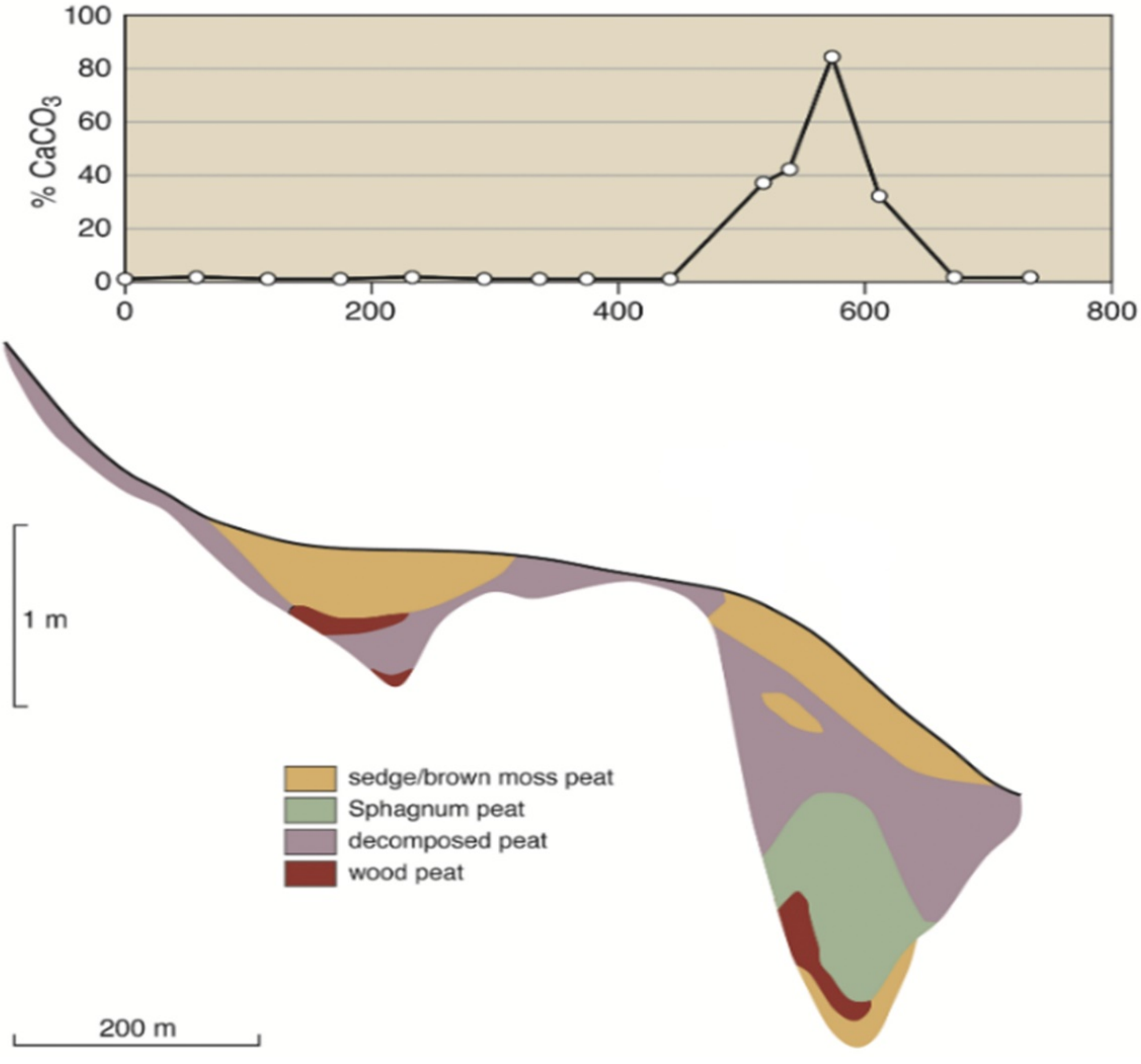

Figure 6: Peat development of Belianske Lúky in Slovakia. The spring fen complex started as an alder wood, then it became a mixed mire (dominated by *Sphagnum fuscum*), dried out, returned to being an alder forest for 3000 years, and finally became an alkaline fen ca. 600 years cal BP (after Hájková *et al*. 2012a).

activities including forest clearance on higher ground, along with mowing, triggered or stimulated calcite formation in the mire (Jamrichová *et al*. 2018, Hájková *et al*. 2020). Human-influenced mire development in Alkaline-fens, may, therefore deviate considerably from the standard autogenic mire succession described in textbooks (Moore & Bellamy 1974, Rydin & Jeglum (1989). In modern times, human interference has usually had devastating effects on mires.

DEGRADATION OF PETRIFYING-SPRINGS AND ALKALINE-FENS

Degradation of Petrifying-springs

Degradation of petrifying springs occurred almost all over Europe because people would try to utilise spring water for all kind of purposes. The use of springs for drinking water does not necessarily alter their spring features, unless the water is captured and removed before it reaches the spring itself (Grootjans & Gojdičová 2011, de Mars *et al*. 2016). The building of water mills to generate power for wood saws, or for making flour, changed the surface water flows but would not necessarily destroy the springs and may even have stimulated the occurrence of springs and spring fens along the edges of the valley.

Large-scale drainage associated with forestry and road building can have devastating effects, however, and has often resulted in exposure of the spring limestone deposits and created new rivulets in which calcium carbonate is deposited on stones, branches and mosses that colonised these new habitats while other parts dried out (Wołejko *et al*. 1994, de Mars *et al*. 2016).

Fossil travertine hills can be found in many parts of Europe where the springs that formed the travertine have dried out due to natural (climatological) changes, or human interference with the hydrology. This does not necessarily mean that, from a botanical point of view, the new but basically degraded sites have no conservation value. Osadowski (2010) gives an example of beech forests in the Parsęta River basin in Western Pomerania, Poland, that constitute a rare and unique type of beech forest with the occurrence of two orchids (*Cephalanthera rubra* and *Neottia nidus-avis*) as well as many other calciphilous and rare plant species. This calcareous soil type (pararendzina) originates from exposed calcareous tufas.

Groundwater pollution can also be very harmful for petrifying spring ecosystems. Particularly in the lowlands of North West Europe, Petrifying-springs are influenced by groundwater pollution from intensive agriculture within the recharge areas (on higher ground) of these springs. De Mars *et al*. (2016), for instance, studied the influence of increased nitrate (NO_3^-) and phosphate (PO_4^{2-}) concentrations in groundwater feeding petrified springs in The Netherlands, Germany, Belgium, France and Luxemburg. They compared their results with published data from 173 other sites in eleven European countries (such as the United Kingdom, Ireland, Poland and Slovakia). They found that in The Netherlands and Belgium, in particular, very high NO_3^- concentrations in the groundwater correlated with a deteriorated vegetation around the spring, and a low cover of those bryophytes usually characteristic for Petrifying-springs. Data from Ireland, Latvia, Poland and Slovakia showed the lowest NO_3^- concentrations (averages between 2 and 100 µmol L^{-1}) while PO_4^{2-} concentrations were on average < 0.32 µmol L^{-1}). The concentrations of NO_3^{-1} in The Netherlands were frequently 1400 µmol L^{-1} (= 80 mg L^{-1}) up to more than 2000 µmol L^{-1} (= 140 mg L^{-1}), and PO_4^{2-} concentrations were up to 2.5 µmol L^{-1} (= 0.25 mg L^{-1}). Intensive land use is also accompanied by liming of agricultural fields. Subsequent leaching appeared to have increased the calcium and bicarbonate concentrations of the groundwater in this region. In various locations this has quite recently started petrifying processes in springs and fens, although usually contributing to a rather eutrophic vegetation development due to high solute concentrations in the groundwater (de Mars *et al.* 2016, 2017).

On the other hand, even slight drainage can decrease the calcium and bicarbonate concentration (calcium saturation), resulting in reduced tufa deposition. Grootjans *et al.* (2015) presented a case in Western Poland in which tufa deposition in a former petrifying spring mire was reduced to almost zero, probably due to changes in groundwater flow as a result of fishpond construction at lower altitude than the springs, that attracted groundwater flow with supersaturated calcium. The springs were still active but they were now fed by shallow groundwater with a neutral calcium saturation index and, thus, no longer capable of tufa deposition.

Degradation of Alkaline-fens

In Europe there are numerous severely degraded Alkaline-fens and Calcareous-fens (Succow 1988, Joosten *et al*. 2017). Below we present some examples of changes that may occur at such sites.

In the lowlands of Eastern Europe lake levels were often lowered before, or during, mediaeval times. The calcareous spring complexes of Mlynskie Lasy and Diabli Skok are examples of the impact of these kinds of events. The Mlynskie Lasy spring fen complex, near Krzemień village in the West Pomeranian Lakeland, had developed alongside a lake that was mostly filled with lake chalk. A sloping fen with well preserved (mesotrophic) peat had developed on the adjacent slope and spring cupolas were present higher up on the slope. Alternating layers of tufa and (now degraded) peat were found there. Nowadays the whole mire consists of eutrophic alder forest with various eroding spring rivulets. The erosion was probably triggered by lowering of the lake water level downstream in the past (Wołejko *et al*. 1994).

In the spring mire reserve of Diabli Skok, a headwater system of the Rurzyca River north of the village of Szwecja, a similar situation was studied by Grootjans *et al*. (1999). They also concluded that lowered lake levels caused enormous erosion upstream, draining away the spring fen that was once present there (Figure 7). In these erosion areas, petrifying spring mosses like *Cratoneuron filicinum* and *Brachythecium rivulare* can now be found.

Both of the foregoing examples mark the end of a severe deterioration process. On the other hand, in the Belianske Lúky spring fen we may recognise the earliest signs of degradation. Improved drainage in the surrounding area, and digging of some ditches within the reserve some decades ago, triggered slight degradation and erosion of the peat and local formation of erosive runnels (Madaras *et al.* 2012).

Based on these findings Grootjans *et al*. (2006b) presented a conceptual model of possible alkaline fen and calcareous spring mire degradation in North Poland (Figure 8).

A quite similar development over time, as described previously for Mlynskie Lasy and Diabli Skok, is known from the small headwater complexes of Bunde-Elsloo Forest (Dutch Limburg) on the steep slopes of the Meuse valley near the village of Geulle. The distribution of fen peat on the slopes was known once to have been quite extensive there. It is no surprise that from the middle of the 19th century until approximately 1950 the area was known by naturalists for the presence of rare characteristic calcareous fen species. This is an indication for the previous presence of alkaline spring-fed fens (de Mars *et al.* 2017). Nowadays, calcareous Alnion spring-forests with deeply eroding petrifying springs and only patches of degraded peat remain. All these springs are also severely polluted by NO_3^- (Smolders *et al*. 2014, de Mars *et al*. 2016). The downfall of the Calcareous-spring-fens was mainly the result of a combination of improved drainage due to afforestation and exploitation of local quarries, as well as groundwater pollution.

Deteriorated counterparts of the Brezové mire (Madaras *et al.* 2012) and Cors Erddreiniog (Farr *et al*. 2014) can be found in the headwater valleys around Voerendaal, (Dutch Limburg; Janssen 1960) and in the Mombeek valley, Belgium (Diriken 1982). Nowadays these areas are also mainly covered by (calcareous) spring forest, brushwood and broadleaf forest with petrifying springs. A few alkaline-fen species sometimes re-occur here but only for a short time (de Mars *et al.* 2016).

An example of severe deterioration is known from Meerssener Heath (Dutch Limburg). Until the beginning of the 20th century a small fen was present here containing base poor as well as calcareous fen habitats (de Mars *et al*. 2017). Due to afforestation and drainage of a nearby quarry which started at the beginning of the 20th century, this peculiar fen was lost. Nowadays broadleaf forest covers the area and there is no evidence of the former fen.

RECONSTRUCTION OF ALKALINE FEN DEGRADATION IN NW-EUROPEAN LOWLANDS

Many authors have suggested that mire development, and even development of this type of alkaline fen, was partly the result of large-scale forest clearance of upstream plateaux in (pre)Roman and mediaeval times (Hajkova *et al.* 2012a,b,c, 2020; Figure 9a). The degradation of spring fens, petrifying springs, and alkaline fens in headwater systems was triggered not only by human interference but also by natural changes in climate and thus in hydrological systems (Madaras *et al*. 2012, Dobrowolski *et al*. 2019). The alternating peat and tufa layers in many alkaline fens show that rewetting restored peat growth. However, severe degradation of both alkaline fens and petrifying springs occurred when people started to change local hydrological conditions by digging small drainage ditches, which also triggered erosion (Figure 9b).

The eroding streams stimulated the further degradation of the spring fens and the solute-rich springs developed when, due to backward erosion, ‘circles’ of springs were formed. Most of the spring fens became eroded and drained, leaving only relics of peat deposits (Figure 9b,c). During the ongoing degradation process open fen areas changed into brush woods, Alnion-with-spring forests or (in more extremely drained situations) even general broadleaf forest. Nowadays most spring systems do not have peat any more (Figure 9c). Springs may be more common than in the past and calcium carbonate is mostly deposited in runnels and spring rivulets that are fed by those springs.

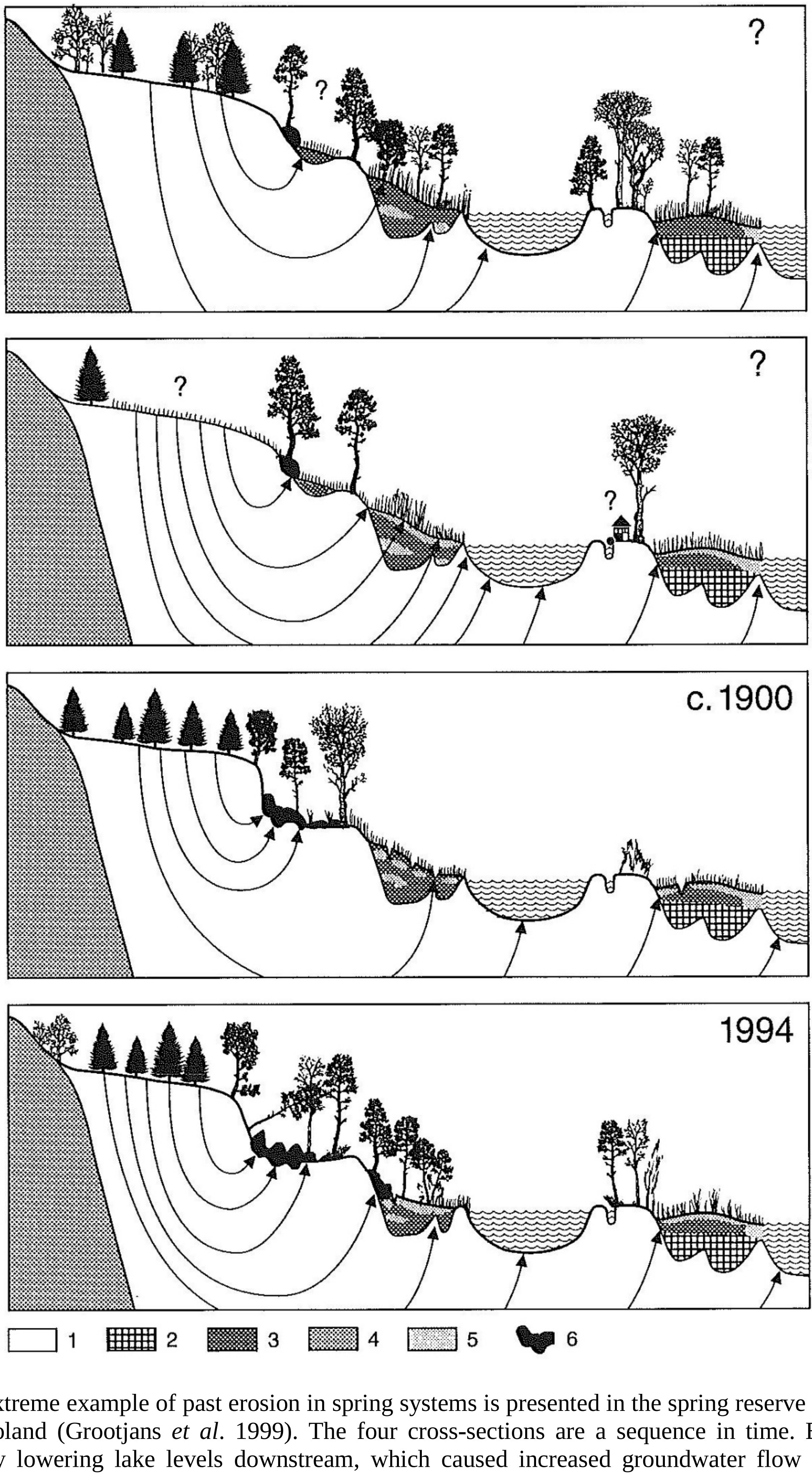

Figure 7. Extreme example of past erosion in spring systems is presented in the spring reserve Diabli Skok in North Poland (Grootjans *et al*. 1999). The four cross-sections are a sequence in time. Erosion was triggered by lowering lake levels downstream, which caused increased groundwater flow and erosion upstream and drying out of spring mires in the centre of the hydrological gradient. Arrowed lines are inferred flows of groundwater. Numbered boxes: 1 = outwash plain (sand), 2 = lake chalk, 3 = tall sedge peat with wood, 4 = front moraine, 5 = sedge peat without wood, 6 = spring ecosystems.

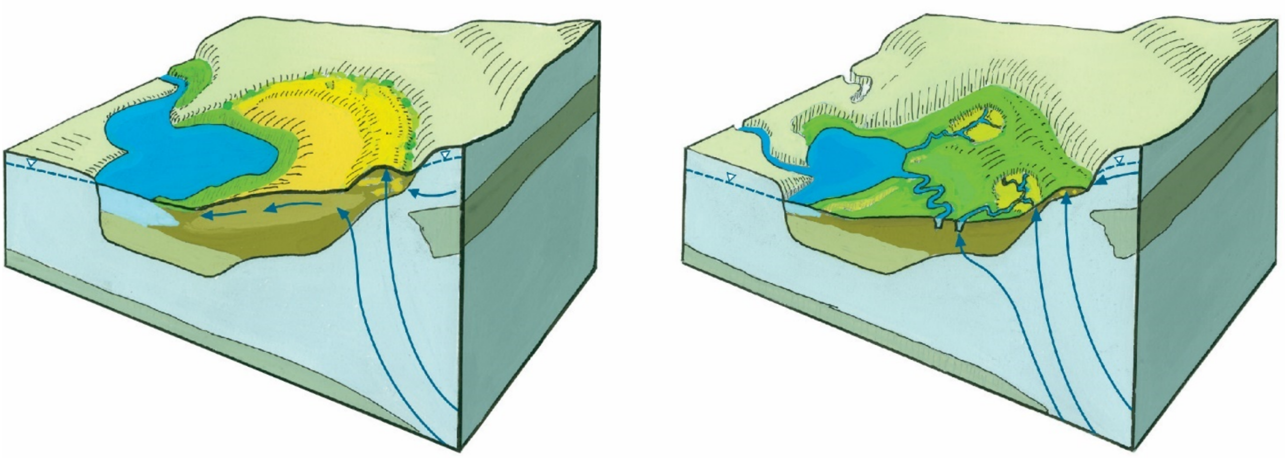

Figure 8**.** Conceptual model of mire development before (left) and after (right) lowering lake water levels in Eastern Europe. Arrowed lines are inferred flows of groundwater. In the lowlands of Eastern Europe lake levels were already lowered in mediaeval times, in some cases by several metres (Grootjans *et al*. 2006b). The steeper hydrological gradient caused erosion in the cupola-shaped spring fens (yellow) that had developed next to the lakes (blue). The eroding spring rivulets caused peat degradation (brown) and establishment of eutrophic alder forest (green).

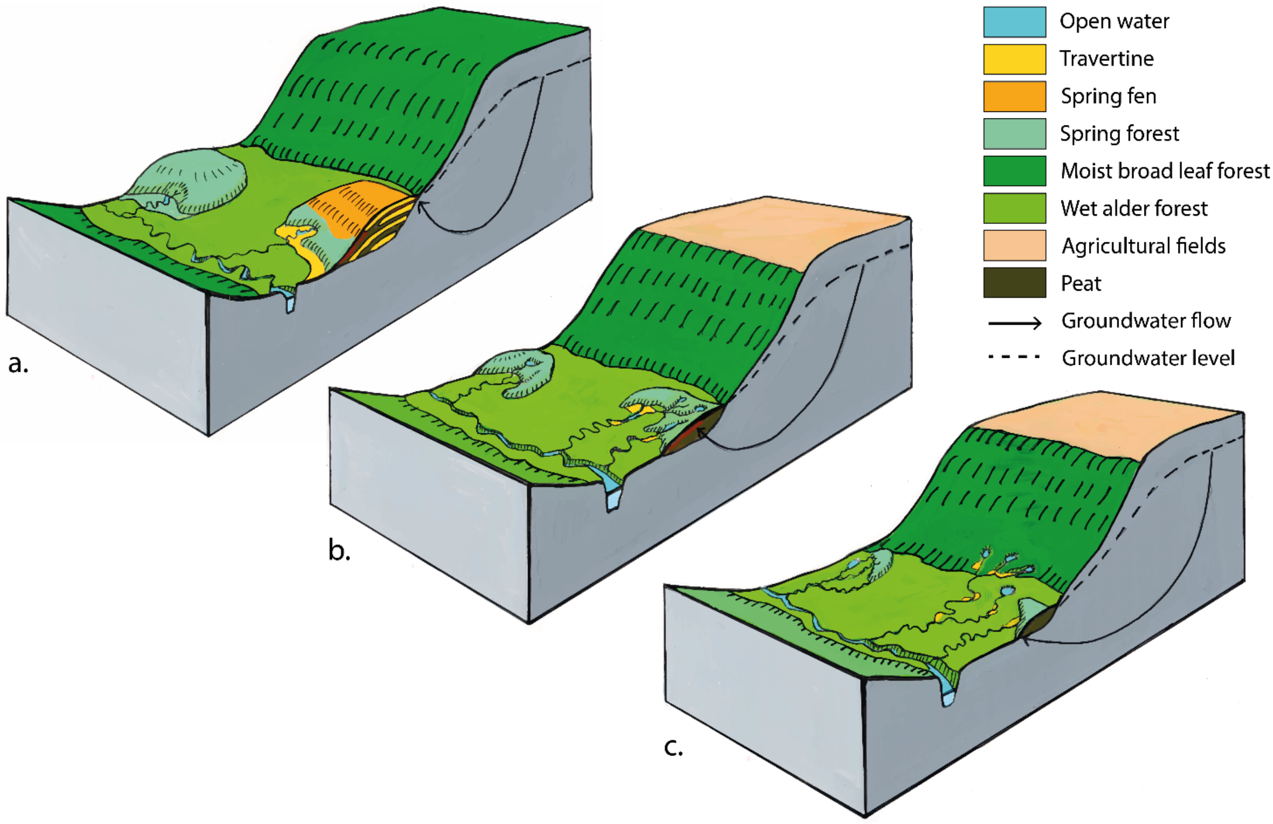

Figure 9: Speculative reconstruction of the degradation of alkaline fens in the NW-European lowlands. (a): undisturbed situation - before cutting of forest on the plateau - with alkaline spring fen and travertine deposition. (b): initial deteriorating phase induced by forest cutting, increased drainage and backward erosion, development of spring forests and petrifying springs with tufa deltas. (c): strongly deteriorated state - strong backward erosion formed groups of springs at a higher position on the slopes and resulted in near disappearance of peat. Only petrifying rivulets may still be present.

CONSEQUENCES FOR RESTORATION MANAGEMENT

In the NW and Central European lowlands, tufa depositing Spring-mires are practically always part of peat forming or former peat forming wetland complexes (Janssen, 1960, Succow 1988, Succow & Joosten 2001, Wołejko 2001, Osadowski *et al*. 2009, Madaras *et al*. 2012). Descriptions of peat profiles taken from such wetland complexes show that peat development and tufa deposition are related to each other in a complex way, in both space and time (Dobrowolski *et al*. 2005, 2012, 2017, 2019). From a landscape ecological point of view many petrifying springs are, or have been in the past, an integral part of alkaline fens or degraded forms of such systems. In many cases hydrological and ecological relationships exist between Petrifying-springs and Alkaline-fens.

Alkaline-fens may or may not deposit tufa on the surface. As we have shown, these mires may shift regularly over time from tufa-depositing systems to peat-forming systems (Wołejko *et al*. 1994, Hájková *et al*. 2012a, Dobrowolski *et al.* 2019). Many Petrifying-springs are very likely relics of former alkaline mesotrophic Spring-fens and in the past the two habitats may have co-occurred in the landscape. They are, in a sense, manifestations of the same conditions resulting in different habitat (types) that alternate in space and time. With respect to water quality the Alkaline-fens are the most vulnerable manifestation of this type of habitat. If Petrifying-springs do occur in the presence of peat deposits within the same hydrological system, they should be considered as part of the Alkaline-spring-fen habitat, not as a separate habitat type. Probably it is only the Petrifying-springs on steeper slopes, petrified cascades, and tufa dams in larger streams that reflect the ecohydrologically natural setting of the habitat type ‘Petrifying-springs (7220)’.

This implies that restoration of damaged Petrifying-springs and Spring-fens should be aimed at restoring the complexes *as a whole* with both habitats included, and should not focus solely on the separate habitat types. Restoration of deeply incised backward eroding gullies is the first real challenge in restoration of the hydrological conditions. It is necessary to stabilise the water outflow in the springs by filling in drainage ditches in order to stop further erosion in the spring complex. Eventually this may lead to the development of peat forming Spring-fens again, either spontaneously or after careful removal of the forest and a subsequent mowing regime. However, to regenerate Spring-fens, the build-up of a new peat layer is an essential but very delicate process (Koska & Stegmann 2001). This is possible only in an environment where (1) a year-round continuous supply of enough groundwater is available and (2) the groundwater feeding the springs is of sufficient quality, at least alkaline and nutrient (NPK) poor. The latter condition requires protection of the direct catchment area and cessation of drainage and fertilisation in such areas (Grootjans *et al*. 2006b). Restoration measures to increase the groundwater outflow in damaged spring complexes may by beneficial for some animal populations in the springs, but conflicts with the restoration of Alkaline-fens or Calcareous-spring-mires (Koska & Stegmann 2001, Grootjans & van Diggelen 2009). Conservation and restoration of a combination of both habitat types stresses the need for quick reduction of negative human influences.

For Petrifying-springs in NW Europe, de Mars *et al*. (2016) defined threshold values for NO_3^- as 450 µmol L^{-1} (= 18 mg L^{-1}) and for PO_4, 0.53 µmol L^{-1} (= 0.04 mg L^{-1}). For lowland petrifying springs in the United Kingdom a threshold value for NO_3^- of 320 µmol L^{-1} (= 12.8 mg L^{-1}) was determined (UKTAG 2012). These threshold values are concentrations above which adverse effects on some characteristic moss species will occur. However, these threshold values for petrification did not consider rarer plant species and small animal species. Moreover, these threshold species cannot be used for peaty/organic-rich spring fed habitats, such as Spring-fens, because of enhanced redox processes in the peat layer due to pollutants (such as NO_3^- or SO_4^{2-}) in the groundwater. Reduction of NO_3^- in the presence of organic matter results in denitrification of NO_3^- but at the cost of organic material (Lucassen *et al.* 2004, Smolders *et al.* 2006, de Mars *et al.* 2016, van Dijk *et al*. 2019), which in the long term will lead to eutrophication and fen degradation (Smolders *et al*. 2006). In (fairly) undisturbed Alkaline-fens, groundwater NO_3^- concentrations are found to be less than 125 µmol L^{-1} (< 5 mg L^{-1} ; Hajek *et al*. 2002, Farr *et al*. 2014, Grootjans *et al*. 2015), which would result in an almost fourfold lower threshold value.

For sustainable conservation and restoration of co-occurring ‘Petrifying-springs (7220)’ and ‘Alkaline-fens (7230)’ the levels of groundwater pollutants such as nitrate must, therefore, be much lower than threshold values defined solely for ‘Petrifying-springs (7220)’. Under conditions with higher nitrate and phosphate concentrations in the groundwater, organic matter will inevitably be lost and new peat formation is hardly possible.

The present paper describes the connection between the two habitat types Petrifying-springs (7220) and Alkaline-fens (7230), and points to differences in their functioning as well as conservation and restoration measures for both. Our considerations indicate that intervention aimed at the restoration of Alkaline-fens will require stricter thresholds and measures than those listed for Petrifying-springs alone.

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APG and LW are lead authors of the article. GvD, HdM and AS provided valuable comments and contributed to editing of the manuscript.

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