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Reconstructing past disturbance dynamics in mountain spruce forests from fossil insect remains

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With this text, I confirm that this PhD thesis “Reconstructing past disturbance dynamics in mountain spruce forests from fossil insect remains” was elaborated independently with the use of quoted literature and consultations with my supervisor and other advisors. I agree with publishing this Ph.D. thesis according to Czech law n. 111/1998 Sb. about the universities in its current valid wording. This agreement is independent from the result of the official defense of this thesis.

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Abstract

The identification of fossil insects has been part of paleoecological studies since the 1960’s, when it became apparent that insect taxa have kept their ecological preferences for thousands of years. As insects use the strategy of dispersal rather than adaptation to local climate, insect remains can be used in climate reconstructions, archaeological reconstructions and landscape reconstructions. Several groups of insects, such as chironomids, ants, mites and beetles can be used in these studies. Of the terrestrial insect groups, beetles (Coleoptera) are most widely used because of their enormous variety, diversity and range of habitat, appearing in almost every environment. Moreover, beetle exoskeletons are one of the hardiest in the insect world, and many fossil insect assemblages consist primarily of beetle remains.

Recently, the use of paleoecology in the reconstruction of natural disturbances has sparked new interest. Under current climate change, natural disturbances such as floods, drought, wildfires, windstorms and insect outbreaks are becoming more frequent, while increasing in magnitude. Paleoecology can contribute to the development of disturbance models which predict future disturbance events, by reconstructing past disturbance events to create a baseline or analogue for these past disturbance events. Currently, several reconstructions of natural disturbances related to fire or windstorms have been published, but no study has focused on reconstructing past bark beetle outbreaks.

This thesis aims to demonstrate how the application of subfossil insect remains can aid in the reconstruction of former landscapes and past disturbances in central Europe, in order to better understand environmental change in this region, and to create a historical analogue of changing landscapes to evaluate current and future adaptation to anthropogenic land-use pressures and climate change.

Fossil insect remains were isolated from a lake core from Šumava National Park in Czechia and from a peat bog in Tatra National Park in Slovakia. In addition to these two new study sites, a data synthesis was conducted to summarize the fossil sites with bark beetle remains currently known from Europe and North America. Results from these studies from central Europe show that conifer bark beetle remains from this region are abundant, when compared to the existing records from Europe and North America (Article I & II). The fossil beetle records produced during this PhD work provide a substantial addition to the knowledge of bark beetle remains recorded from fossil sites in central Europe. The high-resolution beetle record from Diera Hollow forest hollow (Article I) contributes to the reconstruction of the changing mountain landscape through time, affected by natural and anthropogenic

disturbances. Changes in beetle diversity could potentially be used to direct restoration and conservation practices in this region. A peak in conifer bark beetle remains from the beetle assemblages of Diera Hollow (Article III) could be correlated to the recent bark beetle outbreak in the region. These results allow for further interpretation of the presence of conifer bark beetle remains in sediment records. Trichoptera larvae remains from Prašilské Lake (Article IV), used to reconstruct long-term environmental conditions around the lake, show that acidic conditions of this alpine lake were not only prevailing in recent decades but are a natural feature of this glacial lake. Despite the challenges of this PhD project, due to limited local knowledge on Quaternary entomology and limited knowledge on the ecology and distribution of several montane insect species, the results of this study are encouraging further research and an expansion of the field in this region. The articles in this thesis highlight that previous methods, developed to use insect remains in environmental reconstructions, can contribute in several ways to paleoecological research in central Europe.

Contents

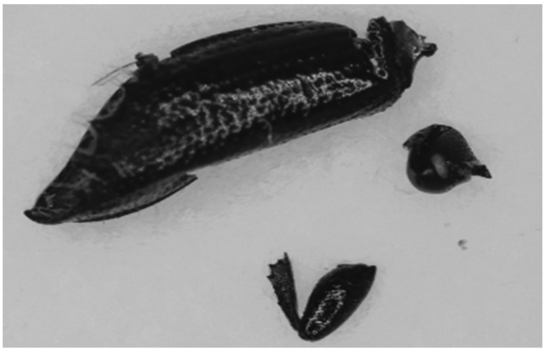
List of original publications

I. **N Schafstall,** NJ Whitehouse, N Kuosmanen, H Svobodová-Svitavská, M Saulnier, RC Chiverrell, P Fleischer, P Kunes, JL Clear (2020). Changes in species composition and diversity of a montane beetle community over the last millennium in the High Tatras, Slovakia: Implications for forest conservation and management. Palaeoecology Palaeoclimatology Palaeogeography 555, 109834.

II. **N Schafstall,** N Kuosmanen, CJ Fettig, M Knižek, JL Clear (2020). Late Glacial and Holocene records of tree-killing conifer bark beetles in Europe and North America: Implications for forest disturbance dynamics. The Holocene 30(6), 847– 857.

III. **N Schafstall,** N Kuosmanen, H Svobodová-Svitavská, K Halsall, M Knižek, P Kuneš, P Fleischer, RC Chiverrell, JL Clear. Using a fossil bark beetle record as indicator of past bark beetle outbreaks in a Norway spruce mountain forest. Manuscript.

IV. Daniel Vondrák, **Nick B. Schafstall,** Pavel Chvojka, Richard C. Chiverrell, Niina Kuosmanen, Jolana Tátosová, Jennifer L. Clear (2019) Postglacial succession of caddisfly (Trichoptera) assemblages in a central European montane lake. Biologia 74(10), 1325 – 1338.



Subfossil *Ips typographus*, ca. AD 1950 (Schafstall, 2018)

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1. Introduction

1.1 Paleoecology and its applications

1.1.1 The practice of paleoecology

Interest in our natural world has been expressed throughout ancient history (Plin. NH; Gessner, 1551-58). The development of the discipline of biology in the 19th century increased our knowledge of botany and zoology, resulting in the foundation of biogeography, ecology and ethology. While fossils were previously regarded as lifeless objects, the development of concepts, such as extinction and evolution, led to these fossils being included as part of our natural history. These advances made us regard our planet Earth as a living object, changing through time (Darwin, 1859; Lovelock and Margulis, 1973). Important advances in understanding the time scales of changes of groups of organisms came with the development of (bio)stratigraphy and, ultimately, dating of the sediments that contain the fossils used to reconstruct aspects of our past (Libby, 1946). Paleoecology is the study of interactions between organisms and/or interactions between organisms and their environments across geological timescales, based on organic as well as inorganic evidence (Birks, 2008). The field of paleoecology can be included in multidisciplinary studies with a variety of fields including; paleontology, ecology, climatology and biology, to inform us about past environments. Therefore, paleoecology is often used in Quaternary sciences and archaeological studies.

1.1.2 Quaternary sciences

Quaternary sciences focus on the Quaternary period, comprising the last 2.6 million years of our Earth's history. During this time, several glacial-interglacial cycles succeeded each other (Petit et al., 1999). An extensive series of studies contributed to the reconstructions of the extension of former ice sheets during periods of glaciation (e.g. Mix and Ruddiman, 1984), but also a significant amount of information has been gathered about the physical condition of our planet during warmer interglacial periods and interstadials (Gallup et al., 1994; Martrat et al., 2004). Not only the geology and climatic aspects of the Quaternary have been reconstructed, but also the flora and fauna of different glacial and interglacial periods (e.g. Stuart, 1974; Velichko et al., 2004; Herzschuh et al., 2016). Adopting the theory that our current flora and fauna has persisted and migrated into refugia during unfavorable climatic periods (Magri, 2007; Bennett and Provan, 2008), the identification of changes in the floral and faunal communities at a site through time allows for detailed reconstructions of interactions between climate and landscapes (e.g. Sher et al., 2005).

1.1.3 Archaeology

In archaeology, paleoecological interpretation of plant and animal species aids in the reconstruction of ancient settlements and their environmental conditions. The evolution and the origin of domesticated plants, as well as the presence of domesticated animals, gives us insight in the development of civilizations and their interaction with people from other geographical regions (Jones et al., 2011; Vigne, 2011). Wild animals and plants are utilized to establish important information about archeological sites, such as the diet of the former inhabitants of a human settlement. Fossils of insect species can be used to identify typical components of a settlement such as a storage space, or identify the location where inhabitants left their waste (Sadori et al., 2006; Grabowski and Linderholm, 2014). Finally, the proportion of forest species versus species living in open terrain, or wetlands, can aid the reconstruction of the type of terrain the settlement was located in (Falconer and Fall, 2013; Tisdall et al., 2018).

1.2 Quaternary entomology

1.2.1 The history and applications of Quaternary entomology

Quaternary entomology, the study of insect fossils, has contributed significantly to the field of Quaternary science because of its suitability for detailed temperature reconstructions. The classical hypothesis that insect fossils from Quaternary deposits belonged mostly to extinct species, was first rejected by Carl Lindroth in the 1940s (Lindroth, 1948). These findings show that the majority of beetle (Coleoptera) species have not changed in appearance for hundreds of thousands of years and only a few beetle fossils have been discovered that do not belong to an extant species. Most of the current known beetle species have been extant since the Late Tertiary or Early Quaternary (e.g. Elias et al., 2006). Russell Coope, the founder of modern Quaternary entomology, demonstrated that beetles were not geographically limited in their dispersal; fossils from glacial deposits in England were found to be from extant species on the Tibetan Plateau (Coope, 1973). Instead of adapting to their environments, not only beetles but all insect groups exert enormous amounts of energy in collective dispersal and migration

(Heydemann 1967; Haek, 1971; Müller, 1982). Many insect groups have wings and migrate rapidly to new areas when the climate of their local habitat becomes unfavorable. An important example of this is the study by Howden and Scholtz (1986), which reports a complete species turnover in a beetle community when a 10-year long increase in precipitation occurred. As insect species reflect clear changes in micro habitats, fossil insect remains can be used for a variety of reconstructions.

1.2.2 Temperature reconstructions

Two main insect groups have been used to reconstruct Glacial-Interglacial temperature shifts; Coleoptera (beetles) and Chironomidae (chironomids; non-biting midges). Certain groups of insects, included beetles and chironomids, are sensitive to changes in temperature and are constrained in their geographical distribution by climatic properties (Elias, 2010).

1.2.2.1 Coleoptera

Climate reconstructions based on fossil beetle assemblages have been published since the 1960's. As it is assumed that climatic requirements for all individual beetle species have not changed through time, modern analogues were identified for fossil beetle assemblages. By plotting the environmental variables from the region(s) where the modern analogue of the fossil assemblage was found, minimum and maximum air temperatures were plotted. Although only a part of the species of Coleoptera is stenothermic, and exact matches with modern analogues were seldom found (Elias, 2010), expertise from the researchers using this so-called 'Range Overlap Method' contributed to proper estimates of paleotemperatures during glacial and interglacial periods. In the 1980's, efforts were made to standardize this method. The Mutual Climatic Range (MCR) method uses climatic ranges of individual beetle species and was developed between 1982 and 1986 by Russell Coope, Timothy Atkinson and Keith Briffa (Atkinson et al., 1987). Data was collected for beetle species in North America and Western Europe, so that the MCR method is only applicable in these regions. In other regions of the world, researchers currently continue to develop different methods (e.g. New Zealand: Marra and Leschen, 2004; Australia: Porch, 2007). Statistical testing shows that the best correlation between calculated and measured temperatures are T_{max} (mean temperature of the warmest month of the year) and T_{range} (the temperature range between warmest and coldest months). An example of overlapping climate envelopes of two beetle species in North America, which currently do not share the same geographical range but could be found in a fossil assemblage together are shown in Figure 2 (page 14). Rapid temperature shifts during the Quaternary have been reconstructed using beetle temperature ranges and the MCR method (Atkinson et al., 1987). These temperature changes occurred so rapidly that they could not be inferred from pollen data but MCR reconstructions captured these changes in such detail that allowed for comparing climatic developments between different regions (Coope et al., 1998). The detailed temperature reconstructions from fossil beetle assemblages have contributed significantly to our understanding of climate fluctuations from the Last Glacial Maximum until today, and data from the various sites made available by Quaternary entomologists such as Russell Coope, Geoffrey Lemdahl and Allan Ashworth are still used widely (e.g. Marks et al., 2016). Currently, only a few recent studies with additional temperature and precipitation reconstructions from beetles have been published as the areas covered in the MCR data sets do not produce any additional novel information about our past climate (e.g. Holden et al. 2017). If more environmental data from beetle species in other regions such as Eastern Europe or Asia is gathered, new and exciting insights into the climate of these regions would likely be published in the near future.

1.2.2.2 Chironomidae

A popular proxy in paleolimnological studies, chironomids can be used to reconstruct summer temperatures, acidity (pH) and quality of a water body (nutrients, trace metals). Studies on chironomids started relatively recently; the earliest publications originate from the 1990's from North America and Europe (e.g. Walker, 1995). From the early 2000's, studies on fossil chironomids became popular and records were often used for local temperature reconstructions in North America and Europe (e.g. Seppä et al., 2002), as well as occasionally in other regions (Andreev et al., 2004). Currently, western and northern Europe are covered by excellent data sets that can reconstruct even moderate climatic changes during the Holocene (Heiri et al., 2003). Recent studies from Europe include temperature reconstructions from countries such as Finland (e.g. Luoto et al., 2014), The Netherlands (Gouw-Bouman et al., 2019) and Czechia (Hájková et al., 2014).

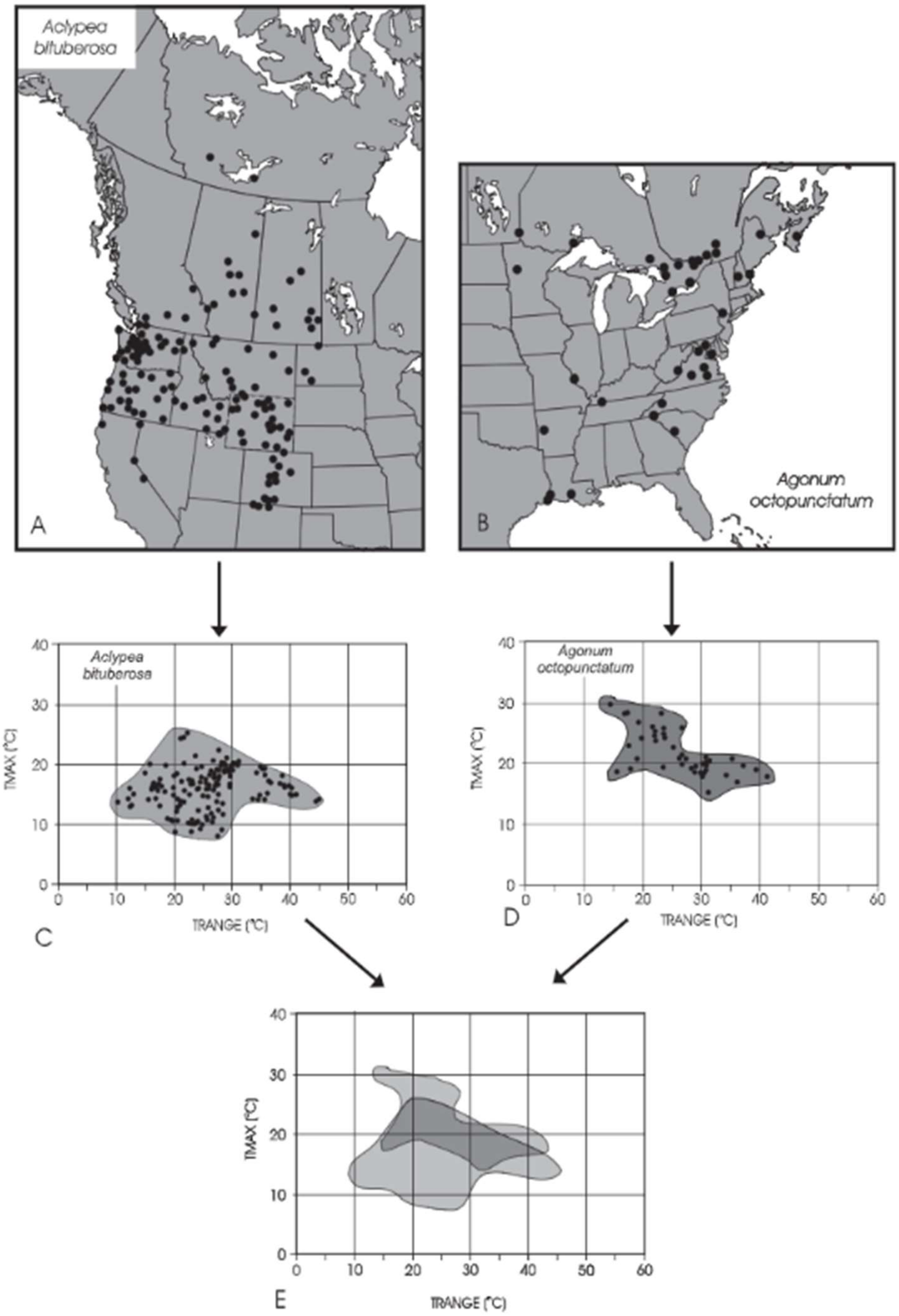

Figure 2. adapted from Elias (2010) showing an example of the Mutual Climatic Range (MCR) method by showing the temperature envelope for two North American beetle species. Modern distribution maps for (A) the carrion beetle (Silphidae) *A. bituberosa* and (B) the ground beetle *A. octopunctatum* correspond to climate envelopes for these respective species (C and D) that overlap to produce a MCR (E), even though the modern distributions of these two beetle species do not overlap. The two variables in the method are *Tmax* (mean temperature of the warmest month of the year) and *Trange* (the temperature range between warmest and coldest months).

1.2.3 Archaeological reconstructions

Insect groups have been used in archaeology as supporting evidence of human presence or human activities such as pasturing, food storage and burying of the dead. Numerous studies have been conducted on insect remains found in buried remains; not only on human mummies in Egypt but also in Greenland (Bresciani et al., 1983), Alaska (Horne, 1979), Chile (Baker, 1990) and from so-called bog bodies in Europe (Dinnin and Skidmore, 1995; Chapman, 2015). The most identified insects from buried humans are lice (Phthiraptera), fleas (Siphonaptera) and larvae of flies (Diptera). Besides aiding the reconstruction of the burial sites, also personal hygiene of these individuals could be discussed (Mumcuoglu, 2008). Other than ectoparasites, mostly Coleoptera have been used in archeological reconstructions.

While by far the most archeological studies with arthropodal identifications are from the United Kingdom, studies have been conducted in regions such as Egypt (Panagiotakopulu, 2001) and Greenland (e.g. Buckland et al., 2009). An interesting example of using archaeology to map the history of civilizations such as the studies on Viking settlements, tracking Viking explorations and colonization from Scandinavia via Iceland and Greenland to North America (Panagiotakopulu et al., 2007; Ledger et al., 2019). Archeological studies using fossil insect remains have contributed to our knowledge about the demise of Norse settlements on Iceland and in Greenland, and the influence of such temporary Norse settlements on the local fauna of Iceland, Greenland and North America (Panagiotakopulu et al., 2007; Ledger et al., 2019). In North America, archeological sites of prehistoric Amerindians are recorded with arthropodal identifications. These studies on insects gained insight in the diet, lifestyle and diseases of the Amerindian people (e.g. Faulkner, 1991). In Europe, the distribution of archeological sites with insect remains are mostly from western Europe and southern Scandinavia, with few other additional sites from southern and southeastern Europe and European Russia. In these European studies, the research mostly focuses on life in cities (e.g. Andersson 1992; Büchner and Wolf, 1997) although there are some exceptions where the natural history of a forest was reconstructed (e.g. Olsson and Lemdahl, 2009). Insect remains identified at archeological sites are often not only used to reconstruct the human settlement but also to reconstruct the surrounding landscape. This way, the interactions between the previous inhabitants of a settlement and their surrounding environment can be better understood.

1.2.4 Landscape reconstructions

Several groups of insects have been used to reconstruct (processes in) natural landscapes; the most frequently used insect groups are Acari (mites), Trichoptera (caddisflies), Chironomidae (nonbiting midges), Formicidae (ants) and Coleoptera (beetles). As these groups include taxa which inhabit a range of habitats, including aquatic habitats, they have been used as supporting evidence for reconstructions of local landscapes.

Acari are occasionally used in Quaternary entomology as they are small, often preserve intact and can be found in high quantities, even when smaller soil samples are used (e.g. Erickson, 1988). Oribatid mites have specific habitat preferences and occupy a variety of ecological niches, varying from aquatic to anthropogenic habitats (Schelvis, 1990). Research on fossil mites has helped reconstruct local landscape composition (Schelvis, 1990), moisture and lake level changes (Schelvis and van Geel, 1989; Salisch et al., 2017) and local sea level changes (Schelvis and Ervynck, 1992). Soil mites are currently studied intensively in studies on arthropod soil communities and although the popularity of soil mites as a study subject in paleoecology seems to have waned, there are occasionally new studies (Moldovan et al., 2016; Salisch et al., 2017).

Trichoptera larvae remains have been used in Quaternary studies as they can often be identified to genus or species level and have specific requirements for water quality and substrates on which the aquatic larvae dwell (Bradt et al., 1999; Hering et al., 2004). Fossil Trichoptera larvae remains have been used to reconstruct past river flow regimes in Denmark, England and France (Wiberg-Larsen et al., 2001; Greenwood et al., 2003, 2006; Ponel et al., 2007). Howard et al. (2009) tested a flow-velocity reconstruction method (Extence et al., 1999) with fossil Trichoptera remains and confirmed the applicability of this method as a paleolimnological tool.

Although Chironomidae are mostly known for their use as a proxy for paleotemperatures, they can also be used to reconstruct physical and chemical properties of water bodies such as nutrient content, lake water levels and salinity. Often, chironomids are studied in combination with other biological proxy indicators such as diatoms (Bigler et al., 2006; Lucas et al., 2015). Furthermore, reconstruction of lake properties can give insight to (changes in) the surrounding landscape (Heinrichs et al., 1999).

Another group of insects whose head capsules are preserved well and are used in landscape reconstructions are Formicidae (ants). Fossil ant remains have been used in various studies as an additional proxy to identify the presence of trees. It has been argued that abundant

ant fossils reflect an abundance of dead wood (e.g. Lavoie, 2001), and thus can be used to establish changes in position of the tree line at high elevation or at high latitudes. Often, the presence of ant fossils is interpreted as an indication of more open conditions as the ant hills of many ant species are found in forest clearings or at forest edges (Ponel et al., 2005). Formicidae fossils have also clearly shown their value as additional proxy for the presence of trees when there were reservations about the interpretations of presence of e.g. bark beetle remains (Elias et al., 1991).

Coleoptera (beetles) are the most popular insect group in landscape reconstructions. One advantage this group has, for instance over oribatid mites, is that the ecological preferences of many beetle species are relatively well known. Beetle remains have been used in various Quaternary studies, adding information about climate reconstructions and the evolving landscape (van Geel et al., 1989; Zazula et al., 2006; Tello et al., 2017). Beetle remains can be found in the strangest places, such as inside fossil mammoth skulls (Scourse et al., 2009), and these accidental finds of beetle remains often contribute to landscape reconstructions. As our climate has been relatively stable over the last 6,000 years, beetle remains from Holocene sites have mostly been used to reconstruct the surrounding landscape in detail (e.g. Olsson and Lemdahl, 2010; Ponel et al., 2011). In Britain, special attention was given to beetle species which have disappeared locally and are currently extant on mainland Europe (Whitehouse, 2004). Many of these species are living in old or dead trees, and have been dubbed ‘Urwald fauna’, as their habitat is confined to old-growth forest. By comparing the timing of disappearance of these species, Whitehouse (2006) mapped the disappearance of primary old-growth forests in Britain and Ireland in the Late Holocene. Another study by Whitehouse and Smith (2010) used a large number of fossil beetle records from Britain to reconstruct the density of the European Holocene ‘wildwood’ by comparing indicator species for closed forests, open landscape and dung beetles. Fossil beetle remains add details about the presence of animal and plant species into past landscape reconstructions and their potential is only limited by the number of sites currently identified with beetle remains to apply these research questions and methodology in other regions of the world.

1.3 Reconstructions of past disturbances in Europe

Disturbances such as windstorms, floods, droughts, fires and insect outbreaks are an essential part of our natural landscapes and have shaped these landscapes into what they are today (Buma, 2015; With, 2019). However, recent climatic changes are increasing the frequency and severity of such disturbance events, causing rapid changes to vegetation structure and the extinction of numerous plant and animal species (Turner et al., 1998; Easterling et al., 2000; Thomas et al., 2004). Many ecosystem services are currently threatened by increased disturbances, and various strategies are being developed to mitigate ongoing changes to our ecosystems under climate change (de Groot et al., 2003; Buma, 2015; Morris et al., 2018).

Forest dieback in Europe is primarily caused by windstorms, droughts and insect or pathogen outbreaks (Seidl et al., 2017). Currently, these processes are being monitored to predict future disturbance events (Temperli et al., 2013; Forzieri et al., 2020; Thrippleton et al., 2020). However, historical data to feed into these disturbance models does not go further back than AD 1850 (Schelhaas et al., 2003). Paleoecological data has clear potential to improve future projections of natural disturbances. By extending data of past disturbances beyond historical records, the frequency and severity of disturbances on longer time scales can be reconstructed to act as baseline to compare with current and future disturbance events (Kuosmanen et al., 2020). Paleoecological reconstructions from insect remains can also be used to reconstruct natural disturbances, by contributing to the reconstruction of vegetation and disturbance dynamics through time. Variation in landscape openness, presence or absence of certain tree or plant taxa, moisture levels at a site and anthropogenic indicators can all be derived from fossil insect remains, complementing other proxies in reconstructing the history of vegetation and disturbance dynamics (see chapters 3.1.1 and 3.2.1).

While proxies such as charcoal records, pollen records, and tree-ring archives are abundant to enable the reconstruction of past disturbances such as fire events and windstorms, fossil records of pest outbreaks in Europe are absent. Outbreaks of conifer bark beetles, mainly species of the genus *Dendroctonus* in North America and the European spruce bark beetle; *Ips typographus* in Europe, have increased in size and duration (Vega and Hofstetter, 2015). The current increase of these primary bark beetle species, so called for their ability to infest and kill living trees, is mainly due to increased annual air temperature which enable them to generate more generations per year (from 1 to 2 in higher latitudes and 2 to 3 in lower latitudes) and to increase their geographical ranges (Hicke et al., 2006; Jönsson et al., 2007; Mitton and

Ferrenberg, 2012; Fleischer et al., 2016). The total amount of timber losses in Europe due to bark beetle outbreaks is expected to increase to 17.9 million m^3 yr^{-1} by 2021 – 2030 (Hlásny et al., 2019). Fossil records of pest outbreaks would provide an extended baseline to compare the magnitude and frequency of these modern-day outbreaks with historical outbreaks. Few attempts have been made in North America to correlate fossil bark beetle records to bark beetle outbreaks but they produced limited quantitative reconstructions, as only few primary bark beetle remains were identified from lake sediments (Brunelle et al., 2008; Morris et al., 2015). However, new opportunities to improve our knowledge on past bark beetle outbreaks have arisen in central Europe, where conifer bark beetle remains have proven to be abundant in the fossil record (see chapter 3.2.2). Analysis of bark beetle records in central Europe could lead to a better understanding of these forest pests and their roles as natural components and agents of change of our landscapes through time.

1.4 Aims of this thesis

Central Europe is a region where Quaternary entomology has been largely absent. This thesis aims to demonstrate how the application of subfossil insect remains can aid in the reconstruction of former landscapes and past disturbances in central Europe. In addition, this thesis aims to create a better understanding of environmental changes in this region, and to create a historical analogue of changing landscapes to evaluate current and future adaptation to anthropogenic land-use pressures and climate change. The first-author publications in this thesis demonstrate the use of fossil beetle (Coleoptera) remains as a tool to reconstruct detailed information about the development of a montane forest site through time, as well as the potential of using bark beetle fossils as indicators of past bark beetle outbreaks. A literature study (chapter 3.2.1) revealed that fossil records with conifer bark beetle remains are rare, therefore the new, original data from this thesis (Chapter 3.1.1; 3.2.2) forms a substantial addition to fossil bark beetle data from the northern hemisphere. A second-author publication (chapter 3.3.1) is included in this thesis to give an example of the use of caddisfly (Trichoptera) remains from lake sediments in reconstructing past environmental conditions over a longer time scale.

2. Methods

2.1 Study area and sites

Fossil data was collected to enable paleoecological reconstructions of the central European montane landscape and natural disturbance dynamics. The studies were conducted in Czechia and Slovakia, where natural disturbances such as windstorms and bark beetle outbreaks have been abundant in recent decades. The sites selected for this study are located in areas with minimum anthropogenic pressure and where the disturbance history of the past few centuries is well-known, allowing for the comparison of fossil records to historical archives.

Šumava National Park is situated in the Bohemian Forest, a small mountain range on the border between Czechia, Germany and Austria. This old mountain range consists of eroded peaks between 800 – 1400 m.a.s.l, densely covered with forest. The area has been previously inhabited but was deserted between 1945 – 1989. In 1963, most of the Bohemian Forest was declared as protected landscape. From 1991, the most valuable part of the forest was declared a national park while the rest of the region serves as buffer zone. Several glacial lakes are found in the protected area of the Bohemian Forest, typically above 1000 m.a.s.l. These lakes were formed during the deglaciation of the region and contain sediment records spanning the extent of the Holocene and beyond into the Last Glacial Maximum.

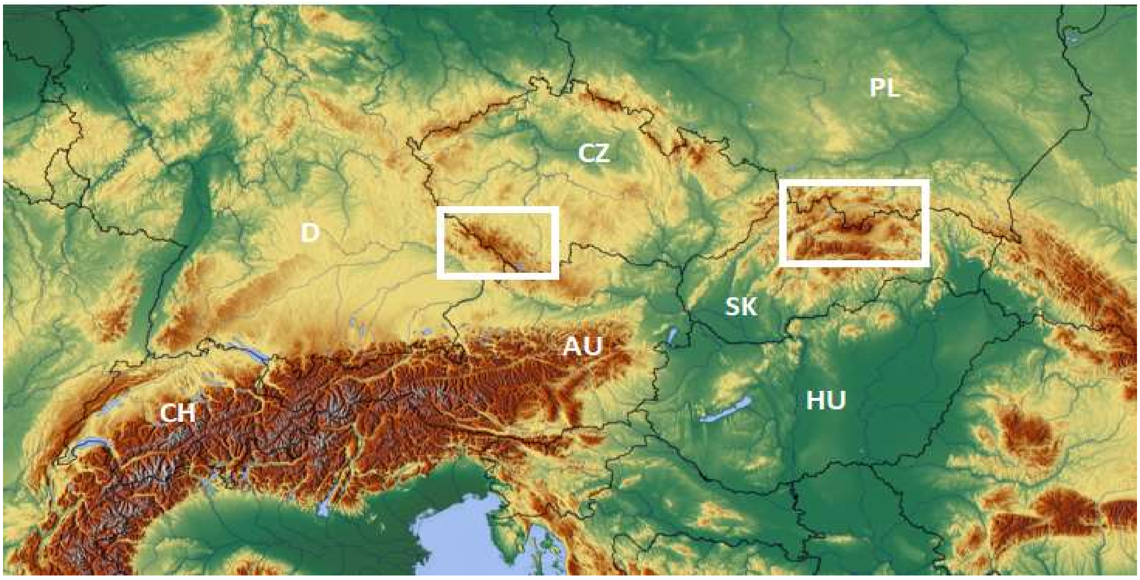

Figure 3. Geographical map of central Europe, with the study areas marked:Šumava National Park in Czechia (CZ) and Tatra National Park in Slovakia (SK)

Tatra National Park in Slovakia is situated in the High Tatra Mountains of the Western Tatras, the highest part of the Carpathian Mountains. The Carpathians range from Austria and Hungary through Slovakia and Romania to Serbia and are of the same age as the Alps. The High Tatra Mountains cover the Slovak-Polish border and inhabit the highest peaks of the Carpathians, reaching altitudes of 2650 m.a.s.l. The area has been subject to several skirmishes between countries over the centuries and transformed from an agricultural area into a tourist destination in the 19th century. Only in the 19th century, when mountain tourism started, these areas became more accessible by cable trains. Tatra National Park was established in 1949 on the Slovakian side, in 1954 on the Polish side, and is currently a UNESCO trans-border biosphere reserve. The area contains few lakes, but many peat bogs can be found on its rocky terrain. Formed when organic material accumulates at the bottom of a depression and preferably waterlogged due to limited soil porosity, peat bogs are excellent archives. In forested areas such as the High Tatras these peat bogs can often be found within the forest canopy, which has given them the name forest hollow (Overballe-Petersen & Bradshaw 2011). One of these forest hollows, namely Diera Hollow features in this thesis.

2.2 Sediment sampling, geochemistry and chronology

Insect remains preserve well under anoxic conditions, typically at waterlogged sites. Data from one lake in Šumava National Park (2015) and from one forest hollow in Tatra National Park (2016 and 2017) are featured in this thesis.

2.2.1 Prašilské Lake

A 2.18 m sediment profile was collected in August 2015 from the deepest (14.8 m) part of Prášilské lake, Šumava National Park in Czechia (49° 04′ N, 13° 24′ E; 1079 m.a.s.l.). The profile consisted of two parallel and overlapping cores (PRA 15-2-1 and PRA 15-2-2). Sampling was done from a floating platform using a hand-percussion Russian-style corer (1.5 × 0.075 m). The sediment–water interface was collected using a 0.1 m diameter gravity corer (PRA15-2GC) (Boyle, 1995). Sediment age-depth relationships were established using 14C radiocarbon dating at Prášilské lake (n = 10), with an additional 210Pb series for the core of the sediment-water interface (Appleby, 1978). Multi-proxy analysis of the cores included insect remains, pollen, charcoal and geochemistry. For all three cores, the geochronological data were compiled within the Bayesian routine "BACON" (Blaauw and Christen, 2011). This analysis partitioned both cores into 0.05 m thick sections and estimated the accumulation rates for each segment using a Markov Chain Monte Carlo (MCMC) approach (Christen and Pérez, 2009). The analyses were constrained by a prior model of sediment accumulation rate (a gamma distribution with mean 50-year cm^{-1} and shape 1.5) and its variability (memory, a beta distribution with mean 0.5 and shape 16). All ^{14}C ages were calibrated and modeled in "BACON" using the IntCal13 curve (Reimer et al., 2013), with a Student-t distribution to account for scatter in the ^{14}C measurements and to allow for statistical outliers (Blaauw and Christen, 2011). The weighted mean modeled ages against depth were smoothed using a 21-point moving average. Results from Prášilské lake are featured in chapter 3.3.1.

Figure 4. Prašilské Lake, 1080 m a.s.l. (picture by P. Kuneš)

2.2.2 Diera Hollow

A master sediment core was retrieved from the forest hollow Diera Hollow in 2016, with a 0.05 x 0.5 m D-section corer (Jowsey, 1965; Aaby and Digerfeldt, 1986). To provide the volumes of material required for quantitative analysis of subfossil beetles, a further 12 very-closely spaced sediment cores were sampled in 2017 using a gridded system, using a 0.1 x 0.5 m D-section corer. Two of these cores covered the top 0.5 m of the sediment, the rest of the cores measured between 0.57 and 0.78 m in total. Multi-proxy analysis of the master core (0.88 m in length) included geochemistry (Energy-Dispersive X-Ray Fluorescence: ED-XRF), pollen analysis, charcoal and radiocarbon dating. Four botanical macrofossil samples from the master core were dated in the Poznan radiocarbon laboratory and were used to establish a site chronology. The ^{14}C ages were calibrated with the IntCal13 curve (Reimer et al., 2013) within a Bayesian age-depth modelling routine 'BACON' (Blaauw and Christen, 2011), which modelled all age information, including the sediment surface, using a Student-t distribution that accounted for scatter and allowed statistical outliers. A Bayesian analysis (Christen and Perez, 2009) partitioned the core into three sections (31.3 cm thick) estimating the accumulation rate for each segment using a Markov Chain Monte Carlo (MCMC) approach. The modelling was constrained by a prior model of sediment accumulation rate.

All 13 cores, including the master profile, were analyzed for geochemistry on a wet-sediment basis using an Olympus Delta Professional ED-XRF mounted on the University of Liverpool Geotek Multi-Sensor Core Logger (MSCL). Patterns in geochemistry were comparable between the master profile and the 12 closely spaced cores. Patterns in concentration of the atmospheric fallout pollutant Pb (Renberg et al., 2000) displayed a strongly repeatable signal, while profiles for conservative lithogenic elements (e.g. Rb) also showed strongly repeatable stratigraphic records. The strong matches between the cores facilitated the transfer of the age-depth model between cores and provided a basis for subsampling the 12 cores. These cores were pooled into 18 samples with total volumes 400 – 1600 ml.

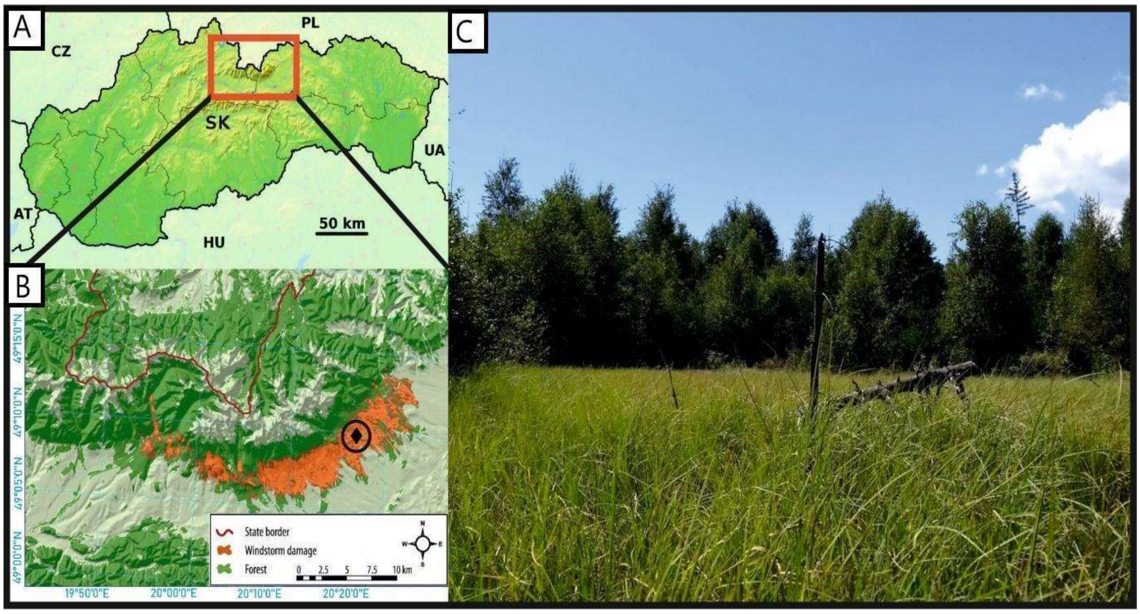

Figure 5. Location (black diamond in B) and impression of Diera Hollow. Base map (B) after Nikolov et al. (2014).

2.3 Fossil beetle analysis

Fossil beetle preparation of the 18 samples followed the methods described in detail by Elias (2010). Samples were wet sieved at 100 µm and the organic remains were soaked in paraffin oil and floated in water. Isolated floats were sieved and rinsed before being stored in ethanol (C_2H_5OH). Beetle remains were picked under a binocular light microscope with 10x magnification and were identified to family, genus and species level with the use of online databases (Kerbtier.de, Cassidae.uni.wroc.pl) and museum collections in the United Kingdom (Plymouth City Museum and Oxford Museum of Natural History) and Czechia (Czech National Museum in Prague, Regional Museum in Roztoky u Prahy and the Moravian Museum in Brno).

Specific ecological attributes of beetle genera and species were derived from literature through online databases; BugsCEP (Buckland and Buckland, 2006) and Biomap (2019). According to their ecological preferences, species or genera were divided into 20 functional groups to facilitate interpretation (Whitehouse, 2004): Eurytopic (appearing in a wide variety of biotopes); Aquatic (living at least partially in water bodies); Aquatic standing water (living in stagnant bodies of water); Aquatic running water (living in flowing water bodies); Marsh/wetland (hygrophilous species living in marshes or wetlands); Bank vegetation (living on vegetation at the banks of water bodies); Hygrophilous (living in a variety of biotopes, with a high humidity as common factor); Heathland/moorland (living in moderately wet, open landscape); Meadow (living in open landscape, often feeding on meadow vegetation); Disturbed/arable (living on disturbed soils, often disturbed by anthropogenic activities); Foul/dung (living in dung and rotting vegetation or other materials); Dung (only living in dung); Dry decomposer (fungivore in dry environments); Wet decomposer (mostly fungivores; found in moist places); Shaded woodland (living in shaded woodland but in the understory); Trees (living on trees); Deciduous trees (living on deciduous trees); Coniferous trees (living on coniferous trees); Deadwood (living in dying trees and decaying wood) and Conifer pest (colonizing healthy trees).The category Conifer pest was added as large quantities of conifer bark beetles (Curculionidae: Scolytinae) were found and these could provide additional information about past disturbances.

2.4 Trichoptera larvae analysis

The cores from Prášilské Lake were used for a multiproxy study (see Carter et al., 2018a) and subsampled in 0.5 cm resolution, while gravity core PRA15-GC-2 was subsampled in 1 cm resolution. Most of the samples from non-overlapping parts of the long cores and the gravity core were analyzed. A total of 318 sediment samples with wet volume of 1.5 – 5 mL for the long cores and 5 – 20 mL for the gravity core were processed. The samples were sieved over 100 µm mesh size to retain all macro-fossils. Caddisfly (Trichoptera) larvae remains were picked using a stereoscopic microscope at 15x magnification, dehydrated in 90 % ethanol, and mounted in Euparal to prepare permanent slides. To avoid an overestimation of individuals, only frontoclypeal apotomes were used for identification. Frontoclypei were identified using a reference collection of Trichoptera larvae from Bohemian Forest lakes and streams, and the identification key by Waringer and Graf (2011). Ecological characteristics of the individual caddisfly species based on Wallace et al. (1990), Braukmann and Biss (2004), Graf et al. (2008), Schartau et al. (2008), together with personal observations by co-authors, were used to derive ecological properties of the identified taxa.

2.5 Other proxies

The Trichoptera data from Prášilské Lake were compared to the geochemical signal from the sediment cores, in order to link changes in species occurrence with changes in water chemistry or erosion of the lake catchment (chapter 3.3.1). Comparison of the other proxies from the cores from Prášilské Lake are published in Carter et al. (2018a).

Beetle data from Diera Hollow were compared to a pollen record (chapter 3.1.1) and a charcoal record (chapter 3.2.1); analysis of these proxies was performed by experts involved in the PEDECO project. Pollen analysis of the Diera Hollow core was performed by Dr. H. Svitavská- Svobodová in continuous 1 cm resolution between 1 – 70 cm and in 2 cm interval for the rest of the core, amounting to a total of 78 samples. Subsamples of 0.5 cm^3 were prepared with standard procedures of KOH-, acetolysis- and HF-treatment (Faegri et al., 1989). The samples were mounted in glycerin and a minimum of 500 terrestrial pollen grains were identified under a light microscope using a 400x magnification. Pollen identification was based on standard pollen keys (Punt 1976,2003; Beug, 2004), microtopographic atlases (Reille, 1992 – 1998), and a reference collection in the Institute of Botany, CAS, Průhonice.

Charcoal analysis was performed on the 2016 master core by Dr. K. Halsall. Macroscopic charcoal (> 180 µm) represents local fire events in the vicinity of the study site

(Peters and Higuera, 2007; Higuera et al., 2007; 2010). Macroscopic charcoal was analyzed following a method adapted from Mooney and Tinner (2011). A known volume of sediment (0.5 – 1 cm^3) was disaggregated using 20 ml sodium hexametaphosphate (Calgon) with 10 ml potassium hydroxide (KOH) and left for a few hours. The sediment was washed gently through a 250 μm sieve, then either 1 or 2 ml of sodium hypochlorite was added to the sediment in water and left for the minimum time necessary to achieve a consistent bleaching effect up to a maximum time of overnight. The sediment was then washed gently through a 125 μm sieve to retain any fragmented particles. A light microscope and pipette were used to sort and remove any dark non-charcoal material, after which the petri dishes were photographed using a 12-megapixel digital camera and light table. The total concentrations and influx of macroscopic charcoal area and counts were calculated for each sample.

2.6 Statistical analysis

A paleoecological data set often exists of dozens of species, which few dominant species and the majority of species or taxa often occurring infrequently and in low numbers. This makes it difficult to discover patterns in the data, even more so as these patterns should be statistically significant. There are several ways to simplify and/or explain variation in ecological data, depending on the required type of information. In this thesis, a cluster analysis was performed on the beetle data, while a diversity index was calculated for both the beetle data and the pollen data.

2.6.1 Shannon’s diversity index

Shannon’s diversity index (Shannon and Weaver, 1949) takes both the number of individuals and the number of taxa into account, by calculating the natural log from the proportion of an individual species of the total sum of individuals. This diversity index is commonly used in ecology as well as archaeology and paleoecology (Pielou, 1967; Liu et al., 2015). Both beetle diversity and pollen diversity were plotted against time to compare forest beetle community dynamics with forest vegetation dynamics. Shannon’s diversity index is calculated with the formula:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

Where H’ is Shannon’s diversity index, p is the proportion (n/N) of individuals of one particular species found (n) divided by the total number of individuals found (N), ln is the natural log, Σ is the sum of the calculations, and s is the number of species.

2.6.2 Hierarchical cluster analysis

To emphasize changes in the terrestrial beetle community, aquatic species were excluded from the following analysis. Raw counts were converted to percentages to account for differences in total sum of individuals per sample (Legendre and Legendre, 2012). The square-chord method (Overpeck et al., 1985) was used to calculate dissimilarities between all samples. The degree of dissimilarity was calculated using the following formula:

$$SQD_{(i,j)} = \sum k \; (div_{ik} - div_{jk})2$$

Where $SQD_{(i,j)}$ is the total distance between the samples i and j, div_{ik} is the diversity of the species k in sample i, and div_{jk} is the diversity of species k in sample j. div_{ik} and div_{jk} are expressed as the number of individuals of species k compared to the total number of individuals in respectively, sample i or sample j.

A hierarchical cluster analysis was then performed on the resulting square-chord dissimilarity (SQD) matrix to identify patterns in the beetle assemblages. Ward's minimum variance criterion (Ward, 1963) was used to implement the hierarchical clustering. This technique produces compact, equal-sized dendrograms by minimizing the total within-cluster variance (Mirkin, 2005). Furthermore, a PCA (Gabriel, 1971) was performed on the samples according to their dissimilarity matrix, to explore which components (species) attributed most to the variance throughout the section. All statistical analyses were performed using the statistical software R (R core team, 2018).

2.6.3 Disturbance Frequency Index

The pollen record from Diera Hollow was used to calculate a Disturbance Frequency Index (after Kuneš et al., 2019). Each pollen found in each sample was assigned to a plant species following Beug (2004) and associated with a disturbance indicator value of that species. Here we used disturbance indicator values from the Whole-Community DF available for Central European flora (Herben et al., 2016), which expresses mean disturbance return time based on various disturbance processes including logging, cutting, mowing, herbivory, trampling, herbiciding, burning, wind-throws, soil erosion, ploughing, hoeing or burrowing, and used without differentiation. If the given pollen taxon covers several species, one of these species was assigned to it randomly (weighted by the present-day frequencies of these species). This process was repeated 100 times to provide mean disturbance indicator value represented by the given pollen grain. Then the mean disturbance frequency of the entire pollen sample is calculated as a mean of estimated disturbance frequency indicator values of all pollen grains in the sample. Disturbance frequency (DF) is expressed on a common logarithm scale and ranges from −2 (once in 100 years) to 0.78 (six times per year). Calculation of the DF was performed by professor P. Kuneš from Charles University.

2.6.4 CharAnalysis

CharAnalysis software was used to detect the peaks in macroscopic charcoal records in order to indicate local fire events (Higuera et al., 2007; 2010; Kelly et al., 2011). First, macroscopic concentrations (particles cm^{-3}) were interpolated to mean temporal sample resolution. Next, the charcoal record was separated into a low-frequency background component (BCHAR) and a peak component using the CharAnalysis software (Higuera, 2010). To determine the background component, smoothing with LOWESS regression within a 500-year moving-window was employed. The peak component was then calculated as residuals between interpolated charcoal records and BCHAR (Cpeak = CHAR-BCHAR) and evaluated using the 99th percentile of a Gaussian mixture model in order to separate fire events reflected by charcoal peaks from the background noise. The detected peaks were screened using a minimum-count peak ($p = 0.05$) test in CharAnalysis. This analysis was performed by Dr. N. Kuosmanen.

2.6.5 Linear regressions

We fitted a series of linear models linking responses (disturbance frequency index and macroscopic charcoal influx) to the total density of primary bark beetles (overall models) and densities of the three most abundant species (species-specific models). Since the reaction of plant communities and occurrence of potential fire events may be delayed in time behind the outbreaks, we evaluated immediate responses using the matched data from the same stratigraphic layers and also delayed responses using first-order lagged data (median lag of 12 years). All models were carefully checked for homogeneity of variances, normality, and temporal autocorrelation using diagnostic plots of residuals. Bark beetle densities and charcoal fluxes were log-transformed to fulfill the assumptions of linear models.

2.7 Literature studies

2.7.1 Data from databases

A literature study was conducted to explore how many Late Glacial and Holocene sites with fossils of destructive bark beetle species are known currently for Europe and North America (chapter 3.2.2). Open access databases Neotoma (Williams et al., 2018) and BugsCEP (Buckland and Buckland, 2006) were used to collate fossil records of bark beetles from 14,000 cal yr BP. An additional data literature search with Elias (2010) provided a detailed overview of all sites <14,000 cal yr BP containing bark beetle remains. Access to data unavailable as supplementary material in the literature was requested directly from the authors of the respective peer-reviewed publications. Modern bark beetle distribution data was collated from the Global Biodiversity Information Facility (GBIF, 2018), to compare modern distributions of bark beetle species with the fossil record of these species.

2.7.2 Human occupation data

To put changes in the beetle community reconstructed from Diera Hollow forest hollow into historical perspective (chapter 3.1.1), Slovak, Polish and Hungarian literature was translated and examined to determine the timing and the extent of human occupation of the region. The book *Terra Scepusiensis* (Gladkiewicz and Homza, 2003) contains gathered information about human activity in the Spiš region in Slovakia from the Bronze Age until modern times. As this region was disputed several times in history, chapters in this book are written in Slovak, Polish and Hungarian. Together, these articles give a comprehensive story of human activities and population densities in different parts of the Spiš region, including the locality of Diera Hollow.

3. Results

The PhD dissertation thesis consists of four articles: three first-author articles and one second-author article. Two first-author articles and the second-author article have been published and one first-author article is in the form of a manuscript, in the process of submission. The first part of the results focuses on using fossil beetle remains as a proxy for changes in a montane landscape over the last 1000 years (section 3.1). The second part elaborates on the use of bark beetle fossils for reconstruction of past beetle bark beetle outbreaks and other (natural) disturbances (section 3.2). The third part (section 3.3) shows how fossil insect remains from lake sediments can be used to reconstruct environmental changes on longer time scales.

Article I (Schafstall et al., 2020b) shows how changes in a mountain landscape in Slovakia over the past 1000 years, based on a fossil beetle assemblage, were mostly linked to changes in the vegetation which surrounded the sample site. The forest beetle community appears to have been influenced by anthropogenic pressure since AD 1250.

Article II (Schafstall et al., 2020a) gives an overview of the Late Glacial and Holocene sites with records of primary and secondary conifer bark beetles in Europe and North America. There are a limited number of records with conifer bark beetles, and only one site in North America recorded larger amounts of conifer bark beetle remains. Many sites in North America are Late Glacial or Early Holocene of age, while a large share of the sites in Europe are archeological sites of a younger age.

Article III (Schafstall et al., manuscript) demonstrates that conifer bark beetle outbreaks can be reconstructed from fossil beetle records. A recent outbreak in Tatra National Park, Slovakia, could be correlated to a large peak in remains of *Pityogenes chalcographus* and *Pityophthorus pityographus*, two smaller species which colonize mainly branches and crowns of living conifer trees. Identification of two peaks in bark beetle remains further back in time allowed for discussion of the use of bark beetle remains as a proxy for past outbreaks, and the conditions under which these took place.

Article IV (Vondrák et al., 2019) shows that, based on remains of Trichoptera larvae, Prašilske Lake appears to have been an acid, dystrophic lake since the onset of the Holocene. This study provides for the first time a record of postglacial succession of caddisfly assemblages from a central European mountain lake.

3.1 Using beetle remains to reconstruct changes in a montane landscape over time

3.1.1 Changes in species composition and diversity of a montane beetle community over the last millennium in the High Tatras, Slovakia: Implications for forest conservation and management

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Authors' contributions:

The study was planned by NS, JLC and NK. NS, NK, RCC, PK and JLC participated in the fieldwork where samples for this study were collected. Radiocarbon dating of the master sediment core was executed at the radiocarbon lab in Poznan, Poland. XRF scanning of the sediment cores was performed by RCC, correlation of sediment cores was performed by NS, RCC and JLC. Subsampling, sample preparation and beetle fossil extraction was performed by NS, initially under guidance of NJW. Beetle taxa identification was performed by NS, with the help of many experts on different beetle families. Ecological classifications were given to beetle taxa by NS, under advice of NJW. A Bacon age-depth model of the study site was created by PK and applied to the pollen data by NK; application of the age-depth model to the beetle data was performed by NS. Figures of beetle data in the program Tilia were created by NS, pollen data was collected by HSS and figures of pollen data were created in the program C2 by NK. MS and NS created the statistical analysis for the article in the program R. NS was responsible for preparing the manuscript, while all co-authors commented and contributed.

Extended summary

Introduction

Temperate mountain forests are under increasing pressure by humans and climate. Humans have progressively modified these ecosystems by altering land-use to their requirements, resulting in the decline of many plant and animal species (e.g. Elsen and Tingley, 2015). More recently, the frequency of extreme events such as drought and windstorms has increased significantly in regions with temperate montane forests, amplified by climate change (Schelhaas et al., 2003; Allen et al., 2010). Forest pest outbreaks have recently increased in central Europe, where large areas of montane forest consist of conifer monocultures with Norway spruce (*Picea abies*) as most common species. Forests which were turned into National Parks during the last century, such as Tatra National Park on the Polish/Slovak border in 1949-1954, currently experience large-scale bark beetle outbreaks which result in the dieback of many hectares of Norway spruce, and occasionally other conifer trees (e.g. Nikolov et al., 2014). Although naturalists and ecologists argue that we should look further back than historical records to assess if the frequency and magnitude of abiotic and biotic disturbances is indeed unprecedented (e.g. Froyd and Willis, 2008), no paleo-records from this region exist to address these questions. The High Tatra Mountains are an ideal region to investigate long-term changes in natural montane conifer forest, as the region was only under moderate anthropogenic pressure until recently (Fleischer et al., 2017). Subfossil beetle remains are a valuable addition to other paleoecological proxies such as pollen, as beetle remains can often be identified to species level and provide detailed information about their habitat. Many beetle species live in specific niche environments, not only with regards to climate but also to their biotope, and species found in a fossil assemblage typically provide information about the area up to 400 meters around the sample site (Smith et al., 2010). By assessing fossil beetle assemblages from a locality through time, changes in local vegetation composition can be reconstructed into detail.

Methodology

Diera Hollow is a forest hollow at the foothills of the High Tatra Mountains, 982 m a.s.l., near the village of Tatranská Lomnica (49.1593° N, 20.26357° E). Twelve cores were taken in 2017, to allow for sufficient material for qualitative analysis of macro remains. Subsampling and pooling of samples was executed based on the geochemical signals of the cores, resulting in 18 pooled samples. Beetle remains were extracted from the sediment by using the flotation method (described in Elias, 2010) and beetle remains picked under a binocular light microscope with 10x magnification. Beetles were identified to family, genus and species level with the use of online species databases ((Buckland and Buckland, 2006; Biomap, 2019) and museum collections. Based on their ecological attributes (Buckland and Buckland, 2006), single ecological niches were chosen for each identified beetle species or taxon. Pollen analysis was performed on a master core from 2016, resulting in 78 samples. Pollen were identified based on standard pollen identification keys (Punt,1976–2003; Beug, 2004; Reille, 1992–1998) and a reference collection. Zonation of the beetle samples was performed by a D-chord hierarchical cluster analysis (Ward, 1963; Overpeck et al., 1985) based on the terrestrial beetle taxa composition in each sample. A principal component analysis (PCA) was performed based on the dissimilarity between the samples, to explore which components (species) contributed most to the variance throughout the section. Furthermore, for both the beetle assemblages and the pollen assemblages the Shannon diversity index (Shannon and Weaver, 1949) was calculated for each respective beetle and pollen sample and plotted against time.

Results

A total of 2860 beetle individuals were identified from 313 taxa and 38 families. According to the D-chord cluster analysis, five beetle zones were established (930 – 1080 CE; 1080 – 1500 CE; 1500 – 1740 CE; 1740 – 1950 CE; 1950 CE – present). The oldest samples (930 – 1080 CE) contain mainly aquatic species and forest species, with the beech leaf miner *Rhynchaenus fagi* and primary bark beetle *Polygraphus poligraphus* in high abundances. In the next zone (1080 – 1500 CE), aquatic species and forest species become less abundant while marsh species and bank species increase significantly. In this zone, dung species start to appear. In the next zone (1500 – 1740 CE), dung species become more abundant and shifts in dominant species occur without significantly changing the contribution of each ecological niche. Zone 4 (1740 – 1950 CE) contains a low amount of primary bark beetles and mainly contains dominant species which were living in the forest hollow or on the surrounding marsh vegetation, although several taxa which are indicative for shaded woodland increased in numbers. The highest amount of dung beetles was recorded around 1780 CE. In the last zone (1950 CE – present), aquatic taxa declined rapidly in numbers while primary bark beetles and species living in deadwood reached a peak in numbers between 2000 CE – present. The primary bark beetle *Pityogenes chalcographus* reached very high numbers in this zone. According to the PCA results, the taxa which contributed most to the beetle diversity of this assemblage were various marshland, meadowland and heathland species, forest pests (primary bark beetles such as *P. poligraphus* and *P. chalcographus*) and the beech leaf miner *R. fagi*. The pollen record extends from 590 CE to present, but the results focus on the record after 900 CE. Between 900 – 1000 CE, *Abies* and *Picea* pollen sums increase to a maximum, which rapidly declines between 1250 – 1350 CE. *Fagus* pollen sums reach a maximum around 1250 CE but also decline quickly afterwards. From 1250 CE, there was a notable increase in human indicator pollen such as *Secale cereale*, *Triticum* sp. and *Plantago lanceolata*. Poaceae and Cyperaceae pollen sums also show a large increase after 1250 CE. A peak in *Pinus* pollen, starting around 1350 CE, is followed by a peak in *Betula* pollen. From 1600 CE, *Picea* and Cyperaceae pollen increased while *Abies* and *Fagus* pollen continued to decline to very low values. The Shannon diversity index of the beetle samples fluctuates between values of 3,7 and 4,4 until around 1500 CE, after which it declines steadily. In the most recent samples (1950 CE – present) the diversity index drops rapidly under a value of 3,25. Pollen diversity fluctuates until a notable increase between 1200 – 1300 CE, followed by a decline until 1500 CE. Pollen diversity then rises to a steady phase, maintained until 1800 CE. Diversity values are lower after that, except for a rapid increase after 2004 CE.

Discussion

Over the last ~ 1000 years, different beetle communities have succeeded each other, many of which can be related to changes in the local vegetation. Reconstruction of the sample site between 930 – 1080 CE shows a shallow, sparsely vegetated peat bog which was surrounded by spruce-dominated forest with a share of fir and beech. In the next period (1080 – 1500 CE), the beetle community increased in diversity and species associated with landscape openness. Beetle diversity appears closely related to floristic diversity, which coincided with the increase of human-indicator pollen ((Behre, 1981; Gaillard, 2013). Around this time the diversity of dung beetles started to increase as well. During the next period (1500 – 1740 CE), indicators of landscape openness are still found. Conifer tree species dominate the indicator species for forest, although the beech leaf miner *R. fagi* was found in samples up to the end of the 19th century. The increasing number of species living on marsh vegetation suggests succession of the peaty pool into a marsh. From approximately 1800 CE, the increased share of shaded woodland taxa and conifer pests suggests a dense conifer forest around the sample site. This coincides with the reported abandonment of the region by humans in the 19th century. From ca. 1500 CE, the Shannon diversity index for beetles appears no longer driven by vegetation diversity. Partitioning of beetle ecological groups shows that from then on, beetle diversity becomes increasingly driven by aquatic taxa. A decrease in moisture at the site might have caused the rapid decline of beetle diversity after 1950 CE. Both climatic data and historical occupation data were studied in order to explain the development of the sample site through time, and the decline in beetle diversity after 1500 CE. Studies on paleoclimate in this region are limited (Niedźwiedź, 2004) and no correlation was found between described changes in temperature and moisture and the reconstructed changes in the beetle assemblage or vegetation. More sources are available which describe the presence of humans in the region through time (e.g. Cichocki, 2003; Pavercsik, 2003; Rączkowska, 2019), and beetle and pollen data support these sources. As the historically recorded increase in anthropogenic activity in the region coincides with the changing pattern in beetle diversity (e.g. Hreško et al., 2015), it is plausible that the decline in beetle diversity was related to anthropogenic activity.

Implications

The fossil beetle and pollen record from Diera Hollow suggest that changes in the local beetle community were related to regional changes, at least partially driven by anthropogenic activity. Evidence for the presence of beech and fir trees at this locality contradicts the common conception that beech trees have long been absent from forests at this elevation in the High Tatra Mountains (Rybníčková and Rybníček, 2006). The coincidence between anthropogenic activity and changes in the beetle community suggests a more pronounced influence of humans on the flora and fauna in this area than was previously assumed. While it can be argued that overall human population density was very low (Rączkowska, 2019), this emphasizes the vulnerability of mountain ecosystems to anthropogenic activities. Results from this study could advise future management of the Tatra National Park by providing clues on the composition of the landscape before it was changed by human activity. Ideally, local policy makers should acknowledge how the landscape of the High Tatras looked like before 1500 CE or even 1250 CE, as our results show a diverse landscape with higher shares of different tree taxa. This study also shows how aquatic beetle and marsh beetle species contribute to local biodiversity and recommends future studies on the conservation of inundated depressions in montane regions. While primarily beetles living in old-growth forest were marked as red-list species for conservation strategies (Nieto and Alexander, 2010), diversification in biotopes would lead to an increase in biodiversity.

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Changes in species composition and diversity of a montane beetle community over the last millennium in the High Tatras, Slovakia: Implications for forest conservation and management

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ABSTRACT

Montane biomes are niche environments high in biodiversity with a variety of habitats. Often isolated, these non-continuous remnant ecosystems inhabit narrow ecological zones putting them under threat from changing climatic conditions and anthropogenic pressure. Twelve sediment cores were retrieved from a peat bog in Tatra National Park, Slovakia, and correlated to each other by wiggle-matching geochemical signals derived from micro-XRF scanning, to make a reconstruction of past conditions. A fossil beetle (Coleoptera) record, covering the last 1000 years at 50- to 100-year resolution, gives a new insight into changing flora and fauna in this region. Our findings reveal a diverse beetle community with varied ecological groups inhabiting a range of forest, meadow and synanthropic habitats. Changes in the beetle community were related to changes in the landscape, driven by anthropogenic activities. The first clear evidence for human activity in the area occurs c. 1250 CE and coincides with the arrival of beetle species living on the dung of domesticated animals (e.g. *Aphodius* spp.). From 1500 CE, human (re)settlement, and activities such as pasturing and charcoal burning, appear to have had a pronounced effect on the beetle community. Local beetle diversity declined steadily towards the present day, likely due to an infilling of the forest hollow leading to a decrease in moisture level. We conclude that beetle communities are directly affected by anthropogenic intensity and land-use change. When aiming to preserve or restore natural forest conditions, recording their past changes in diversity can help guide conservation and restoration. In doing so, it is important to look back beyond the time of significant human impact, and for this, information contained in paleoecological records is irreplaceable.

1. Introduction

Montane biomes are diverse multi-functional environments with a variety of habitats often occupied by specific, endemic animal and plant communities constrained by environmental conditions (Kessler and Kluge, 2008; Dimitrov et al., 2012; Amori et al., 2019). Humans have progressively modified these ecosystems by altering land-use to their requirements, resulting in the decline of many plant and animal species. The establishment of national parks during the 20th century serves to preserve the remaining biodiversity in remote mountain areas, yet these montane forests are increasingly impacted by extreme climate events and their ecosystems are changing rapidly (McCain and Colwell, 2011;

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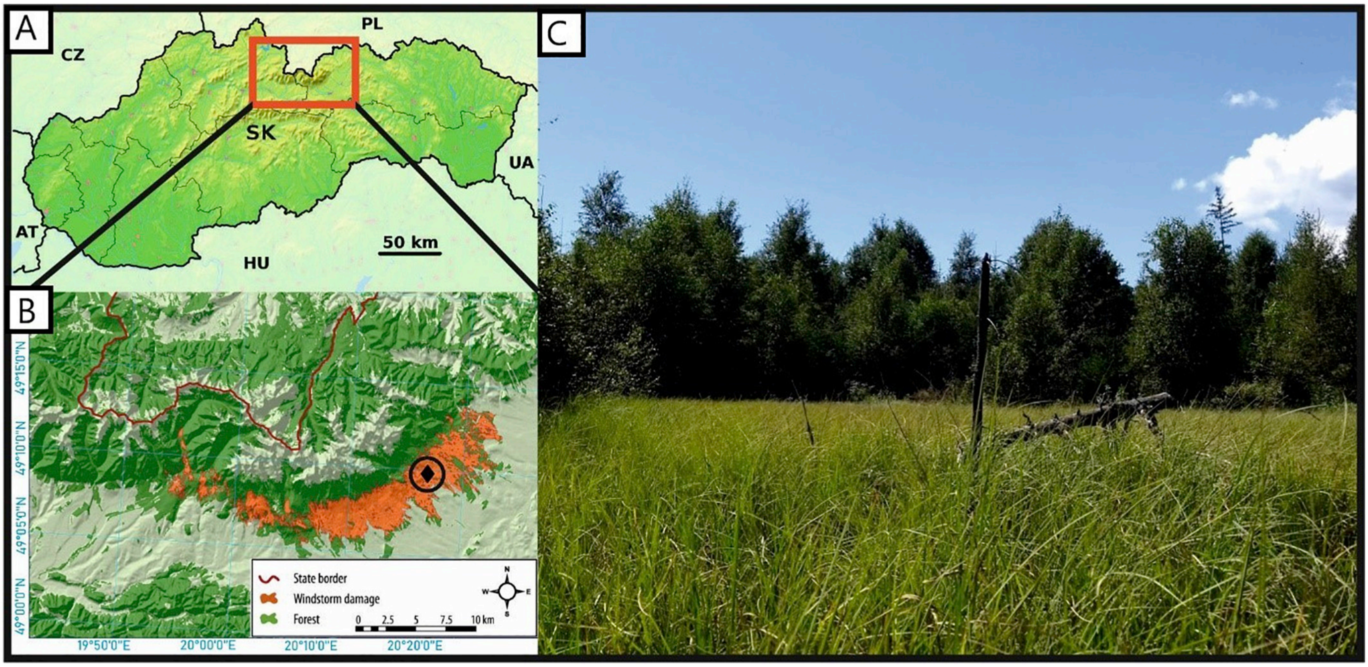

Fig. 1. A The study site Diera Hollow, located in the High Tatra Mountains on the Slovak-Polish border. Depicted countries are Slovakia (SK), Czechia (CZ), Poland (PL), Ukraine (UA), Hungary (HU) and Austria (AT). Fig. 1B Terrain map after Nikolov et al. (2014), highlighting the area affected by the 2004 windstorm Alžbeta, with the black diamond marking the location of Diera Hollow (49.09885° N, 20.15814° E). Fig. 1C shows the sample site during fieldwork in 2017.

Elsen and Tingley, 2015). In particular, the frequency of extreme events disturbing forest ecosystems, such as drought and windstorms, have increased significantly in North America and Europe during the last 50 years (Schelhaas et al., 2003; Allen et al., 2010). However, historical recordings of disturbance agents are rare in some regions (Schelhaas et al., 2003). Paleoecological reconstructions can be used to understand the long-term effects of changing climate and anthropogenic pressure on the landscape structure and the flora and fauna in montane regions (La Sorte and Jetz, 2010; McCain and Colwell, 2011). In the last decades it has become apparent that linking paleoecology with conservation management is key to understand the effects of current conservation efforts (Froyd and Willis, 2008). Ecological data on longer time scales allow for a better reconstruction of natural variability in a landscape and give clearer results about ecological thresholds and resilience within a natural system. Furthermore, by addressing ecological data on longer time scales it can be argued if the current disturbance events in montane forests are unprecedented (Froyd and Willis, 2008; Kidwell, 2015).

Fossil pollen and botanical macrofossils are the most commonly used proxies for reconstructing paleoenvironment and vegetation structure (e.g. Magyari et al., 2012). Subfossil beetle (Coleoptera) remains are a valuable additional proxy to pollen as these can often be identified to species level and provide detailed information about past beetle habitats (e.g. van Geel et al., 1989). Many beetle species live in specific niche environments because of their preferences for certain temperature and moisture levels, landscape openness and host plants (Elias, 2010). Local communities (< 400 m; Smith et al., 2010) are the source area for beetle remains at fossil sites. In previous studies, the comparison of fossil beetle assemblages with modern beetle communities provided valuable information about the timing and drivers of local beetle taxa extinctions (e.g. Whitehouse, 2006). Therefore, fossil beetle records provide not only detailed information to reconstruct landscape composition through time, but also contribute to solve issues in conservation and management (e.g. Buckland and Kenward, 1973; Gustavsson et al., 2009). Lindbladh et al. (2013) highlight fossil beetle remains as an underused, yet valuable proxy in forested landscape reconstructions as fossil beetles can contribute to the reconstruction of forest composition, (relative) amounts of old trees and coarse woody debris, and to reconstruct natural disturbances. Even insect outbreaks could potentially be quantified from fossil beetle remains.

Central Europe has a diverse landscape with high flora and fauna species diversity, and is currently under pressure from intensive land use (Turnock, 2002). The High Tatra Mountains are located on the border between Slovakia and Poland and are part of the Western Carpathian range, the highest range of the Carpathian Mountains. The area is a prominent UNESCO biosphere reserve with species such as brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*) and wolf (*Canis lupus*), and many endemic plant and animal species (unesco.org UNESCO, 2016). In the last decades, extreme events such as windthrows and droughts have increased significantly in this region (e.g. Fleischer, 2017). Consequently, the Tatra Mountains are an ideal region to investigate long-term (millennial) changes in the local flora and fauna, based on pollen and beetle remains. In this study, we aim to 1) Reconstruct changes in diversity of the local forest beetle community and 2) Identify the drivers behind changes in beetle community and vegetation diversity. Understanding the drivers behind species composition and diversity change over the last 1000 years can be used as a potential analogue to help understand the response and resilience of these ecosystems to future climate and anthropogenic changes.

2. Methods

2.1. Site area

Diera Hollow is a small forest hollow of 30 m × 80 m in size and located at 982 m a.s.l. on a former end moraine of the High Tatra Mountains near the village Tatranská Lomnica, Slovakia (49.09885° N, 20.15814° E; Fig. 1). The region has a sub-continental climate with an average minimum temperature of −5.3 °C and an average maximum temperature of 15.4 °C. The mean annual rainfall is 830 mm (Tatranská Lomnica weather station, 830 m a.s.l.). Forest hollows are waterlogged anoxic peat depressions within a forest canopy. Due to their small to moderate size (~100–2000 m^2) their sediments reflect a local environmental signal. The pollen signal is representative of the vegetation recorded within a radius approximately 100 m of the site (Overballe-Petersen and Bradshaw, 2011), and comparable to the source area radius of 400 m for beetle remains (Smith et al., 2010). The site was heavily damaged by the autumnal storm Alžbeta in 2004 and is currently surrounded by pine (*Pinus*), spruce (*Picea abies*), larch (*Larix decidua*), birch (*Betula*) and bilberry (*Vaccinium myrtillus*). Seedlings of birch, bedstraw (*Galium* sp.), rosebay willowherb (*Epilobium angustifolium*) and sedges (*Carex* spp.) are present at the site. Prior to the windstorm in 2004, the area surrounding the study site was densely forested, with spruce as the dominant species.

2.2. *Field methods*

A master sediment core was extracted from Diera Hollow in 2016, with a 5 × 50 cm D-section corer (Jowsey, 1965; Aaby and Digerfeldt, 1986). To provide the volumes of material required for analysis of fossil beetles, a further 12 proximal sediment cores were sampled in 2017 using a gridded system, with a 10 × 50 cm D-section corer. To minimize the disturbance of the sampling site inside the nature reserve, sampling was performed by collecting multiple parallel cores instead of digging trenches, a sampling method often used in paleoentomological studies (e.g. Forbes et al., 2019). Cores measured between 50 cm and 78 cm in total length due to variable moraine deposits and bedrock. The master core (88 cm in length) was radiocarbon dated and analyzed for geochemistry (Energy-Dispersive X-Ray Fluorescence: ED-XRF), subfossil beetles and pollen, while the additional cores were analyzed for beetle remains.

2.3. *Chronology, geochemistry and core correlation*

Four botanical macrofossil samples from the master core were dated in the Poznan radiocarbon laboratory (see supplementary data Table S1) and were used to establish a site chronology. The ^{14}C ages were calibrated with the IntCal13 curve (Reimer et al., 2013) within a Bayesian age-depth modelling routine 'BACON' (Blaauw and Christen, 2011), which modelled all age information, including the sediment surface, using a Student-t distribution that accounted for scatter and allowed statistical outliers (Fig. 2). The Bayesian analysis (Christen and Perez, 2009) partitioned the core into three sections (31.3 cm thick) estimating the accumulation rate for each segment using a Markov Chain Monte Carlo (MCMC) approach. The modelling was constrained by a prior model of sediment accumulation rate.

All 13 cores, including the master profile, were analyzed for geochemistry on a wet-sediment basis using an Olympus Delta Professional

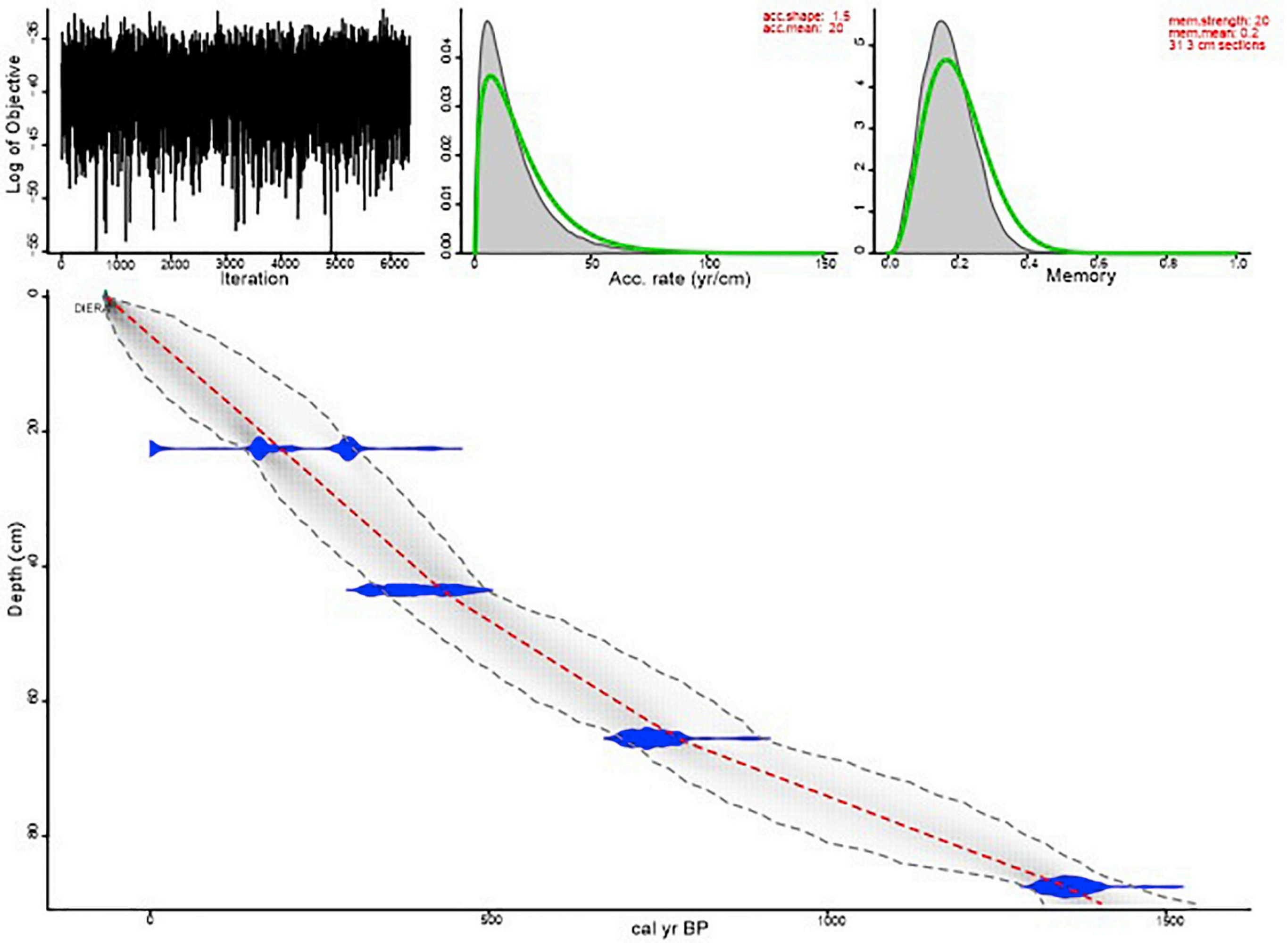

Fig. 2. Age-depth model based on four radiocarbon dates (Table S1) of master core DIE-16. Calibrated with the IntCal13 curve (Reimer et al., 2013) within a Bayesian age-depth modelling routine 'BACON' (Blaauw and Christen, 2011), which modelled all age information, including the sediment surface, using a Student-t distribution that accounted for scatter and allowed statistical outliers. The Bayesian analysis (Christen and Perez, 2009) partitioned the core into three sections (31.3 cm thick) estimating the accumulation rate for each segment using a Markov Chain Monte Carlo (MCMC) approach. The modelling was constrained by a prior model of sediment accumulation rate (a gamma distribution with mean 20-year cm-1 and shape 1.5) and its variability (memory, a beta distribution with mean 0.2 and shape 20).

ED-XRF mounted on the University of Liverpool Geotek Multi-Sensor Core Logger (MSCL). XRF core scanning is a non-destructive, rapid approach for quantifying elemental concentrations in a sediment core (Croudace et al., 2006) and has been used frequently in paleolimnological studies (Davies et al., 2015) and, to lesser extent, studies on peat cores (Poto et al., 2015; Longman et al., 2019). Patterns in geochemistry were comparable between the master profile and the 12 proximal cores; patterns in concentration of the atmospheric fallout pollutant Pb (Renburg et al., 2000) displayed a strongly repeatable signal. Profiles for conservative lithogenic elements, e.g. Rb, also showed strongly repeatable stratigraphic records. The strong matches between the cores (Figs. S1 – S4) facilitated the transfer of the age-depth model between cores and provided a basis for subsampling the 12 cores. These cores were pooled into 18 samples with total volumes 400–1600 ml, with narrower 1–4 cm intervals to provide greater detail for the last 100 years (400–500 ml) and the remainder in 4–7 cm depth intervals (800–1600 ml). Details on the subsampling can be found in Fig. S4.

2.4. Fossil beetle analysis

Fossil beetle preparation of the 18 samples followed the methods described in detail by Elias (2010). Samples were wet sieved at 250 µm and the organic remains were soaked in paraffin oil and floated in water. Isolated floats were sieved and rinsed before being stored in ethanol (C_2H_5OH). Beetle remains were picked under a binocular light microscope with 10 × magnification and were identified to family, genus and species level with the use of online databases (Kerbtier.de, Cassidae.uni.wroc.pl) and museum collections in United Kingdom (Plymouth City Museum and Oxford Museum of National History) and Czechia (Czech National Museum in Prague, Regional Museum Roztoky u Prahy and the Moravian Museum in Brno). The minimum number of individuals (MNI) was calculated by adding up all elytra, heads and dorsal plates(pronota) identified as Coleoptera.

2.5. Ecological attributes

Specific ecological attributes of beetle genera and species were derived from literature through online databases; BugsCEP (Buckland and Buckland, 2006) and Biomap (2019), which contained full species descriptions. According to their ecological preferences, species or genera were divided into 20 functional groups to facilitate interpretation. Functional groups are personal interpretations used to summarize the ecology of beetle taxa and can vary to certain degree according to the type of study they are used for (e.g. archaeological vs. paleoecological). The functional groups in this study are based on previous work from the United Kingdom (e.g. Whitehouse, 2004). Many beetle species can be found in more than one type of landscape, and the ecology of taxa is as well often constrained by their feeding strategies. Unless beetle taxa were clearly eurytopic, the most dominant ecological feature was chosen for each beetle taxon: Eurytopic (appearing in a wide variety of biotopes); Aquatic (living at least partially in water bodies); Aquatic standing water (living in stagnant bodies of water); Aquatic running water (living in flowing water bodies); Marsh/wetland (hygrophilous species living in marshes or wetlands); Bank vegetation (living on vegetation at the banks of water bodies); Hygrophilous (living in a variety of biotopes, with a high humidity as common factor); Heathland/moorland (living in moderately wet, open landscape); Meadow (living in open landscape, often feeding on meadow vegetation); Disturbed/arable (living on disturbed soils, often disturbed by anthropogenic activities); Foul/dung (living in dung and rotting vegetation or other materials); Dung (only living in dung); Dry decomposer (fungivore in dry environments); Wet decomposer (mostly fungivores; found in moist places); Shaded woodland (living in shaded woodland but in the understory); Trees (living on trees); Deciduous trees (living on deciduous trees); Coniferous trees (living on coniferous trees); Deadwood (living in dying trees and decaying wood) and Conifer pest (colonizing healthy trees). The category Conifer pest was added as large quantities of conifer bark beetles (Curculionidae: Scolytinae) were found and these could provide additional information about past disturbances. Beetle data was displayed using the program Tilia (Grimm, 1990), zonation was performed by D-chord cluster analysis (see Section 2.7).

2.6. Pollen analysis

Pollen analysis of the 2016 master core was performed in continuous 1 cm resolution between 1 and 70 cm and in 2 cm interval for the rest of the core, amounting to a total of 78 samples. Subsamples of 0.5 cm^3 were prepared with standard procedures of KOH-, acetolysis- and HF-treatment (Faegri and Iversen, 1989). The samples were mounted in glycerine and a minimum of 500 terrestrial pollen grains were identified under a light microscope using a 400 × magnification. Pollen identification was based on standard pollen keys (Punt, 1976–2003; Beug, 2004), microtopographic atlases (Reille, 1992–1998), and a reference collection in the Institute of Botany, CAS, Průhonice. Pollen data was plotted using the program C2 (Juggins, 2003). The full pollen dataset can be accessed upon personal request to the authors and will be published elsewhere.

2.7. Statistical analysis

Shannon's diversity index (Shannon and Weaver, 1949) takes both the number of individuals and the number of taxa into account, by calculating the natural log from the proportion of an individual species of the total sum of individuals. This diversity index is used commonly in ecology as well as archaeology and paleoecology (Pielou, 1967; Liu et al., 2015). Both beetle diversity and pollen diversity were plotted against time to compare forest beetle community dynamics with forest vegetation dynamics.

To emphasize changes in the terrestrial beetle community, aquatic species were excluded from the following analyses; 266 out of 313 taxa remained. Raw counts were converted to percentages to account for differences in total sum of individuals per sample (Legendre and Legendre, 2012). The square-chord method (Overpeck et al., 1985) was used to calculate dissimilarities between all samples. A hierarchical cluster analysis was then performed on the resulting square-chord dissimilarity (SQD) matrix to identify patterns in the beetle assemblages. Ward's minimum variance criterion (Ward, 1963) was used to implement the hierarchical clustering, to define beetle zones. This technique produces compact, equal-sized dendrograms by minimizing the total within-cluster variance (Mirkin, 2005). Furthermore, a PCA (Gabriel, 1971) was performed on the samples according to their dissimilarity matrix, to explore which components (species) attributed most to the variance throughout the section. All statistical analyses were performed using the statistical software R (R Core Team, 2018) and different packages: vegan (Oksanen et al., 2019), usedist (Bittinger, 2017), factoextra (Kassambara and Mundt, 2017), ggplot2 (Wickham, 2016), dplyr (Wickham et al., 2019) and tidyverse (Wickham, 2017).

3. Results

3.1. Beetle assemblages

A total of 2860 individuals were identified from 313 taxa and 38 families (Table S2). The number of individuals per sample ranged between 58 and 279 (Table S2, Fig. 3). In Fig. 3, depths are according to core 11, which matched best with the master core from 2016 and was used to correlate all other cores to (see Fig. S1 – S4). The beetle record was divided into five distinctive zones according to the hierarchical cluster analysis (Fig. 4): Zone 1 (930–1080 CE), Zone 2 (1080–1500 CE), Zone 3 (1500–1740 CE), Zone 4 (1740–1950 CE) and Zone 5 (1950 CE – present).

Zone 1 (930–1080 CE) has a high abundance of aquatic species

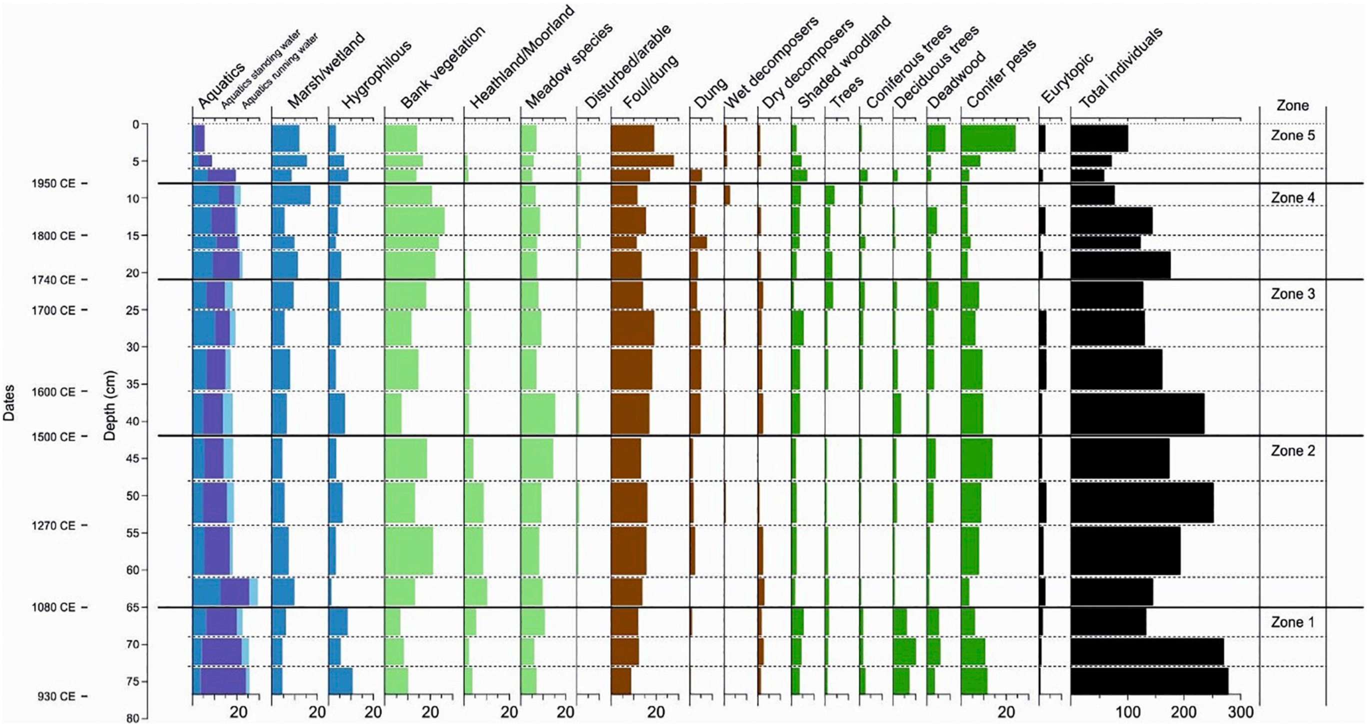

Fig. 3. Coleoptera functional groups (in percentage of the total number of individuals) from Diera Hollow. According to a D-chord cluster analysis, the section was divided into five zones. Depth and age are presented on the y-axis according to chronology based on a Bacon age-depth model (Fig. 2).

(21.8–24.4%). Especially species living in standing water (e.g. the diving beetle *Hydroporus tristis* and the water scavenger beetle *Anacaena lutescens*) were found but also species living in running water such as *Limnius perrisi*, which feeds on moss from stones in mountain streams (Koch, 1989a, 1989b). Marsh/wetland species (4.4–6%) consist mostly of species in the families Carabidae and Staphylinidae. Species living on or hunting within bank vegetation (6.8–10.1%) consist primarily of *Cyphon* spp. and *Stenus* spp. (Koch, 1989b). Species living in rotting materials (Foul/dung; 9–12.2%) primarily consist of a variety of rove beetles, among which many species of the subfamily Aleocharinae. This zone contains a high proportion of species living on deciduous trees (6–10%) which consists almost entirely of the species *Rhynchaenus fagi*, a leaf-mining weevil which colonizes beech trees (Koch, 1989a). The proportion of conifer pests is high in this zone as well (6–11.5%), consisting mostly of the species *Polygraphus poligraphus*, a species which attacks depressed stands of spruce (Pfeffer, 1989). Species living in meadows or glades, such as *Eusphalerum alpinum*, which visit flowers in mountain meadows (Koch, 1989a), are also abundant (5.9–10.5%). *Arpedium quadrum*, a predator in heathlands and alluvial meadows and an indicator of heathland/moorland (Koch, 1989a), is the most

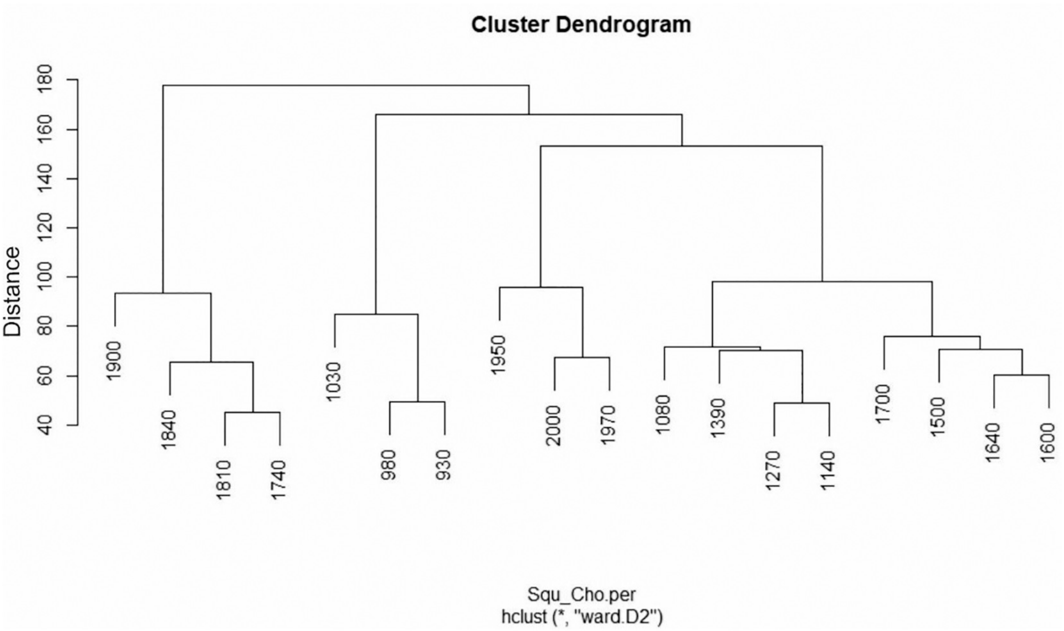

Fig. 4. Cluster diagram of the 18 samples of Diera Hollow, based on the terrestrial beetle taxa of the assemblages. A square-chord distance matrix was calculated in the program R, after which Ward's minimum variance criterion was used to implement hierarchical clustering.

abundant species (5.3%) from the remaining ecological groups.

In Zone 2 (1080–1500 CE), common species are *Stenus* spp. (16.1%), *A. quadrum* (9%), *Pityogenes chalcographus* (7.5%), *Pityophthorus pityographus* (5.8%), *Cyphon* spp. (4.7%) and *Eusphalerum anale* (3.1%). The proportion of aquatic beetles declines while marsh/wetland species such as *Trechus* spp. and *Olophrum piceum* increase (Koch, 1989a). Bank species (primarily *Stenus* spp. and *Cyphon* spp.) increase significantly. *Pit. chalcographus* and *P. pityographus* replace *P. poligraphus* as abundant conifer pests (Pfeffer, 1989), but species indicative for shaded woodland, deciduous trees and deadwood species all decline to values below 4%. Dung species, such as *Aphodius abdominalis* (Koch, 1989b), start to appear in this zone. In the upper part of Zone 2, species living in meadows (such as *Eusphalerum* spp.) increase to 15.3%.

Zone 3 (1500–1740 CE) shows a shift in dominant species: *Cyphon* spp. (8.7%), *Anotylus tetracarinatus* (6.9%), *Stenus* spp. (5.5%), *Pit. chalcographus* (5%), *Gabrius pennatus* (4.3%), *Enochrus quadripunctatus* (3.8%), *A. quadrum* (3.1%), and *Platystethus arenarius* (3.1%). *A. tetracarinatus*, *G. pennatus* and *P. arenarius* are found in dung or other rotting substances (Koch, 1989a) while *E. quadripunctatus* is an aquatic generalist (Koch, 1989a). Heathland/moorland species and meadow species decrease in number. Different classes related to woodland do not change significantly in this zone but shaded woodland species such as *Molops piceus* increase slightly to 5.4% (Koch, 1989a). Dung species (Koch, 1989a, 1989b), such as *Aphodius* spp., *Onthophagus* cf. *joannae* and *Sphaeridium lunatum/scarabaeoides*, increase to about 5% of the total beetle assemblage.

Zone 4 (1740–1950 CE) contains mainly dominant species connected to the inundated site and its (bank) vegetation: *Cyphon* spp. (18.1%), *Hydroporus erythrocephalus* (living in a wide range of still water habitats (Koch, 1989a; 4.9%), *Phyllotreta* spp. (4.2%), *A. lutescens* (3.9%), *E. quadripunctatus* (3.5%), *Donacia* spp. (3.5%) and *Coelostoma orbiculare* (3.4%). *Cyphon* spp., *Phyllotreta* spp. and *Donacia* spp. feed on bank vegetation while the other taxa are all aquatic (Koch, 1989a, 1989b, 1992). This zone contains a lower amount of species living in running water (0.7–2.6%) as well as lower amounts of conifer pests (2.6–4.1%). Heathland/moorland species decline even further. Sample 6 in this zone (1780 CE) has the highest proportion of dung species (e.g. *Aphodius* spp., *Onthophagus* cf. *joannae* and *Sphaeridium lunatum/scarabaeoides*; 7.4%) of all samples.

Zone 5 (1950 CE – present) has the lowest number of individuals recorded. Aquatic species decline rapidly (down to 5%) and aquatic beetles living in running water are absent. Marsh species remain between 8.6 and 15.3% but bank vegetation species decline to levels similar to Zone 2 and 3 (13.8–16.7%). Meadow species and species living in disturbed/arable areas remain consistent. Foul/dung species increase (27.8%) and dung species are absent between 1970 CE and present. Shaded woodland species such as *Anoplotrupus stercorosus* (Koch, 1989b) increase in the bottom sample of this zone (6.9%) while conifer pests (e.g. *Pit. chalcographus*) (24%) and species living in deadwood (8%) peak between 2000 CE – present. Conifer pest *Pit. chalcographus* reaches high values of 13% of the total assemblage in this zone.

3.2. Pollen assemblages

In order to compare the changes in the beetle community to changes in the vegetation, the zonation of the pollen diagram (Fig. 5) follows the zonation used for beetle communities. Zone 1 (< 1080 CE) is dominated by pollen from *Picea, Abies* and *Fagus*, with *Pinus* contributing to 10% of the total pollen sum. Zone 2 (1080–1500 CE) consists of two phases: in the first phase there is a maximum of *Abies* and *Picea* pollen, which decline around 1350 CE. Maximum values of *Fagus* pollen occur between 1250 and 1350 CE. Between 1250 and 1500 CE, there are peaks in Poaceae and Cyperaceae, after which *Pinus* pollen increase considerably and *Betula* pollen starts to increase. In contrast, *Fagus* pollen decrease. From 1250 CE, there are notable increases in human indicator taxa, including cultivated plants such as *Secale cereale* and *Triticum avellana* and plants growing on open mineral soil connected to human settlements such *Plantago lanceolata* (Behre, 1981; Gaillard, 2013). The green alga *Botryococcus neglectus*, indicative for oligotrophic or mesotrophic reservoirs (Komárek and Fott, 1985), increases around 1250 CE. In Zone 3 (1500–1740 CE), the peak in *Pinus* pollen is followed by a peak in *Betula* pollen. When the *Betula* pollen peak declines around 1600 CE, *Picea* and Cyperaceae pollen increase, while *Abies* and *Fagus* pollen continue to decrease. *Quercus* and *Corylus* pollen also increase in Zone 3. In Zone 4 (1740–1950 CE) *Picea* pollen values reach their second maximum, while *Pinus* pollen gradually increases. Green alga *B. neglectus* decreases to very low values. From 1950 CE (Zone 5), *Pinus* pollen values are as high as in Zone 2. There is also a decrease recorded in Cyperaceae and human indicator pollen taxa.

3.3. Beetle and vegetation diversity

The pollen diversity data extends from 590 CE to present, and the beetle diversity data extends from 930 CE to present (Fig. 6). Beetle diversity fluctuates until the highest Shannon diversity occurs around 1500 CE. After this period, beetle diversity declines steadily, with a rapid decline to the lowest Shannon Index values in the most recent samples (from 1950 CE). Pollen diversity fluctuates until a notable increase between 1200 and 1300 CE, followed by a decline until 1500 CE. Pollen diversity then rises into a consecutive steady phase until 1800 CE. After that, pollen diversity drops to minimum values. There is a rapid increase in pollen diversity in the last sample (2004 CE).

3.4. Patterns in beetle diversity

The PCA biplot (Fig. 7) shows the 10 beetle taxa that contribute most to the total variance. The first principal component (PC1) explains 34.3% of the variance whereas the second rotated factors PC2 contribute to 17.9%. PC1 has the highest loadings from *Cyphon* spp. (bank species, positive loadings), *Stenus* spp. and *A. quadrum* (marsh/wetland and heathland species, respectively, negative loadings). PC2 has the highest loadings of *Pit. chalcographus* (forest pest, positive loadings), *P. poligraphus*, *E. alpinum* and *R. fagi* (forest pest, meadow species and deciduous tree indicator, respectively, negative loadings). The oldest samples (930–1030 CE) are located within the negative portion of PC2; younger samples are located in the positive portion of PC2. The positive portion of PC1 groups the other, with highest values for samples from Zone 4 (1740–1900 CE). Samples from Zone 2 (1080–1390 CE) and Zone 5 (1950–2000 CE) overlap in the PCA biplot.

4. Discussion

4.1. Forest diversity and ecosystem dynamics over the last millennium

A variety of functional beetle communities enabled the reconstruction of past changes in forest composition and biodiversity at Diera Hollow. The high abundances of tree/forest beetle taxa are indicative of a closed forest ecosystem (Robinson, 1991, 2000; Smith et al., 2010), with Norway spruce as the dominant species at the site over the past 1000 years. However, despite relatively consistent dominant forest cover, different beetle communities have succeeded one another, many of which can be related to changes in the local vegetation.

4.1.1. Montane spruce-dominated forest (930–1080 CE)

At the beginning of the last millennium, the dominance of forest/tree beetle taxa suggests a predominantly forested environment. Dominant species *R. fagi* and *P. poligraphus* indicate the presence of beech and spruce trees at the site, respectively (Koch, 1992; Pfeffer, 1989). Low abundances of *Pityokteines vorontzowi* indicate the presence of fir trees (Pfeffer, 1989). This is further supported by the pollen record with the presence of *Abies*, *Picea* and *Fagus* pollen. The dominance of

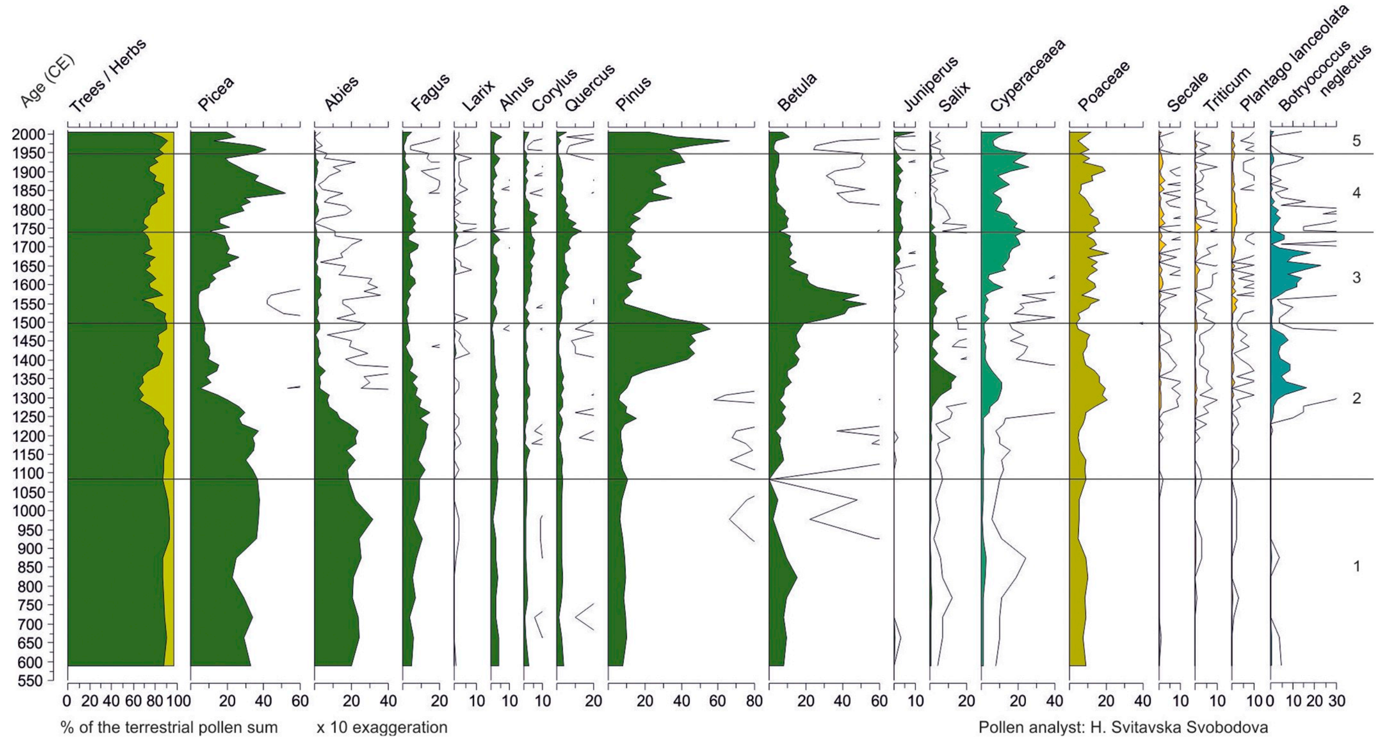

Fig. 5. Percentage pollen diagram from Diera Hollow. The pollen curves show the percentages of each taxa calculated from the terrestrial pollen sum, with trees/shrubs and herb taxa pooled together in the most-left column. Zonation is based on the cluster analysis of the fossil beetle assemblage from the same site.

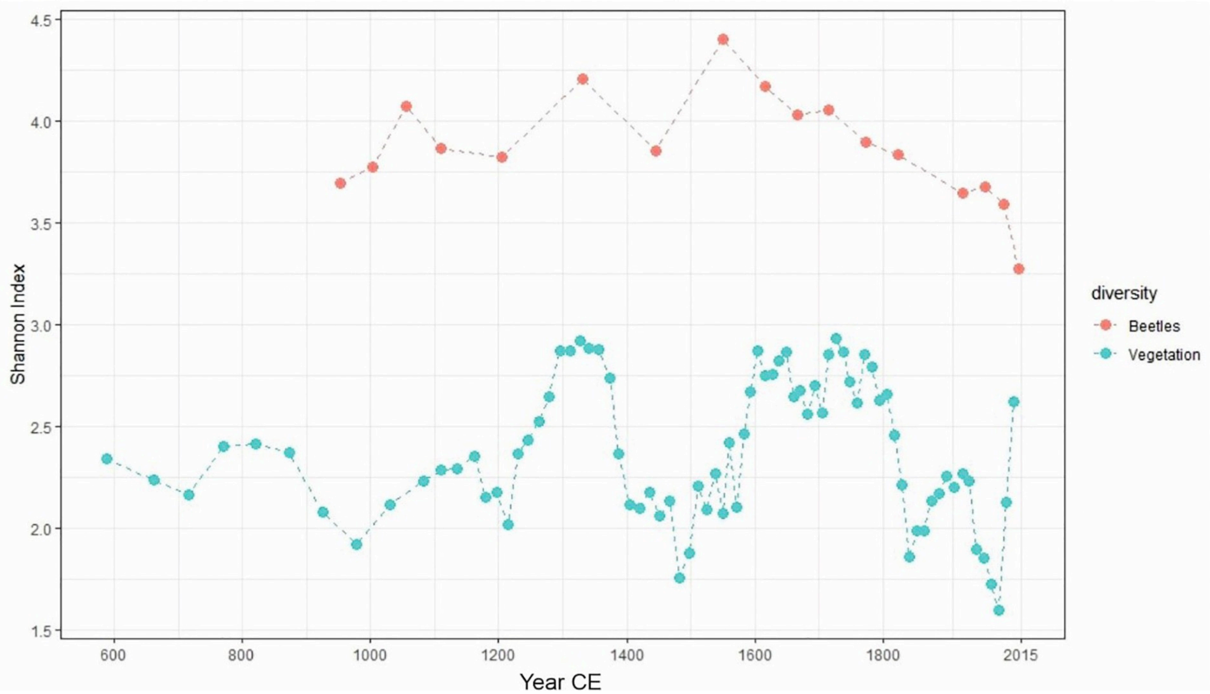

Fig. 6. Shannon diversity index of beetle data and vegetation data (pollen) from Diera Hollow, with added trend lines. Samples run between 590 CE and 2004 CE for the vegetation data and between 930 CE and 2011 CE for the beetle data.

dytiscid *H. tristis*, together with an abundance of other diving beetles typically living in peaty pools (Koch, 1989a), suggests that the site was a shallow peat bog. The high abundance of the species *A. quadrum* and *Stenus* spp. suggest that the banks of the peat bog were not densely covered with vegetation (Brundin, 1934; Koch, 1989a). Besides, a variety of species populating open areas was present, such as *Eusphalerum* spp. living on flowers in (alpine) meadows (Koch, 1989a), but also *Silpha tristis*, known to feed on carrion (Koch, 1989a), *Limonius aeneoniger* living at forest edges (Laibner, 2000) and various species of flea beetles living on herbs in open areas (e.g. *Chaetocnema* sp.; Koch, 1989b).

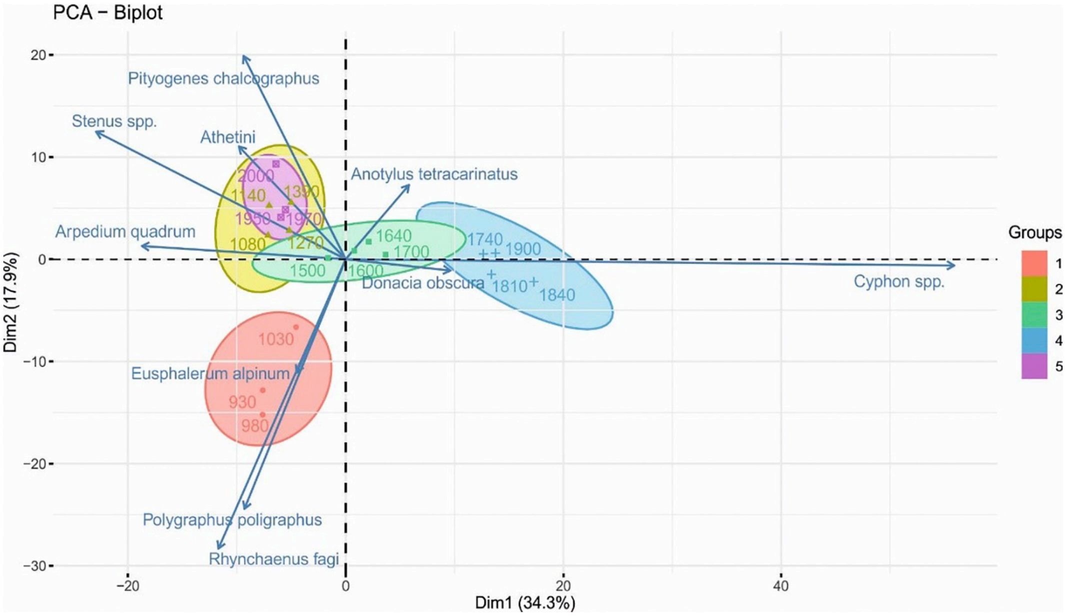

Fig. 7. PCA biplot of the beetle data from Diera Hollow. Samples (defined by sample age CE) are divided into five zones according to a D-chord cluster analysis performed on percentage-transformed data. The vectors of the ten species which contribute most to the variance in the data are displayed.

4.1.2. Increased beetle diversity associated with landscape openness and floristic diversity (1080–1500 CE)

From around 1250 CE, increasing changes in the species composition of the beetle community indicate landscape openness and an increase in human activity in the region. Beetle diversity appears to be closely linked to floristic diversity in this period, with an increase of taxa living in open landscapes (Fig. 4). There is a decline in species living on deadwood (e.g. *Rhizophagus* spp. and *Anobium* sp.) and shaded woodland species (e.g. ground beetle *Pterostichus foveolatus;* Koch, 1989a), suggesting a decline of old-growth forest directly around the forest hollow. *R. fagi* indicates that beech trees remain present but in low numbers. Several taxa living in forest clearings or at open water edges (e.g. *Eusphalerum* spp. and *A. quadrum*) increase to become the dominant taxa and are indicative of landscape openness (Koch, 1989a). Additionally, the presence of *Hydrobius fuscipes* indicates that the peat bog was sun-exposed at this time (Fossen et al., 2016). The increased presence of conifer pests, *Pit. chalcographus* and *P. pityographus* between 1430 and 1500 CE to 7.5% of the total beetle assemblage, indicates an abundance of their primary host, Norway spruce (Pfeffer, 1989). However, the pollen record shows lower amounts of *Picea* pollen, suggesting a lower presence of trees. As these bark beetle species are known to colonize thin branches or otherwise young trees, the high presence of these species might have delayed the establishment of mature spruce trees around the site. The presence of *Ips acuminatus* and *Pityogenes quadridens* colonizing *Pinus* spp. (Pfeffer, 1989) coincides with an increase in *Pinus* pollen values, suggesting that pine became the dominant tree species at Diera Hollow during this time. The increase of dung beetles living on dung from sheep, cattle and horses (*P. arenarius*, *S. lunatum/ scarabaeoides*, *Onthophagus* cf. *joannae*, *Aphodius mixtus, A. rufipes, A. prodromus;* Koch, 1989b) from 1500 CE suggests an increase in herding activities. Since both *S. lunatulum/ scarabaeoides* and *O. joannae* prefer horse, cattle or sheep dung (Koch, 1989b), it is likely that the increase of dung beetles near the site was caused by the presence of dung from domesticated animals. However, values of dung beetles between 0.4 and 5% does not suggest pasturing (Robinson, 1991, 2000) and therefore, the site was likely located near routes where cattle and sheep were herded to alpine meadows higher up in the mountains (as hypothesized by Zámečniková, 2008).

4.1.3. Mixed deciduous-coniferous forest with patchy landscape openness (1500–1740 CE)

From 1500 CE onward *Cyphon* spp., *Donacia* spp. and *Phyllotreta* spp., all known to live on bank vegetation (Koch, 1989b, 1992), start to increase and become the dominant taxa. An increase in species living on bank vegetation around 1700 CE coincides with a pronounced increase of Cyperaceae, the general food source for these species. The presence of high amounts of *Quercus* pollen suggests an increase in light availability (e.g. Annighöfer et al., 2015). Therefore, it is likely that the landscape openness increased during this time. Low occurrences of the weevil *R. fagi* together with *Fagus* pollen indicate that beech trees remained present near to the site until the end of the 19th century. The presence of *A. stercorosus*, which is found in semi-humid deciduous and mixed forest (Koch, 1989b), confirms the occurrence of deciduous trees around the site, while the presence of conifer pests and species living on conifer trees (e.g. *Polydrusus pallidus*; Koch, 1992) suggests that conifer trees were still present. As dung beetle species continue to occur in the record, the area likely remained impacted by herding activities.

4.1.4. Semi-natural closed forest and decline in beetle diversity (1740 CE – present)

Conifer pests and shaded woodland taxa start to increase from approximately 1800 CE, suggesting that the vicinity of Diera Hollow became dominated by Spruce-Pine forest during this time. This process coincides with human abandonment of the region in the 19th century (Olah et al., 2009). Tatra National park was established in 1949 CE and the effects of forest management such as reforestation in the area are visible in the beetle record with shaded woodland species increasing and dung beetles no longer present. Although the PCA biplot (Fig. 6) shows that samples after 1950 CE are mostly similar to samples between 1080 and 1500 cal CE (Zone 4), many forest beetle species did not reappear, and the original Spruce-Fir-Beech woodland was not restored. The decline in beetle diversity according to the Shannon Index started around 1500 CE and continued before a rapid decrease from 1950 CE. Partitioning of the Shannon Index for different functional groups (see Figure S5) shows that from 1500 CE, the diversity of the beetle assemblages becomes increasingly driven by aquatic taxa. The rapid decline of beetle diversity between 1950 and 2017 CE could be attributed to the infilling or drying out of Diera Hollow, due to the sharp decline of the total amount of aquatic species and the disappearance of species living in running water. Decline of the alga *B. neglectus* from ~1750 CE is also an indication that the pool was decreasing in size (Jankovská and Komárek, 1982). Apart from the slow infilling of the basin, both climatic and anthropogenic changes could have contributed to the drying out of Diera Hollow. During the period 1881–2008, the average annual precipitation in Slovakia decreased by 3.4% (Ministry of Environment of the Slovak Republic, 2005). However, it has been argued that forest plantations can have a negative effect on forest hydrology and affect surface water generation and groundwater recharge, as young forests demand large amounts of water in order to grow (van Dijk and Keenan, 2007).

4.2. Drivers behind changes in the local beetle community and vegetation

Climatic conditions, especially moisture fluctuations, are likely to have played a significant role in the changes in the local vegetation and beetle community. In a study on the Little Ice Age in the High Tatra Mountains (Niedźwiedź, 2004), the highest decrease in temperature and increase in moisture was identified between 1575 and 1676 CE. An increase in pollen from cultivated plants co-occurs with appearances of beetle species living on animal dung from 1250 CE onwards (Fig. 2) suggesting farming in the surrounding area. Moreover, an increase in vegetation and beetle diversity associated with landscape openness can be correlated to regional human activity. Even though limited sources are available, one describes a village called Maklar or Matrei. This was a settlement for livestock herders that was inhabited until 1360 CE (Greb Greb, 1934). From 1400 CE onward, several wars resulted in abandonment of a large part of the region (Cichocki, 2003; Pavercsik, 2003), enabling forest succession (Fig. 2, Fig. 4). As soon as the region became more stable from ~1500 CE, human recolonization started. Many settlements were founded as mining communities in search for ore and metals, similar to villages in nearby mountain ranges (Jambrich, 2007). A well-recorded example of recolonization in the area itself is Ždiar, located ten kilometres north of Diera Hollow at an altitude of 850 m a.s.l. and founded in the 16th century (Hreško et al., 2015). Socio-economic activities in the village were mainly related to agriculture, farming, logging and charcoal burning, activities which had a pronounced effect on the surrounding landscape (Rączkowska, 2019). As the onset of increased anthropogenic activities around 1500 CE coincides with the changing patterns in beetle diversity compared to vegetation diversity (Fig. 6), it is plausible that the decline in local beetle diversity was related to anthropogenic activity. However, as there are no archaeological evidence or historical documents of human settlement in the vicinity of the sampling site, these indications should be considered with caution.

4.3. Implications for nature conservation

This study recorded several saproxylic beetles (European Red List, Nieto and Alexander, 2010), as well as the rare species *Dapsa denticollis* and *Graphoderus zonatus*. The cryptic endomychid *D. denticollis* has been collected in xerothermic grassland and forest steppe habitats in eastern and south-eastern Europe (Franc and Hemala, 2014) and a single individual was found in sample 16 (1080 CE). *G. zonatus* is a large diving beetle which inhabits peaty pools (Koch, 1989a) and was found in samples up to 1840 CE. This species is currently rare in many regions in Europe due to a decline of its habitat (Knoblauch and Gander, 2019). The identified saproxylic species in our study were only identified sporadically and no trend in their occurrence was found. A study by Majzlan (2015) confirms that all identified saproxylic species are currently found within 5–10 km from the sampling site Diera Hollow. However, several of the beetle species identified in this study have a mostly unknown ecology and distribution. This especially concerns species with a strictly montane habitat, living in or near peat bogs and marshes (e.g. the leaf beetle *Chrysolina lichenis*; Burakowski et al., 1990). It gives reason to look beyond the standardized red-list saproxylic species (Nieto and Alexander, 2010) and consider the beetle community as a whole. At Diera Hollow, not only beetle taxa indicative for (old-growth) forest changed drastically over the last millennium but also taxa living in the forest hollow. Our findings suggest that the current forest ecosystem and forest beetle species composition remain affected by changes in the landscape that started centuries ago, possibly by the legacy of previous human impact in the area as was found in other European montane regions (e.g. Valsecchi et al., 2010). As argued by Froyd and Willis (2008), the identification of these past baselines and ecological thresholds would contribute to the conservation of insects and other groups of plants and animals in Tatra National Park. Based on our results, we recommend stakeholders of the national park to 1) look further back in time than only a few hundreds of years when considering restoration strategies (e.g. before 1080 CE), 2) include insect diversity in the targets and monitoring of restauration efforts; and 3) include forest hollows and other inundated depressions in conservation strategies for the national park.

5. Conclusions

The fossil beetle and pollen record from Diera Hollow suggest that changes in the local beetle and vegetation record were linked to regional changes, most likely driven by anthropogenic activity. The site developed from a semi-closed to closed montane Spruce-Fir-Beech forest at 930 CE, to a more open landscape from 1080 CE onward. Human activities in the region were first recorded in the beetle and pollen record around 1250 CE. From around 1740 CE, human abandonment of the region and subsequently, the establishment of Tatra National Park in 1949 CE resulted in the reestablishment of a closed woodland, but of a different composition than the ancient woodland. While climate was an important driver behind changes in the vegetation and beetle community, anthropogenic activity likely played a significant role in determining the beetle and floristic diversity during the past millennium. Our results suggest that diversity indices such as the Shannon Index can be used to assess ecological thresholds of local flora and fauna through time. Based on our findings, initiatives to restore the original landscape of this region should compare with the situation before 1080 CE. Furthermore, we recommend including beetles and other insect communities in the monitoring of restoration efforts of flora and fauna biodiversity in montane nature reserves as they could contribute to understanding the baselines and ecological thresholds in these regions. Due to the recorded historical presence of rare beetle species connected to peat bogs, we also advise to include mountain peat bogs in studies on biodiversity and nature conservation.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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3.2 Fossil bark beetle records as indicator of bark beetle outbreaks and other natural disturbances

3.2.1 Late Glacial and Holocene records of tree-killing conifer bark beetles in Europe and North America: Implications for forest disturbance dynamics.

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Authors' contributions

The study was planned by NS and JLC. Data from online databases and literature was collected by NS. Data preparation and creation of maps was performed by NS, with the help of J. Pettit. Information on destructive bark beetles and their outbreaks was collected by NS, CJF and MK. NS was responsible for preparing the manuscript, while all co-authors commented and contributed.

Extended summary

Introduction

Conifer bark beetles inflict density-dependent tree mortality and help maintain a diversity of tree species, ages, sizes, and spatial heterogeneity. Conifer bark beetle outbreaks have however increased in frequency and magnitude during the last decades, causing increasing economic damage in Europe and North America (e.g. Bentz et al., 2009). Economic losses due to forest dieback are mainly attributed to the European spruce bark beetle *Ips typographus*, while several bark beetle species in North America attack conifer trees in different regions of the continent (e.g. Morris et al., 2016). Under projected climate change, frequency and magnitude of bark beetle attacks is expected to increase further (Berg et al., 2006; Kurz et al., 2008; Negrón and Fettig, 2014).). Although many projections of bark beetle outbreaks under climate change exist, the data for these models does not extend further back in time than AD 1850 ((Hicke et al., 2006; Schelhaas et al., 2003). This study synthesizes available data of past occurrences of primary (tree-killing) bark beetles by 1) summarizing the amount of fossil bark beetle data and 2) summarizing historical observational data from publicly available sources. Ultimately, we aim to improve knowledge on patterns (localities, frequency, mechanisms) of primary bark beetle outbreaks in Europe and North America.

Methodology

Fossil records of bark beetles spanning the past 14,000 cal yr. BP were collected from the online databases BugsCEP and Neotoma (Buckland and Buckland, 2006; Williams et al., 2018). Access to some data and metadata was requested directly from the owners of published data, as well as additional unpublished data sets. In Europe, the genera *Ips*, *Dendroctonus* and *Pityogenes* were selected for the query, while in North America the genera *Ips*, *Dendroctonus*, *Dryocoetes* and *Scolytes* were selected based on species which are currently, or are projected to be tree-killing species. Sites were divided into time periods according to a formal subdivision of the Holocene (Walker et al., 2012); late Glacial (14,000 ~ 11,500 cal yr. BP), early Holocene (~11,500 – 8200 cal yr. BP), middle Holocene (~8200 – 4200 cal yr. BP), and late Holocene (~4200 – 1000 cal yr. BP). An additional time period, called 'Historical' included the last ~1000 cal yr. BP. From selected sites, not only data from the queried genera but all primary and secondary bark beetles were recorded. Identification to genus level were also included in these records. Modern, as well as historical bark beetle distribution data were collated from the

Global Biodiversity Information Facility (GBIF, 2018). For North America, additional distribution data described by Wood (1982) was added as point coordinates. The locations of fossil sites with identified primary bark beetle remains were compared with modern distribution data by comparing their point locations. Mapping of all point locations was executed in the statistical program R. In addition, the historical observation data from GBIF were divided into 20-year time periods (AD 1750 – 2018).

Results

A total of 53 sites from North America and Europe, ranging from late Glacial to Historical, were found to contain records of at least one of the queried primary bark beetle genera. The type of fossil deposit included archeological sites, beach deposits, river deposits, lake deposits and peat deposits. Archeological sites with identified bark beetle remains were only located in Europe, while sites with a late Glacial age were more common in North America. In Europe, several fossil records of *Ips typographus* and *Pityogenes chalcographus* were found, as well as one record of *Dendroctonus micans*. Some species which are potential primary bark beetles were not found, however. Records from North America contained only 8 out of 20 of the current and potential primary bark beetles, and mostly species from the genus *Dendroctonus* were found. No discrepancies between fossil distribution data and modern distribution data were found in Europe or North America, although the fossil data are considered too infrequent to make direct comparisons with modern distribution data.

Discussion

Fossil sites with primary bark beetles were scattered and often only included the identification of a single specimen. In North America, the only exception in this is the record from Lake Emma in Colorado (Elias, 1985). From these lake deposits of early Holocene age, several individuals of *Dendroctonus rufipennis* were identified. As outbreaks of this species currently occur in the region where the lake is located, it might be argued that these outbreaks are not a novel development in this region. From other records, lower amounts of 1 – 2 individuals per sample could only confirm the presence of these species at that locality. European fossil sites were more frequently containing primary bark beetle species, with the species *I. typographus* and *P. chalcographus* co-occurring at several of the sites. This suggests co-occurrence of these two species in central Europe at least since the Holocene. While fossil data of primary bark beetles can be compared to historical distribution data from GBIF in Europe, less data is available for North America. Nevertheless, fossil bark beetle data records hold great potential for inference of changes in forest composition and other disturbance regimes.

Implications

Data generated for this thesis increased the records of primary bark beetles in Central Europe notably, with new primary bark beetle records from southern Czech Republic and eastern Slovakia. We suggest that fossil bark beetles are not by definition scarce in the fossil record, but that it might require purposeful identification to reconstruct the presence of bark beetles, and significant amounts of sediment to make quantitative reconstructions. The significance of reconstructing past bark beetle population densities is currently increasing as climate changes affects tree mortality and bark beetle outbreaks are increasing in frequency and magnitude. For studies which aim to reconstruct changes in forest composition and disturbance regimes through time, fossil primary bark beetle remains might be an important additional proxy. It has been argued that bark beetle outbreaks currently affect ecosystem services such as forest biomass, Studies on past bark beetle outbreaks, if conducted on the right scale, could reconstruct the frequency and magnitude of past bark beetle outbreaks, the past relationships between bark beetle outbreaks and other natural disturbances, the environmental conditions under which these bark beetle outbreaks took place and any effects of these outbreaks on the environment in return. This would significantly improve the knowledge of policy makers to help them decide what management practices to engage in to mitigate or to deal with bark beetle outbreaks.

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Late Glacial and Holocene records of tree-killing conifer bark beetles in Europe and North America: Implications for forest disturbance dynamics

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Abstract

Outbreaks of conifer bark beetles in Europe and North America have increased in scale and severity in recent decades. In this study, we identify existing fossil records containing bark beetle remains from the end of the Last Glacial Maximum (~14,000 cal. yr BP) to present day using the online databases Neotoma and BugsCEP and literature searches, and compare these data with modern distribution data of selected tree-killing species. Modern-day observational data from the Global Biodiversity Information Facility (GBIF) database was used to map recorded distributions from AD 1750 to present day. A total of 53 fossil sites containing bark beetle remains, from both geological and archeological sites, were found during our searches. Fossil sites were fewer in Europe ($n = 21$) than North America ($n = 32$). In Europe, 29% of the samples in which remains were found were younger than 1000 cal. yr BP, while in North America, remains were mainly identified from late Glacial (~14,000–11,500 cal. yr BP) sites. In total, the fossil records contained only 8 of 20 species we consider important tree-killing bark beetles in Europe and North America based on their impacts during the last 100 years. In Europe, *Ips sexdentatus* was absent from the fossil record. In North America, *Dendroctonus adjunctus, Dendroctonus frontalis, Dendroctonus jeffreyi, Dendroctonus pseudotsugae, Dryocoetes confusus, Ips calligraphus, Ips confusus, Ips grandicollis, Ips lecontei, Ips paraconfusus*, and *Scolytus ventralis* were absent. Overall, preserved remains of tree-killing bark beetles are rare in the fossil record. However, by retrieving bulk material from new and existing sites and combining data from identified bark beetle remains with pollen, charcoal, tree rings, and geochemistry, the occurrence and dominance of bark beetles, their outbreaks, and other disturbance events can be reconstructed.

Keywords
Archeological sites, BugsCEP, fossil sites, GBIF, historical data, Holocene, insect outbreaks, late Glacial, natural disturbances, Neotoma, peat deposits, synthesis

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Introduction

Conifer bark beetles (Curculionidae: Scolytinae) often inflict density-dependent tree mortality (i.e. population growth rates and associated levels of tree mortality are partially regulated by the density of suitable hosts) and help maintain a diversity of tree species, ages, sizes, and spatial heterogeneity (Berryman, 1976). Endemic populations create small gaps in the forest canopy by killing trees usually stressed by age, drought, defoliation, or other factors. During outbreaks, large amounts of tree mortality may occur in short periods (e.g. 1 to several years) negatively affecting timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, biodiversity, endangered species, carbon sequestration and storage, and cultural resources, among others (Morris et al., 2018). In recent decades, bark beetle outbreaks in Europe and North America have increased in severity and scale (e.g. Hicke et al., 2016; Thorn et al., 2017) and several recent outbreaks are recognized among the most severe in recorded history, with high economic impacts (Bentz et al., 2009; Fettig et al., in press). Bark beetles are highly sensitive to thermal conditions conducive to population survival and growth (Bentz et al., 2010), and temperature-related drought stress negatively affects host tree vigor (Kolb et al., 2016). As such, outbreaks have been correlated with recent shifts in temperature and precipitation attributed to climate change. Forest densification has exacerbated this effect in many locations (Fettig et al., 2007).

Detailed, historical records document numerous outbreaks of different species of bark beetles in forests of Europe and North America since the 19th century (Bentz et al., 2009; Schelhaas et al., 2003; Wood, 1982). In Europe, outbreaks of the European spruce bark beetle (*Ips typographus*) on Norway spruce (*Picea abies*) are the most important cause of timber losses with millions

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of hectares of forest impacted annually (Schelhaas et al., 2003; Skuhravý, 2002). However, during the 20th century, the Great spruce bark beetle (*Dendroctonus micans*) has been expanding its geographic range and impacts across Europe (O'Neil and Evans, 1999). While the forest structure and economic damage from bark beetle outbreaks in Europe is substantial (Lieutier et al., 2004), the damage in North America is much higher (e.g. Hicke et al., 2012). There are several species in North America, from four different genera, which cause high tree mortality (Drooz, 1985; Fettig, 2016; Furniss and Carolin, 1977). The most notorious of these are in the genus *Dendroctonus* (Erichson). For example, species like *Dendroctonus ponderosae* and *Dendroctonus rufipennis* have had major impacts on forests in western North America in recent decades, destroying large numbers of trees and leading to major changes in forest function, structure, and composition (e.g. Berg et al., 2006; Kurz et al., 2008; Negrón and Fettig, 2014). Over the past 30 years, tree mortality caused by bark beetles in the western United States has exceeded tree mortality caused by wildfires (Hicke et al., 2016), raising concerns about the sustainability of some western forests to provide certain ecological goods and services over time. Most notable, *D. ponderosae* impacted ~10.3 million hectares of forest from 2000 to 2016, which represents almost half of the total area impacted by all bark beetles combined in the western United States during this period (Fettig et al., in press).

Although challenging, it is important to gain more insight in the relationships between other natural disturbance agents and bark beetle outbreaks (Dale et al., 2001; Fettig et al., 2013; Jenkins et al., 2014; Seidl and Rammer, 2017; Seidl et al., 2017; Thom and Seidl, 2016). A variety of models have been created to predict bark beetle outbreaks (e.g. Hicke et al., 2006; Stadelmann et al., 2013). These models allow us to calculate the chances of future bark beetle outbreaks on a regional as well as local scale, in order to assess their effects and to mitigate negative impacts (e.g. Fettig et al., 2007). The historical records of natural disturbances and bark beetle outbreaks, used in these models, go back as far as AD 1850 (Hicke et al., 2006; Schelhaas et al., 2003). In a few isolated studies, tree-ring records have been used in North America to identify local bark beetle outbreaks (Jarvis and Kulakowski, 2015; Zhang et al., 1999) which at certain locations date back to AD 1640. Dendroecological data sets from Central Europe (e.g. Čada et al., 2016) have been created to identify past natural disturbance events back to AD 1700. These records give us, up to a certain level, insight into what role bark beetles played in our forested landscapes before the significant increases in frequency and severity of outbreaks of the last several decades. In addition, identification of fossil bark beetle remains from sedimentary records can provide firsthand information of past outbreaks (Brunelle et al., 2008). Fossil beetle assemblages have been used to establish baselines of natural situations in managed parks (e.g. Mansell et al., 2014) as well as broader regional contexts (e.g. the reconstruction of Britain's landscapes by Whitehouse and Smith, 2010). However, fossil records containing beetle remains are scattered and lacking from many regions, and an overview of fossil sites containing remains of tree-killing (primary) bark beetles is currently not available.

This study synthesizes available data of past occurrences of primary bark beetles by (1) summarizing the amount of fossil bark beetle data in publicly available databases and in the literature and (2) summarizing historical observational data from publicly available databases. Ultimately, we aim to improve knowledge on patterns (localities, frequency, mechanisms) of primary bark beetle outbreaks in Europe and North America.

Methods

Fossil records of bark beetles spanning the past 14,000 cal. yr BP were collated from sites in Europe and North America using the databases BugsCEP (Buckland and Buckland, 2006) and Neotoma (Williams et al., 2018). An additional data literature search with Elias (2010) provided a detailed overview of all sites <14,000 cal. yr BP containing bark beetle remains. Access to data and metadata unavailable as supplementary material in the literature was requested directly from the authors of the respective peer-reviewed publications. Additional unpublished data obtained directly from authors completed the final data collection (see unpublished; Supplemental Appendix C, available online). Taking the age constraint of 14,000 cal. yr BP and geographical limits into regard, ~500 sites from BugsCEP (Buckland and Buckland, 2006), 70 sites from Neotoma (Williams et al., 2018), and 20 additional sites were examined for primary bark beetle species remains. In Europe, the genera *Ips, Dendroctonus*, and *Pityogenes* were selected for query. Although species of the genus *Pityogenes* do not cause substantial damage to conifers in Europe, historical and recent outbreaks have been frequent (e.g. Göthlin et al., 2000; Grodzki, 1997; Zúbrik et al., 2008). Furthermore, as *Pityogenes chalcographus* favors the same host trees as *I. typographus* and *D. micans* (Göthlin et al., 2000; Novotný et al., 2002), its presence in the fossil record could indicate past conditions favorable for outbreaks of *I. typographus* or *D. micans*. The genera *Ips, Dendroctonus, Scolytus*, and *Dryocoetes* were selected for the query of North American sites. Metadata including location, latitude, longitude, altitude, site type (e.g. archeological site, peat bog), additional paleoecological proxies, age of sediments, number of samples, and reference were recorded (see Supplemental Data, available online). Sites were divided into time periods according to a formal subdivision of the middle Holocene and late Holocene by Walker et al. (2012): late Glacial (~14,000–11,500 cal. yr BP), early Holocene (~11,500–8200 cal. yr BP), middle Holocene (~8200–4200 cal. yr BP), and late Holocene (~4200–1000 cal. yr BP). In addition, the last ~1000 cal. yr BP to present were defined as an extra time period called 'Historical', which includes archeological sites as well as lake and peat bog sites. Samples with bark beetle remains were attributed to a certain time period by comparing the depth of the sample with the published age-depth model of the respective site. From the selected sites, not only data from the queried genera but all identified primary and secondary bark beetles were recorded. Identifications to genus level (e.g. *Ips* sp.) were also included in these records.

Modern observational data

Modern bark beetle distribution data were collated from the *Global Biodiversity Information Facility* (GBIF, 2018a). Recordings without coordinates were deleted and recurring coordinates were combined if these observations were recorded during the same year. Records from museums were removed from the results as well, as these do not reflect the original locality of the beetles. For North America, additional observational data were added from approximated localities described by Wood (1982). The locations of fossil sites with identified primary bark beetle remains were compared with the observed modern species distribution by plotting point locations in R (R Core Team 2018, version 3.5.0). In addition, the historical observation data from GBIF (2018a) were divided into 20-year time periods (AD 1750–2018).

Results

A total of 53 fossil records, 21 from Europe and 32 from North America, were identified as containing bark beetle remains of the queried genera (Figure 1; Supplemental Appendix A, available online). The age of sites ranged from late Glacial to present day, and all but two sites contained radiocarbon dated samples. Site classifications included archeological sites, (paleo) beach deposits, river deposits, lake deposits, and peat deposits. Three of the 21 sites found in Europe were records from archeological studies, while none of the 32 sites in North America were archeological

Figure 1. Sites with fossil records in Europe and North America, dated 14,000 cal. yr BP to present, where *Ips, Dendroctonus*, and/or *Pityogenes* (Europe) or *Dendroctonus, Ips, Scolytus*, and/or *Dryocoetes* species (North America) remains were identified. Based on the data obtained from BugsCEP (Buckland and Buckland, 2006) and Neotoma (Williams et al., 2018).

Table 1. Bark beetle species (Scolytinae) that caused substantial damage to stands of conifer trees in Europe and North America in recent decades.

Species (Europe)	Common host(s)	Examples of outbreaks
Dendroctonus micans	*Picea* spp., *Pinus* spp.	1970s (Georgia), 1970s–2019 (Turkey), 1980s (France, Great Britain)[1,2,3,4]
Ips sexdentatus	*Pinus* spp.	1980s (Turkey), 2001, 2009 (France, Spain)[5,6,7,8]
Ips typographus	*Picea* spp., *P. sylvestris*	1990s (Central Europe, France, Sweden), 2000–2019 (Austria, Czech Republic, Germany, France, Poland, Switzerland, Slovakia, Sweden)[9,10,11,12,13,14,15,16]
Species (North America)	Common host(s)	Examples of outbreaks
Dendroctonus adjunctus	*Pinus* spp.	1990 (Colorado), 1990–2000 (Arizona, Utah), 1991–1994 (Arizona, New Mexico), 2001–2003, 2013 (Arizona, New Mexico)[17,18,19,20]
Dendroctonus brevicomis	*P. ponderosa*, *P. coulteri*	1990s (Alberta, British Columbia), 2001–2008 (California, Colorado, Idaho, Montana, Oregon, Utah, Washington), 2009 (Colorado), 2009–2019 (California, Colorado, Idaho, Oregon, Utah, Washington)[17,18,19,20,21]
Dendroctonus frontalis	*Pinus* spp.	1990–1992 (Alabama, Arkansas, Georgia, Lousianna, North Carolina, South Carolina, Tennessee, Texas, Virginia), 1995 (Alabama, Arkansas, Florida, Georgia, Lousianna, North Carolina, South Carolina), 1999–2002 (Alabama, Florida, Georgia, Kentucky, North Carolina, South Carolina, Tennessee, Virginia), 2000 (Alabama, Kentucky, North Carolina, Tennessee, Virginia), 2010–2015 (New Jersey), 2015–2019 (New York)[17,18,20]
Dendroctonus jeffreyi	*P. jeffreyi*	2009, 2013–2018 (California)[17,18,20]
Dendroctonus ponderosae	*Pinus* spp.	1999–2015 (British Columbia, California, Colorado, Idaho, Montana, Oregon, South Dakota, Utah, Washington, Wyoming), 2003–2019 (Alberta)[17,18,19,20,22,23,24]
Dendroctonus pseudotsugae	*Pseudotsuga menziesii*	1992 (Idaho, Oregon, Washington), 1998 (Colorado, Idaho, Montana), 2002–2019 (Idaho, Utah, Montana, Wyoming), 2009, 2017–2018 (British Columbia)[17,18,19,20,22]
Dendroctonus rufipennis	*Picea* spp.	1990–1997, 2016–2019 (Alaska), 1995–2000 (Yukon), 2000–2007 (Arizona, New Mexico), 2003, 2008–2019 (Alberta, British Columbia, Colorado, Montana, New Mexico, Utah, Washington, Wyoming, Yukon)[17,18,20,20,22,25,26]
Dendroctonus simplex	*L. laricina*	1980s (New Brunswick, Newfoundland, Nova Scotia, Prince Edward Island), 1999 (Alaska, Maine), 2003–2005 (Alaska, Michigan, Minnesota), 2005–2019 (Michigan, Minnesota, Wisconsin)[17,18,20,26,27,28]
Dryocoetes confusus	*A. lasiocarpa, Abies* spp.	1991–1994 (Idaho, Utah, Wyoming), 1992 (Montana), 2001–2008 (Colorado, Idaho, Montana, Nevada, Utah, Wyoming), 2014–2018 (British Columbia)[17,18,19,20,22]
Ips calligraphus	*Pinus* spp.	2002–2005 (Arizona, New Mexico), 2015–2018 (Georgia)[17,20]
Ips confusus	*P. edulis, P. monophylla*	2002–2004 (Arizona, Colorado, New Mexico, Nevada, Utah)[17,20]
Ips grandicollis	*Pinus* spp.	2006–2009 (Minnesota), 2015–2018 (Georgia)[17,20]
Ips lecontei	*P. ponderosa*	2002–2005 (Arizona, New Mexico), 2018 (Arizona)[17,20]
Ips paraconfusus	*P. ponderosa*	2004, 2014 (California), 2012–2018 (Oregon, Washington)[17,21,29]
Ips perturbatus	*Pi. glauca, Picea* spp.	1990s, 2004–2010, 2016 (Alaska)[17,18,20,26]
Ips pini	*Pinus* spp.	1980–1994 (Montana), 2003–2006 (Colorado, Montana, Nebraska, South Dakota, Washington, Wyoming), 2012–2013 (Wisconsin), 2018–current (Arizona)[17,18,19,20]
Scolytus ventralis	*A. concolor, A. grandis, A. magnifica*	1985–1989 (California, Oregon, Washington), 1997 (Idaho), 2002–2018 (California, Colorado, Idaho, Oregon, Washington), 2003–2006 (Nevada), 2004–2005, 2014 (Utah)[17,18,19,20,21]

Numbers of affected trees differ greatly among species. References: [1]Khobakhidze et al. (1970), [2]Akinci et al. (2009), [3]Gregoire et al. (1985), [4]Bevan and King (1983), [5]Schönherr et al. (1983), [6]Goldazarena et al. (2012), [7]Lopez and Goldarazena (2012), [8]Rossi et al. (2009), [9]Kärvemo and Schroeder (2010), [10]Krehan et al. (2010), [11]Steyrer and Krehan (2011), [12]Zahradník and Zahradníková (2019), [13]Lausch et al. (2013), [14]Grodzki (2016), [15]Fleischer et al. (2016), [16]Marini et al. (2016), [17]USDA Forest Service, National Insect and Disease Survey Database (Portal Pest Summaries) (2018), [18]USDA Forest Service, Annual National Forest Health Monitoring Reports (2001–2018), [19]Fettig et al. (in press), [20]USDA Forest Service, Forest Insect and Disease Conditions in the United States (1955–2014), [21]California Forest Pest Condition Reports (1960–2018), [22]British Columbia Ministry of Forests, Lands, Natural Resource Operation and Rural Development (1999–2018), [23]Natural Resources Canada (2013), [24]Cudmore et al. (2010), [25]Garbutt et al. (2006), [26]USDA Forest Service, Forest Health Conditions in Alaska (2002–2017), [27]Langor and Raske (1989), [28]Crocker et al. (2016), [29]Murray et al. (2013).

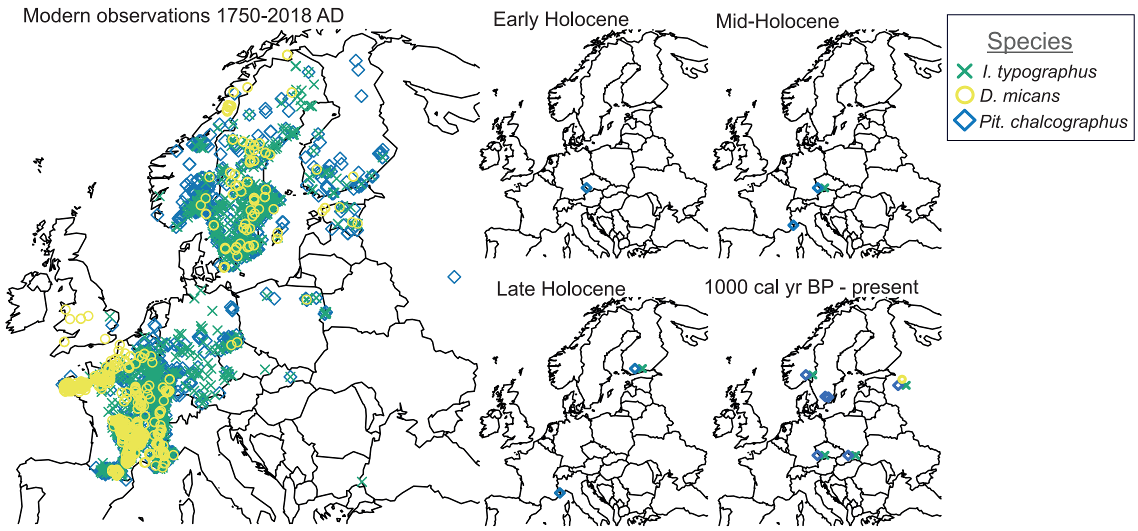

Figure 2. Modern distributions of three tree-killing bark beetle species in Europe, next to locations of the fossil sites with their identified remains which were dated Early Holocene (~11,500–8200 cal yr BP), Mid-Holocene (~8200–4200 cal yr BP), Late Holocene (~4200-1000 cal yr BP) and 1000 cal yr BP-present. Coordinates of modern observations were downloaded from GBIF.org. *Ips typographus* (green crosses), *Dendroctonus micans* (yellow circles), and *Pityogenes chalcographus* (blue diamonds). Depicted sites with Early Holocene fossils are Prašilske Lake (unpublished data); Mid-Holocene sites are Prašilske Lake (unpublished data), Lac Long Inferior (Ponel et al., 2001); Late Holocene sites are Piilonsuo (Koponen and Nuorteva, 1973) and Lac Long Inferior (Ponel et al., 2001); <1000 cal yr BP sites are Oslo: Gamlebyen (Kenward, 1988), Stavsåkra (Olsson and Lemdahl, 2009), Storasjö (Olsson and Lemdahl, 2010), Novgorod: Troitski (Hellqvist, 1999), Prašilske Lake (unpublished data), Laka Lake (unpublished data) and Diera Hollow (unpublished data).

sites. Many of the sites found in North America were used to identify the extent and timing of deglaciation (e.g. Ashworth et al., 1981; Mott et al., 1981). This difference in research foci is reflected in the ages of the different sites in Europe and North America. While only 2 of the 21 sites containing bark beetle remains of the queried genera in Europe included late-Glacial sediments (Ponel et al., 2001, 1999), 12 of the 32 sites in North America were late Glacial sites. In North America, only four fossil sites contained samples younger than 1000 cal. yr BP, but none of these samples contained any of the bark beetle species which are considered to cause substantial damage (Bentz et al., 2009; Fettig et al., in press; Morris et al., 2017; Table 1).

Europe

In Europe, the species identified from fossil remains that cause substantial damage to trees were *I. typographus* (six sites) and *D. micans* (one site), but also fossil remains of *Pit. chalcographus* (nine sites) were found (Figure 2; Supplemental Appendices B and C, available online). All fossil records with these three identified species were younger than late Glacial. In samples covering the early Holocene, one site (Prašilske Lake, Czech Republic) contained remains of *Pit. chalcographus*. During the middle Holocene, two sites (Lac Long Inferior, France; Prašilske Lake, Czech Republic) contained remains from *Pit. chalcographus*, where at the Czech site, these remains were found together with those of *I. typographus*. *Pit. chalcographus* was found in samples from the late Holocene at two sites (Lac Long Inferior, France; Piilonsuo, Finland), and the Finnish site Piilonsuo (Koponen and Nuorteva, 1973) contained remains of *I. typographus* as well. Historical (~1000 cal. yr BP to present) sites in Europe contained most of the bark beetle remains of *I. typographus, Pit. chalcographus*, and *D. micans*. The Medieval archeological site of Novgorod, Russia (Hellqvist, 1999), contained fossil records of all three species *I. typographus, Pit. chalcographus* and *D. micans*. Five more historical (~1000 cal. yr BP to present) sites contained remains of *Pit. chalcographus*, three of these also contained remains of *I. typographus* (Oslo: Gamlebyen, Norway; Stavsåkra, Sweden; Storasjö, Sweden; Laka Lake, Czech Republic; and Diera Hollow, Slovakia; Oslo: Gamlebyen being an archeological site). Unpublished data from Diera Hollow in Slovakia (unpublished data by author) showed higher numbers of individuals of *Pit. chalcographus* between 950 and 400 cal. yr BP.

North America

In North America, the species identified from fossil remains that cause substantial damage were *D. ponderosae* (two sites), *D. rufipennis* (eight sites ranging from late Glacial to late Holocene), *Dendroctonus brevicomis* (one site), *Dendroctonus simplex* (two sites), *Ips perturbatus* (two sites), and *Ips pini* (two sites) (Figure 3; Supplemental Appendices B and C, available online). During the late Glacial, four different species were found: *D. rufipennis, D. simplex, I. perturbatus*, and *I. pini*. During the early Holocene, *D. rufipennis, I. perturbatus*, and *I. pini* were found. Here, *D. rufipennis* was identified at three different sites in two different regions of North America (Rocky Mountains (Elias et al., 1986, 1991) and Eastern Canada (Ashworth, 1977)). One site (Lake Emma, Colorado: Elias et al., 1991) showed an indication of a higher abundance of *D. rufipennis* in two samples dated 10,000–9000 cal. yr BP. Two sites located in the Rocky Mountains in the United States contained remains from *D. rufipennis* (Elias, 1985; Elias et al., 1986), and two other sites in the same region contained remains from *D. ponderosae* during the middle Holocene (Brunelle et al., 2008). A fifth site located in Eastern Canada contained remains of *D. simplex* (Morgan et al., 1985). During the late Holocene, two sites in North America contained remains of *D. rufipennis* and *D. brevicomis*. One of the sites, located west of Hudson Bay, Canada (Elias, 1982), contained remains of *D. rufipennis*, and the other site, located in the Rocky Mountains in the United States (Elias et al., 1986), contained remains of *D. rufipennis* and *D. brevicomis*.

In total, the fossil records contained 8 out of the 20 species that are considered (potentially) destructive bark beetles (Table 1). In Europe, no remains of *Ips sexdentatus* were found. In North America, the species *Dendroctonus adjunctus, Dendroctonus frontalis, Dendroctonus jeffreyi, Dendroctonus pseudotsugae, Dryocoetes confusus, Ips calligraphus, Ips confusus, Ips grandicollis, Ips lecontei, Ips paraconfusus*, and *Scolytus ventralis* were absent from the fossil record. Remains which were identified to genus

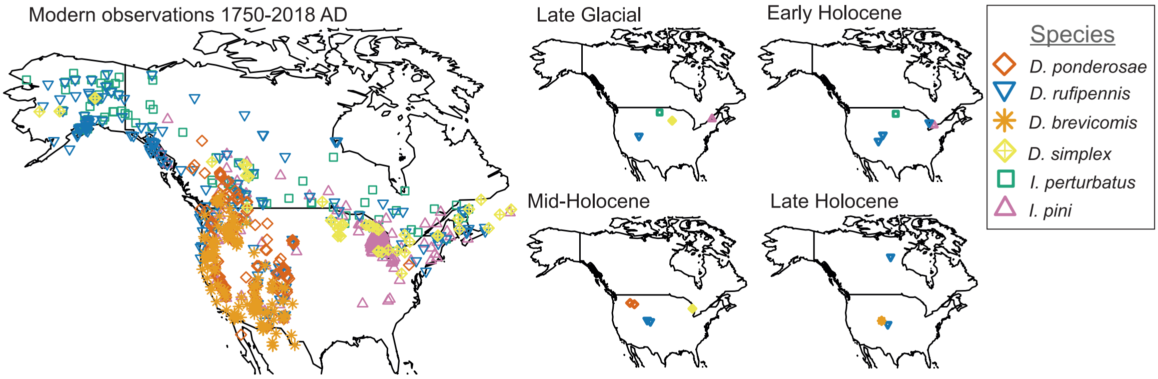

Figure 3. Modern distributions of six tree-killing bark beetle species in North America, next to locations of the fossil sites with their identified remains which were dated Late Glacial (~14,000-11,500 cal yr BP), Early Holocene (~11,500-8200 cal yr BP), Mid-Holocene (~8200-4200 cal yr BP) and Late Holocene (~4200-1000 cal yr BP). Coordinates of modern observations were downloaded from GBIF.org and supplemented with approximate locations from Wood (1982). *Dendroctonus ponderosae* (red diamonds), *Dendroctonus rufipennis* (blue triangles), *Dendroctonus brevicomis* (orange stars), *Dendroctonus simplex* (yellow diamonds), *Ips perturbatus* (green squares) and *Ips pini* (pink triangles). Depicted sites with Late Glacial fossils are St. Hillaire (Mott et al., 1981), Johns Lake (Ashworth and Schwert, 1992), Norwood (Ashworth et al., 1981) and Huntington Dam (Elias 1991); Early Holocene sites are Seibold (Ashworth and Brophy, 1972), 18 Miles River (Ashworth, 1977), Gage Street Site (Schwert et al., 1985), Lake Isabella Delta (Elias et al., 1986) and Lake Emma (Elias et al., 1991); Mid-Holocene sites are Hoodoo Lake (Brunelle et al., 2008), Baker Lake (Brunelle et al., 2008), Au Sable River (Morgan et al., 1985), La Poudre Pass LP5 (Elias et al., 1986) and Lake Isabella Peat (Elias, 1985); Late Holocene sites are Ennadai II (Elias, 1982) and Roaring River (Elias et al., 1986).

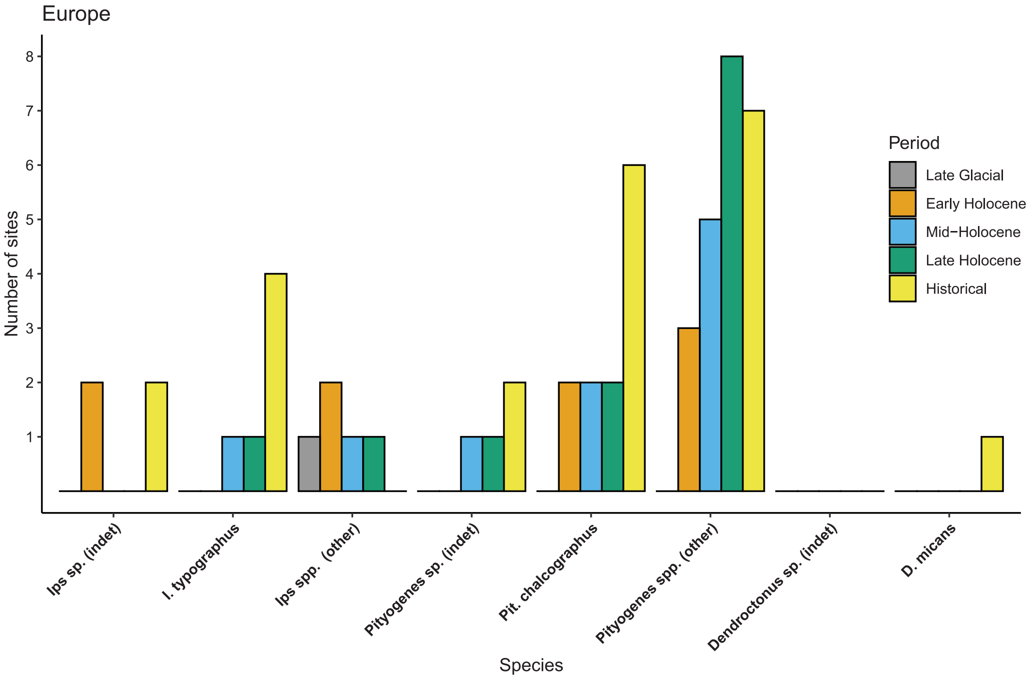

Figure 4. Fossil sites in Europe with occurrences in different time periods of the three queried taxa *Ips*, *Pityogenes* and *Dendroctonus* and the target species *I. typographus*, *Pit. chalcographus* and *D. micans*. A single fossil site can contain multiple time periods.

level could account for some of these missing species, although this concerns a low number of identifications (data from two sites in Europe with identified *Ips* sp., and six sites in North America: five with identified *Dendroctonus* sp. and one with identified *Ips* sp.; see Supplemental Data, available online). Figures 4 and 5 give an overview of the collated data and show the number of sites with target species, remains identified to genus level, and different species from the same genera as were queried.

Modern observational data

Modern observational data from GBIF (2018b-i, 2019a) for Europe and North America are shown in Figures 6 and 7. For North America, the lowest amount of data points for the query species was found for *D. simplex* (14 data points) and the highest for *I. pini* (144 data points), the latter one of the most common bark beetles in North America (Furniss and Carolin, 1977).

Discussion

Distribution and abundance of fossil and historical primary bark beetles

Here, we present the first synthesis of fossil records of primary bark beetles in Europe and North America. Fossil sites that contained remains of primary bark beetles were scattered, and most consisted of a single identification of a species within a fossil record. In North America, the only exception was the site Lake Emma, Colorado (37.90211°N, 107.61537°W), where remains of 3 to 11 individuals of *D. rufipennis* were found in three sediment

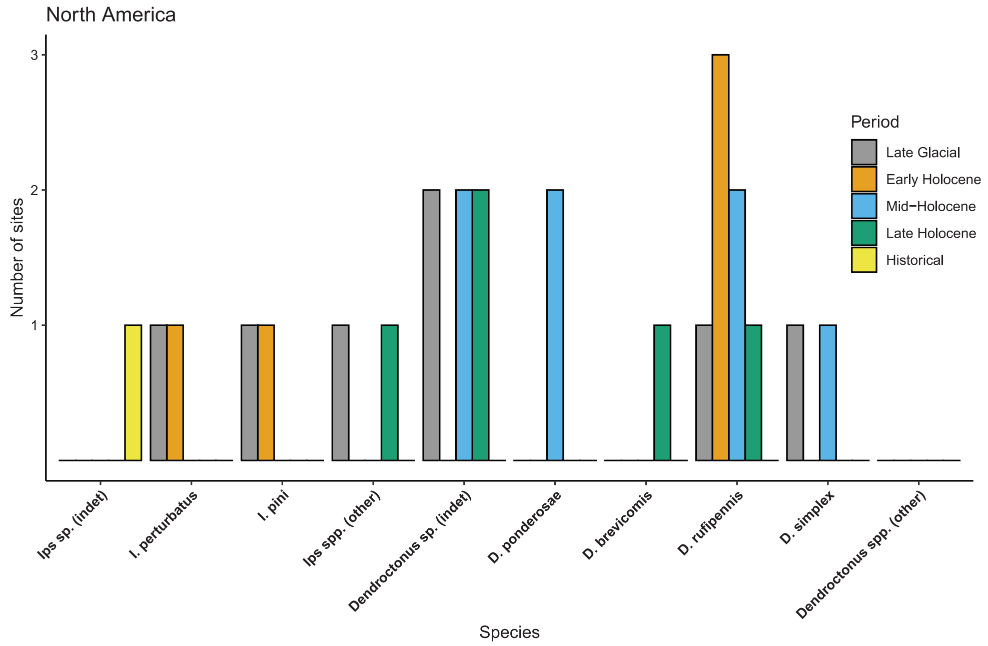

Figure 5. Fossil sites in North America with occurrences in different time periods of the queried taxa *Ips* and *Dendroctonus* and the target species *I. perturbatus*, *I. pini*, *D. ponderosae*, *D. brevicomis*, *D. rufipennis* and *D. simplex*. A single fossil site can contain multiple time periods.

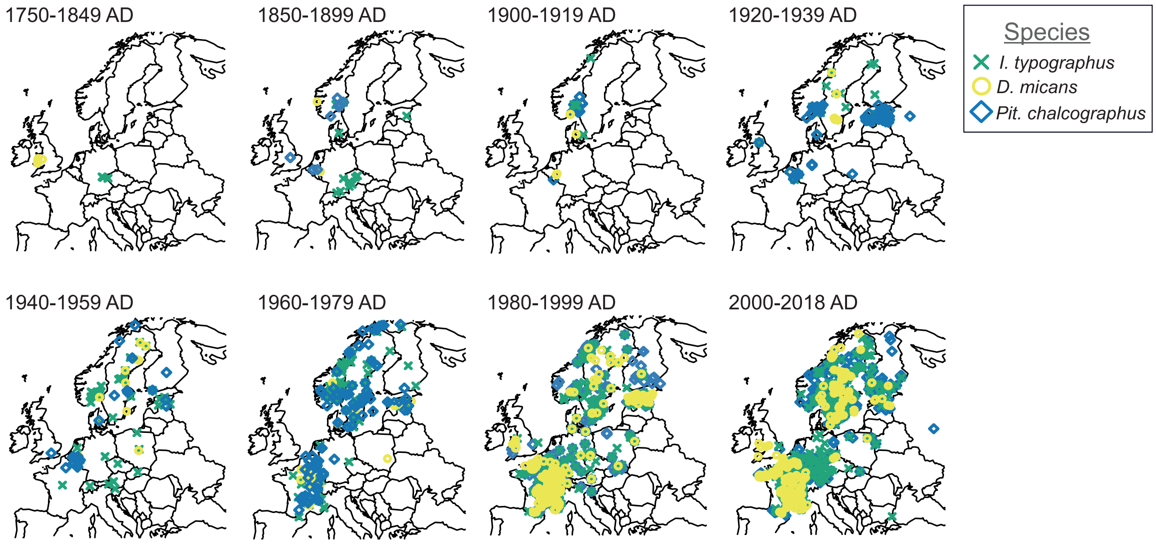

Figure 6. Historical and modern-day observations of *Ips typographus* (green crosses), *Dendroctonus micans* (yellow circles) and *Pityogenes chalcographus* (blue diamonds). Downloaded observational data from GBIF.org was split into one time period of 1750-1849 AD, one time period of 1850–1899 AD, and afterwards time periods of 20 years.

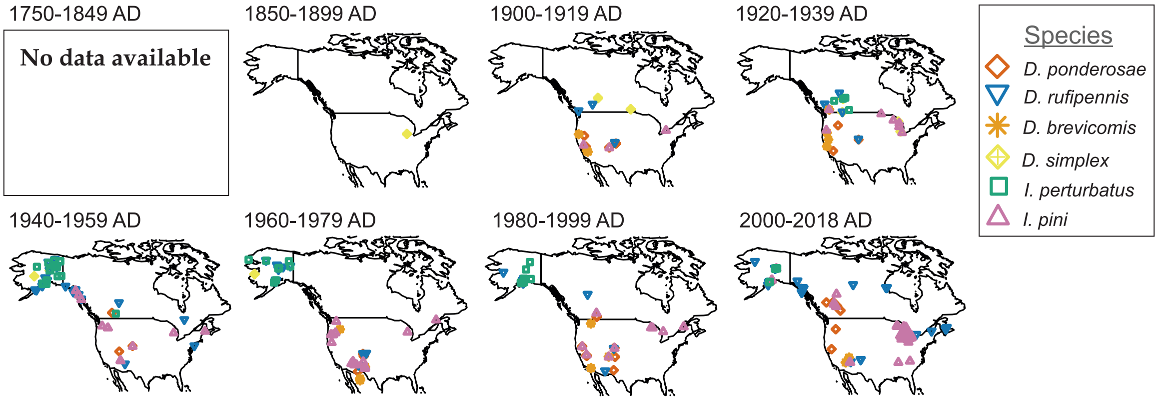

Figure 7. Historical and modern-day observations of *Dendroctonus ponderosae* (red diamonds), *Dendroctonus rufipennis* (blue triangles), *Dendroctonus brevicomis* (orange stars), *Dendroctonus simplex* (yellow diamonds), *Ips perturbatus* (green squares) and *Ips pini* (pink triangles). Downloaded observational data from GBIF.org was split into one time period of 1750–1849 AD, one time period of 1850–1899 AD, and afterwards time periods of 20 years.

samples from ~10,000 cal. yr BP (Elias, 1991). In the region where Lake Emma is located, severe outbreaks of *D. rufipennis* have been occurring since AD ~2000 (Colorado State Forest Service, 2017). Such a high abundance of *D. rufipennis* in the fossil record of a site, which lies in a region where outbreaks are occurring currently, provides strong evidence that this area has been subjected to *D. rufipennis* outbreaks at least since the early Holocene. Due to the low abundances of bark beetle fossils in general, presence of species in the fossil record has previously been interpreted in a qualitative way (e.g. Schwert et al., 1985) to indicate the presence of certain plant or tree species or climatic conditions (although bark beetle species have been pooled with other species living in dead wood to form functional groups in paleoenvironmental reconstructions; e.g. Olsson and Lemdahl, 2010). In many of the studies where bark beetles were used to indicate the presence of trees or forests, no more than one or two individuals were found per sample and no species had a continuous presence throughout a stratigraphic sequence (e.g. Brunelle et al., 2008). Other species, such as *D. frontalis, D. pseudotsugae*, and *S. ventralis*, are missing completely in the fossil record, even though extensive outbreaks of these species have occurred historically (Table 1). For some species (*D. frontalis, Ips* spp.), this absence can be explained by a lack of fossil sites within their modern distribution range. For example, Neotoma (Williams et al., 2018) shows no fossil sites with insects <14,000 BP for a large portion of the southeastern United States. Possible explanations include a lack of suitable sites for preservation of remains and/or an absence of research interests (for an overview, see Elias, 2010). It is important to note that sites in this study might have been poorly dated, and although great care was taken to attribute samples with bark beetle remains to their appropriate time period, this has been highly dependent on the recorded age of the sites. Nevertheless, fossil records with primary bark beetles are scarce.

There were more sites with fossil records of primary bark beetles found in North America, but the European sites contain more occurrences. *I. typographus* and *Pit. chalcographus* co-occurred at six (29%) fossil sites. At Novgorod (Hellqvist, 1999), *I. typographus* was found together with both *D. micans* and *Pit. chalcographus*. Results from these fossil sites are a good indication that at least in historical times (since ~1000 cal. yr BP) primary bark beetle species were co-occurring in the same areas of Europe as they are today (Figure 2). A lack of occurrences of *I. typographus* in the fossil record of France, one of the countries that has experienced several notable outbreaks (Sallé et al., 2005; Viiri and Lieutier, 2004), is difficult to explain although the location of fossil sites likely has some influence as older publications report *I. typographus* populations were confined to mountainous areas (Komárek, 1925; Pfeffer, 1930). Despite this, fossil sites from France and Sweden, incorporated in the current data set, yielded remains from other *Ips* spp. such as *Ips accuminatus* (Storasjö, Sweden during the early Holocene; La Borde, France during the early Holocene; Tailefer Massif, France during the late Holocene). As *I. accuminatus* colonizes *Pinus sylvestris* in France (e.g. Herard and Mercadier, 1996), it might be worthwhile to consider this species in future research.

Differences in the types of fossil sites and original study objectives in Europe and North America seem to have resulted in differences between the fossil records from these continents, as well as low amounts of recorded bark beetle remains for certain time periods. In North America, some of the studies that recovered primary bark beetle remains focused on reconstructing late-Glacial to early-Holocene temperatures (e.g. Morgan and Morgan, 1979), while others focused on the retreat of the Laurentide Ice Sheet after the Last Glacial Maximum and subsequent landscape dynamics (e.g. Schwert et al., 1985). For these type of studies, single occurrences of primary bark beetle remains were sufficient evidence of the presence of host trees at the study site (e.g. Ashworth et al., 1981; Elias, 1982). In Europe, fossil insect remains have been used to reconstruct late-Glacial to early-Holocene climates (Coope et al., 1998). Many of these sites are located in Great Britain (Elias, 2010), a region where few remains of conifer bark beetles have been found. All identified species from records of Great Britain are colonizing *Pinus* spp. rather than *Pi. abies*. Moreover, the majority of bark beetle species found in Great Britain are species that colonize deciduous trees. This likely clarifies why the relatively large number of fossil sites in Europe yield a very low abundance of the queried species.

We only found one study, conducted by Brunelle et al. (2008), which attempted to specifically identify primary bark beetle remains in the fossil record of a site. This study was conducted at Hoodoo Lake, Idaho, US, and correlated the occurrence of remains with past disturbance events. Given the assumption that bark beetle outbreaks are likely to occur when stands of trees are experiencing stress, such as during drought (Kolb et al., 2016), their study focused on identifying bark beetle remains from lake sediments in an area that experienced frequent bark beetle outbreaks. The only remains of *D. ponderosae* were found originated from sediments that were dated at 8200 cal. yr BP, and as such it was speculated that bark beetle outbreaks may have occurred during the 8.2 Ka event (Brunelle et al., 2008). However, attempts to reproduce these results proved difficult as additional cores from Hoodoo Lake, and other nearby lakes, yielded no remains of *D. ponderosae* (Morris et al., 2015). In Europe, recent unpublished multiproxy data from Prašilske Lake and Laka Lake, Czech Republic and Diera Hollow, Slovakia (see unpublished in Supplemental Data, available online) indicate that fossil remains of primary bark beetles from lake sediments and peat cores could be used to detect fluctuations in bark beetle populations through time. In these three studies, bark beetle remains were used as one of the proxies to detect other natural disturbances.

The data from GBIF (2018b-i, 2019a) for Europe and North America provide a good overview of the regional representation of modern bark beetle distributions. For example, observational records from GBIF (2018b) for *D. ponderosae* appear to demonstrate its northward range expansion between 1980 and 2018 (e.g. Robertson et al., 2009). However, many areas that have experienced substantial outbreaks of *D. ponderosae*, as well as other primary bark beetles in North America, are not well represented in GBIF (2018b-g) but are available elsewhere (e.g. for the United States, see www.fs.fed.us/foresthealth/publications). Modern distribution data for *I. typographus, D. micans*, and *Pit. chalcographus* are concentrated in Western Europe and Scandinavia and lacking in Eastern Europe, coherent with the fact that the majority of GBIF data collectors reside in Western Europe and Scandinavia. As with similar databases, GBIF (2018a) depends on individuals for uploading data and some regions as well as certain species are better represented than others. Furthermore, it can be argued that a rapid increase of data from 1980 onwards could also be explained by improved methods of data collation and a rise in interest in the occurrences of certain bark beetle species.

Primary bark beetles as indicators of disturbance dynamics

Fossil bark beetle records hold great potential for inference of changes in forest composition and other disturbance regimes. However, records from the British Isles, where the majority of the studies on fossil beetle remains have been executed contained few conifer bark beetles. The few attempts to correlate trends in pollen fluctuations with bark beetle remains were criticized as circumstantial (Girling and Grieg, 1985). As no evidence exists for fluctuations in deciduous bark beetle populations from the numerous British records, the focus in historical landscape studies shifted to the ‘Urwald fauna’, beetle species indicative of primary forests (e.g. Whitehouse, 2006). At several sites in Britain, however, specimens of *Pityogenes quadridens* and *Pityogenes bidentatus* were found (see Supplemental Appendix B, available online), species with *Pinus* spp. as host or main host. As shown in GBIF (2019b), *Pi. abies* is not common in all regions of the British Isles, and future studies on conifer bark beetles in this region should include species colonizing *Pinus* spp.

Together with other proxies such as fossil pollen and sedimentary charcoal, fossil bark beetle remains may be used to reconstruct past disturbance history of sites (unpublished data by author). For example, fossil records with the absence of primary bark beetles but the presence of secondary bark beetles that only colonize dead or dying trees (see Supplemental Appendix B, available online) might indicate large amounts of dead wood resulting from other causes than a bark beetle outbreak. Combining all this information, the history and mechanisms of natural disturbances in conifer forests could be reconstructed. This could provide valuable new information for models to predict future bark beetle outbreaks (Morris et al., 2017). At many sites in Europe and North America, data from proxies such as pollen, charcoal, tree rings, and geochemical data already exist and have been used to reconstruct disturbance histories on local to regional scales (e.g. Tinner et al., 2008; Willis et al., 2000). Additional bulk material from waterlogged sites like peat bogs or small lakes could yield insect remains, in many cases in amounts large enough to make qualitative (small lakes) or even quantitative (peat bogs) reconstructions. These reconstructions could be used to establish baselines for primary bark beetle species abundance from the early to late Holocene, as well as to provide additional information about the distribution of these species in historical times (Figures 2–7).

Conclusion

In this study, we take the initial steps toward identifying and integrating fossil and historical data of primary bark beetle occurrences in Europe and North America. The scarcity of bark beetle remains in fossil records, especially in North America, represents a critical gap in our understanding of ecological history, and a fruitful area of future research in the field of paleoecology. Historical observational data from GBIF (2018b-g) for North America are also scarce. As such, we encourage researchers in North America to consider contributing more records to this and similar databases in hopes of increasing their overall utility. Both fossil and historical records in Europe are more numerous, but concentrated in Western Europe. New unpublished data from Central Europe show an abundance of primary bark beetle remains at sites located in coniferous forests. By retrieving bulk material from new and existing sites and combining data from identified bark beetle remains with pollen, charcoal, tree rings, and geochemistry, the dominance, presence, or absence of primary bark beetles during natural disturbance events could be reconstructed. Further synthesis of fossil and historical data, from geological sites as well as archeological sites, will increase our understanding of past disturbances.

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Supplemental material

Supplemental material for this article is available online.

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3.2.2 Using a fossil bark beetle record as indicator of past bark beetle outbreaks in a Norway spruce mountain forest

Finished manuscript:

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Using a fossil bark beetle record as an indicator of past bark beetle outbreaks in a Norway spruce mountain forest.

Authors' contributions:

The study was planned by NS, JLC and NK. NS, NK, RCC, PK and JLC participated in the fieldwork where samples for this study were collected. Radiocarbon dating of the master sediment core was executed at the radiocarbon lab in Poznan, Poland. XRF scanning of the sediment cores was performed by RCC, correlation of sediment cores was performed by NS, RCC and JLC. Subsampling, sample preparation and beetle fossil extraction was performed by NS, initially under guidance of NJW. Bark beetle taxa identification and ecological interpretation was performed by NS, under guidance of MK. Pollen data was collected by HSS, charcoal data was collected by KH. Analysis of pollen data was performed by PK, analysis of bark beetle data by NS. Data from the other proxies was compiled by NK, addition of bark beetle data and display with the program Tilia was performed by NS. MS performed linear regression analysis on the different proxies in the statistical program R. NS was responsible for preparing the manuscript, while all co-authors commented and contributed.

Extended summary

Introduction

Disturbance events in montane conifer forests in the northern hemisphere, such as windstorms, fires and insect outbreaks, are increasing in frequency and magnitude under climate change (Hicke et al., 2016; Thorn et al., 2017). Currently, bark beetle outbreaks have increased to unprecedented numbers and it is expected that the geographical range and host selection will expand for certain bark beetle species (e.g. Cullingham, 2011). However, only a few paleoecological studies have been conducted to gain more understanding about the long-term outbreak history (>200 years) of tree-killing bark beetle species in their primary habitats (Zhang et al., 1999; Morris et al., 2015; Jarvis and Kulakowski, 2015). In order to address the absence of fossil bark beetle records in central Europe, this study aims to reconstruct past bark beetle outbreaks using fossil bark beetle remains from a peat core from a small forest hollow in Slovakia. We aimed to answer the following questions: 1) Can peaks in conifer bark beetle remains from small forest hollow records be used as indicators of past outbreaks; and 2) Do peaks in conifer bark beetle remains coincide with disturbance events reconstructed from other proxies and historical archives?

Methodology

A forest hollow at the southern slope of the High Tatra Mountains was selected for paleoecological studies, to reconstruct changes in forest composition, fire events and the associated changes in abundance of primary bark beetle species over the last 1000 years. Diera Hollow is a small forest hollow located at the eastern edge of the area affected by a windstorm in 2004 subsequent bark beetle outbreaks. In 2016, a master core was retrieved which was radiocarbon dated and analyzed for geochemistry and pollen. Twelve additional cores were collected in 2017. Both the master core and additional cores were analyzed for geochemistry (ED-XRF; e.g. Longman et al., 2019) and the additional cores were subsampled according to matching geochemical patterns, resulting in 18 samples with beetle remains. Bark beetle species were classified as either primary or secondary bark beetle species, according to their ability to successfully attack and invade healthy trees. Pollen and charcoal analysis were performed on the 2016 master core, according to standard procedures (Fægri and Iversen 1989; Higuera et al., 2007). CharAnalysis software (Higuera et al., 2009, 2010; Kelly et al., 2011) was used to detect the peaks in macroscopic charcoal records indicating local fire events. The pollen record from Diera Hollow was used to calculate a Disturbance Frequency Index (DFI; Kuneš et al., 2019). Finally, a series of linear models were fitted to link responses (DFI and macroscopic charcoal influx) to the total density of primary bark beetles (overall models) and densities of the three most abundant species (species-specific models). The linear regression analyses were performed in R (Wickham, 2016, Bjornstad, 2020).

Results

A total of 302 individuals from 22 taxa of the subfamily of Scolytinae was identified from the beetle assemblages from Diera Hollow. Three taxa of primary bark beetles; *Polygraphus poligraphus* (L.), *Pityogenes chalcographus* (L.) and *Pityophthorus pityographus* (Ratz.) appear in numbers of five individuals or more in at least one of the 18 samples. The pollen and charcoal records from the 2016 master core extend from AD 590 until present, while the bark beetle record extends from AD 930 until present. The first distinctive peak in bark beetle remains was found in samples 17 and 18 (AD 930 – 1030), with high numbers of *P. poligraphus*. Starting from sample 14 (AD 1140), but most prominently in sample 12 (AD 1390), a distinctive peak in the numbers of *P. chalcographus* and *P. pityographus* was found. Finally, samples 1 and 2 contain high amounts of *P. chalcographus* and *P. pityographus* in sample 1 (AD 2000 – present). Notable changes occur in the pollen record of the main conifer tree taxa, namely *Picea, Pinus* and *Abies*. A short peak in *Abies* pollen occurs around AD 1000, otherwise values remain relatively constant between AD 590 – 1250. Between AD 1300 – 1400, pollen values of *Abies* and *Picea* decreased significantly. Around AD 1400 a peak in the *Pinus* pollen curve occurs, which subsides ~ AD 1550. *Picea* pollen increased around AD 1600 while *Abies* pollen continued to decrease; *Pinus* pollen gradually started to increase from AD 1750. At AD 1850, *Picea* pollen values reached their second maximum while *Pinus* pollen simultaneously showed a brief decrease. From AD 1950, *Pinus* pollen values were as high as around AD 1500. *Abies* pollen are nearly absent by this time. The disturbance frequency index (DFI) shows continuously lower values before AD 1250. Between AD 1250–1400, high values of the DFI indicate disturbance of the vegetation surrounding the sample site. A second, more moderate period of vegetation disturbances occurs between AD 1550–1850. Between AD 1900–1950, a short disturbance event is recorded of similar magnitude as between AD 1550–1850. Macroscopic charcoal influx values (particles cm^{-2} year^{-1}) are higher in the lower part of the core (AD 560 – 1450) and drop notably after AD 1450. CharAnalysis detected 12 significant peaks indicating fire events around AD 725, 850, 930, 1220, 1260, 1420, 1620, 1720, 1770, 1830, 1870 and 1960. Models with time-lagged responses revealed a significant lagged relationship between primary bark beetle densities and the charcoal influx. The amount of macroscopic charcoal particles increased with the total number of primary bark beetles in the previous stratigraphic layer.

Discussion

The modern bark beetle outbreak which started after AD 2004 (e.g. Nikolov et al., 2014) is apparent in the fossil bark beetle record, with a distinctive peak in numbers of *P. chalcographus* and *P. pityographus*. There also appears to be a relation between the disturbances between AD 1250 – 1400 and the higher numbers of *P. chalcographus* and *P. pityographus* fossils shortly thereafter. The increase in macro charcoal and DFI during this time period coincides with the first evidence of human activity in the region, according to human-indicator pollen. The significant lagged relationship between primary bark beetle densities and the charcoal influx suggests a lagged response in local fire events, on average 20 years after increases in bark beetle populations. The peak in remains of the primary bark beetle *P. poligraphus* around AD 930 – 1030 could have been related to fire events, although no significant changes in the vegetation structure were found. *P. poligraphus*, however, was recorded to only very infrequently cause serious dieback of its host during an outbreak. *I. typographus*_was found frequently, especially in samples younger than AD 1500, but always in low amounts (1-2 individuals per sample) which made statistical analysis impossible. *P. chalcographus* and *P. pityographus* are much more frequent in the fossil record and it was found that population density of these two species is currently primarily correlated to Norway spruce density (Schroeder, 2012), while local population density and attack patterns of *I. typographus* are much more influenced by different variables in the forest structure (Schroeder, 2012; Økland et al., 2016; Stereńczak et al., 2020). Therefore, it is plausible that *P. chalcographus* and *P. pityographus* fossils might be a better proxy for past conifer bark beetle outbreaks in central Europe. Two bark beetle outbreaks in 1968 and 1993 - 1998 which occurred approximately 10 km away on the other side of the mountain (Koren, 2006; Grodzki et al., 2010), are not evident in the fossil bark beetle record. As the DFI and charcoal likely recorded signals from a wider source area than the 400 m for beetles, all emphasizes that the bark beetle record only shows outbreaks which took place in close proximity to the sample site.

Implications

This study presents the first fossil record with high numbers of conifer bark beetle remains in mountain spruce forests in Central Europe (Schafstall et al., 2020a and references therein) and shows that bark beetle outbreaks can be directly reconstructed from the fossil record. It represents an important step in the development of new proxy records for long-term forest dynamics in central Europe, adding to recent studies on vegetation development and fire events in this region (e.g. Jamrichová et al., 2017; Feurdean et al., 2017; Carter et al., 2018). Future studies on past bark beetle outbreaks are advised to regard the whole bark beetle community instead of focusing on the species of interest only, as the main primary bark beetle species might be ambiguous in the fossil record. A lagged correlation between bark beetle densities and macro charcoal densities highlights the role of bark beetles in the natural disturbance regimes of this region. Our study shows that in the High Tatra Mountains, bark beetle outbreaks were a natural part of forest dynamics which was altered after the increase of anthropogenic activities in the region. Long-term records of fire events, bark beetle outbreaks and other disturbance agents which can be indirectly reconstructed from organic sediments, would be useful in reconstructing past disturbance events in several national parks in central Europe which are currently discussing strategies on dealing with bark beetle outbreaks, such as Šumava National Park (Zyval et al., 2016), Białowieża National Park (Grodzki, 2016) and many more. Any inundated organic despression in de direct vicinity of a bark beetle outbreak is likely to contain sufficient bark beetle remains to allow for quantitative reconstructions. By increasing our knowledge of past bark beetle outbreaks, the general public and policy makers would be better informed about the frequency and magnitude of bark beetle outbreaks on a longer time scale, and their effect on the vegetation structure of nature parks. Increases in deadwood by other natural disturbances such as windthrows have stirred up bark beetle outbreaks, which now are said to have more pronounced effects on our ecosystem services such as biomass, biodiversity and water quality (Morris et al., 2018). Recently, several studies have argued against negative effects of bark beetle outbreaks on forest ecosystem services on a longer time scale (Beudert et al., 2014; Kopáček et al., 2020; Seedre et al., 2020), which are an ongoing subject of debate between forest managers and conservationists (Müller, 2011). By better informing the general public and policy makers, this subject could become less polarized and lead to a discussion on how we would manage our nature parks on the long run, instead of making decisions with short-term effects. On a longer time scale, bark beetle outbreaks might even lead temperate conifer ecosystems into a new stable state which could be more resilient to our current climate (e.g. Müller et al., 2008). In this sense, is advisable to let nature take its course and allow for a long-term development of our nature parks.

Using a fossil bark beetle record as an indicator of past disturbance events in a temperate spruce mountain forest

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Abstract

Temperate conifer forests are greatly affected by environmental changes, with an increase in the frequency and severity of natural disturbance events such as droughts, fires, windstorms and insect outbreaks. In recent decades, bark beetle outbreaks have caused significant dieback of conifer forests in Central Europe and efforts have been made to model and predict future bark beetle outbreaks. However, to predict future bark beetle outbreaks, historical baseline information is required to quantify the magnitude of current and potential future outbreaks. A fossil beetle record from a forest hollow in the High Tatra Mountains, Slovakia, was analyzed to reconstruct insect outbreaks during the last millennia. The bark beetle record was compared to a pollen and charcoal record from the same site in order to assess if peaks in conifer bark beetle remains can be related to past disturbance events, documented in historical records or reconstructed from the fossil record.

Three peaks in bark beetle remains were detected, of which abundant species *Pityogenes chalcographus* and *Pityophthorus pityographus* around AD 2004 could directly be correlated to a large bark beetle outbreak which commenced in the High Tatra Mountains after 2004. Two earlier peaks in bark beetle remains occurred between AD 1140 - 1440 (*P. chalcographus* and *P. pityographus*) and between AD 930 -1030 (*Polygraphus poligraphus*). The most prominent conifer bark beetle in central Europe, *Ips typographus*, was found in most of the samples but always in very low numbers. It is plausible that *P. chalcographus* and *P. pityographus* fossils might be useful proxies for past conifer bark beetle outbreaks in Central Europe, as they occur together with fossils of *I. typographus* but in much greater numbers. A significant lagged correlation of 20 years was found between primary bark beetles and macroscopic charcoal densities in the sediment, highlighting the role of bark beetles in the complex interactions between disturbance agents in the long-term regime of natural disturbances in central Europe. Assumed negative effects of bark beetle outbreaks on forest ecosystem services such as water quality and total biomass appear to be much less pronounced on a longer time scale. Our 1400-year disturbance record shows how bark beetle outbreaks appear to have been an important component of the disturbance regimes in this

region and how the disturbance regimes changed after the onset of anthropogenic activity. On a longer time scale, bark beetle outbreaks might lead temperate conifer ecosystems into a new stable state which could be more resilient to our current climate.

1. Introduction

Temperate conifer forests cover large parts of the northern hemisphere, often in montane areas, and are typically occupied by endemic flora and fauna communities (Jenik, 1998; Amori et al., 2019). During recent decades, environmental change has had a significant impact on these forested areas. Amplifying the changes in forest cover and composition related to anthropogenic factors, climate change has increased the frequency and severity of droughts, fires, windstorms and insect outbreaks (e.g. Schelhaas et al., 2003; Seidl et al., 2017). Insect outbreaks in Europe and North America have been caused by species such as the gypsy moth (*Lymantria dispar*; Elkinton and Liebhold, 1990), spruce budworm (*Choristoneura fumiferana*; MacLean, 2019) and several species of bark beetles (Scolytinae Primary bark beetles are species which successfully invade and kill healthy trees. In Europe, the primary bark beetle species *Ips typographus* and in North America beetles of the genus *Dendroctonus* have caused substantial damage and caused economical losses in managed forests (Vega and Hofstetter, 2015). The main host of *I. typographus* is Norway spruce (*Picea abies*), which is common in central Europe, while different species of *Dendroctonus* in North America have their specific host tree species in the conifer taxa *Picea*, *Pinus* and *Pseudotsuga* and are confined by the geographical range of their host tree (for an overview, see e.g. Morris et al., 2017).

Bark beetle outbreaks have increased rapidly both in severity and scale across Europe and North America in the recent decades (Hicke et al., 2016; Thorn et al., 2017). Large quantities of trees are currently killed by bark beetle attacks annually, often triggered after other disturbance events such as fires and droughts (Geiszler et al., 1984; Kolb et al., 2016). Major recurring bark beetle outbreaks have, to certain extent, changed the forest structure in regions throughout Europe and North America, creating extensive areas with dead standing trees which are often regarded negatively by nature tourists (Werner et al., 2006; Hacket, 2007; Müller, 2011). Under current climate change, the geographic range of many primary bark beetle species is expanding into uncolonized territory (e.g. Cullingham, 2011). In North America, several species of *Dendroctonus* are expanding their range northwards (Bentz, 2009; Robertson et al., 2009; Trân et al., 2007) and in Eurasia, *Ips typographus* populations are increasing and spreading westwards as well as eastwards (Jeger et al., 2017). In many cases, increased annual temperatures have led to increases in fecundity of bark beetles, leading to a build-up of bark beetle populations (Jönsson et al., 2007; Mitton and Ferrenberg, 2012). *I. typographus* historically has only caused outbreaks on healthy trees when large quantities of deadwood have been available to build up a large population (e.g. after windstorms; Skuhravy, 2002), and such outbreaks quickly subsided after a few years. In the last decades, however, populations of *I. typographus* have been able to maintain themselves at higher abundance over longer periods of time and have spread through spruce stands throughout Europe (Krehan et al., 2010; Grodzki, 2016; Marini et al., 2016). Recent observations show that *I. typographus* can also utilize other tree species as hosts, if their main host tree becomes scarce (Knížek et al., 2019).

Due to increasing losses in the timber industry, studies have been conducted with the aim to mitigate future bark beetle outbreaks to prevent large-scale death of conifer trees (e.g. Fettig et al. 2007; Seidl et al., 2017). These studies vary from developing and improving methods to avoid en masse colonization of trees by bark beetles (e.g. Jakuš and Šimko, 2000), to modelling approaches to predict under which conditions bark beetle outbreaks are more likely to happen in the near future (e.g. Hicke et al., 2006; Stadelmann et al., 2013). Several studies point out that bark beetle outbreaks are a natural component of forest dynamics and that the increase in outbreaks in the current decades is mainly a cause of human manipulation of natural forest systems into forest plantations (e.g. Zemek & Herman, 2010; Nagel et al., 2017). The current outbreaks are unprecedented compared to the existing historical records (Schelhaas et al., 2003; Raffa et al., 2008), which date back a few hundred years. Only a few paleoecological studies have been conducted to gain more understanding about the long-term outbreak history (>200 years) of tree-killing bark beetle species in their primary habitats (Zhang et al., 1999; Morris et al., 2015; Jarvis and Kulakowski, 2015). Such paleoecological studies have great potential to provide important information on the current and future outbreaks through reconstructing the frequency and magnitude of past outbreaks, and the conditions under which past outbreaks took place (Froyd and Willis, 2008; Schafstall et al., 2020a). Past natural disturbance events on longer time scales have been revealed in a range of studies, primarily focusing on fire events (Kilgore and Taylor, 1979; Anderson et al., 2008; Carter et al., 2018) as these events could be identified from sediment records. As a proxy for vegetation composition, landscape structure and insect outbreaks, fossil beetles have a high potential to be used for paleo-reconstructions on various spatial and temporal scales (Olsson and Lemdahl, 2009; Smith et al., 2010; Whitehouse and Smith, 2010; Lindbladh et al., 2013). Currently, there has been little effort made to reconstruct bark beetle outbreaks from sediment records. To reconstruct conifer bark beetle outbreaks, large amount of bark beetle remains are required (Schafstall et al., 2020a), and previous attempts to correlate fossil bark beetle remains from lake sediment records to past disturbance events on longer time scales were qualitative reconstructions based on small amounts of lake sediment (Brunelle et al., 2008; Morris et al., 2015).

In order to address the absence of fossil bark beetle records in central Europe (Schafstall et al., 2020a), this study aims to reconstruct past bark beetle outbreaks using fossil bark beetle remains from a peat core from a small forest hollow in Slovakia. The High Tatra Mountains in Slovakia are a unique nature reserve, which is currently influenced by intense anthropogenic pressure and climate change (Fleischer et al., 2005; Rączkowska, 2019). Several large windstorms were documented in this area over the last century and a large part of the nature reserve was damaged by a large windstorm in 2004, with consecutive outbreaks of *I. typographus* from 2007 onward (Nikolov et al., 2014). In addition to fossil bark beetle remains, fossil pollen was used to detect changes in vegetation and sedimentary charcoal to reconstruct past fire events, allowing comparison between different proxies for past disturbances. Disentangling the different types of disturbance within the source area of a fossil site in the High Tatra Mountains reveals past bark beetle outbreaks and their relation to other natural disturbances in this region, and could improve the knowledge of mechanisms behind current bark beetle outbreaks in central Europe. We aim to answer the following questions:

1. Can peaks in conifer bark beetle remains from small forest hollow records be used as indicators of past outbreaks?
2. Do peaks in conifer bark beetle remains coincide with disturbance events reconstructed from other proxies and historical archives?

2. Methods

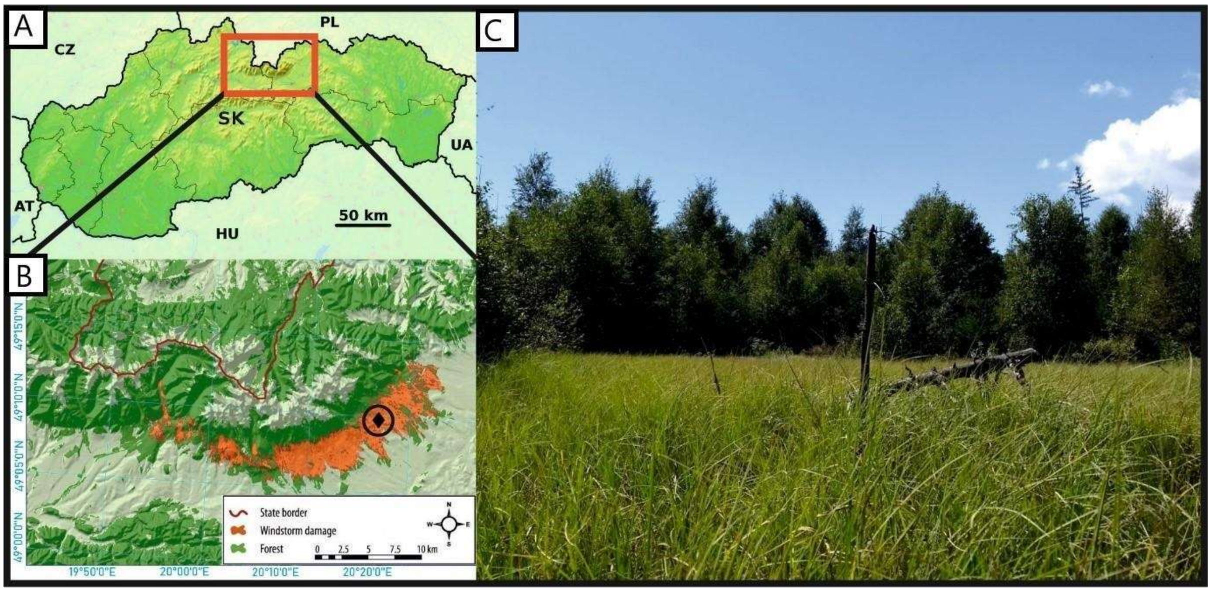


Figure 1 The study site, Diera Hollow (B; black diamond) located in the Tatra Mountains on the Slovak-Polish border (A). Base map after Nikolov et al. (2014) highlighting the area affected by the 2004 windstorm Alžbeta.

2.1 Site area

Tatra National Park is situated in the High Tatra Mountains, and forms a natural boundary between Poland and Slovakia. In both countries, national parks were established in the early 1950’s and the parks were joined in 1993 as a transboundary UNESCO biosphere reserve (unesco.org). (I think you need to state here the focus is on Slovakia). The area gradually developed since the end of the 19th century, from a cultural landscape into a tourist destination, and currently a large ski resort is located in the area (Chrenka and Ira, 2011). The region has a sub-continental climate with average monthly temperatures between -5.3 °C – 15.4 °C (Tatranská Lomnica weather station). It is densely forested with Norway spruce (*Picea abies*) as the predominant tree species, with pine (*Pinus sylvestris; P. cembra*), larch (*Larix decidua*), fir (*Abies alba*) and birch (*Betula* spp.; Fleischer & Homolová, 2011). Two autumnal storms, in 2004 and 2014, damaged a great number of trees in a large portion of the Slovak side of the national park (Potterf et al., 2019). Bark beetle outbreaks started on lying deadwood shortly afterwards and continued every consecutive year. Outbreaks of *Ips typographus* were ongoing in this region at the time of sampling in 2017 and have destroyed large amounts of (mostly) large spruce trees between 2004 and 2017 (Kunca et al., 2019), in many localities expanding far beyond the area which was initially affected by the windstorms (Potterf et al., 2019).

A forest hollow at the southern slope of the High Tatra Mountains was selected for paleoecological studies, to reconstruct changes in forest composition, fire events and the associated changes in abundance of primary bark beetle species over the last 1000 years. Forest hollows are waterlogged anoxic peat depressions within a forest canopy. Due to their small to moderate size (~100 – 2000 m^2) the fossil remains from these sites reflect a local signal of past disturbances, ideal for local studies (Overballe-Petersen and Bradshaw, 2011). The source area for beetle remains is 400 m from the sample site at most (Smith et al. 2010). Macroscopic charcoal, analyzed from forest hollows, records primarily local fire events as charcoal from more distant fires is filtered out by the vegetation (Higuera et al., 2007). Diera Hollow is a small forest hollow of 30 x 80 m in size and located at 982 m a.s.l. at the Eastern edge of the area affected in 2004 and 2014, near the village Tatranská Lomnica, (49.1593° N, 20.26357° E; Fig. 1). The site was heavily affected by the autumnal storm Alžbeta in 2004 and is currently surrounded by pine, spruce, larch, birch (*Betula*) and bilberry (*Vaccinium myrtillus*). Seedlings of birch, bedstraw (*Galium* sp.), rosebay willow herb (*Epilobium angustifolium*) and sedges (*Carex* spp.) were found growing on the site during fieldwork.

2.2 Field methods

A master sediment core was extracted from Diera Hollow in 2016, with a 5 x 50 cm D-section corer (Jowsey 1965; Aaby & Digerfeldt 1986). To provide the volumes of material required for quantitative analysis of fossil beetles, a further 12 proximal sediment cores were sampled in 2017 using a gridded system (50 cm between cores), with a 10 x 50 cm D-section corer. Cores measured between 50 cm and 78 cm in total length due to variability of peat accumulation on top of the underlying bedrock. The master core (88 cm in length) was radiocarbon dated and analyzed for geochemistry (Energy-Dispersive X-Ray Fluorescence: ED-XRF), fossil beetles, fossil pollen and charcoal particles, while the additional cores were analyzed for geochemistry and fossil beetles. For further information on core correlation see Schafstall et al. (2020b).

2.3 Chronology, geochemistry and subsampling

Four botanical macrofossil samples from the 2016 master core were dated in the Poznan radiocarbon laboratory and were used to establish a site chronology (Supplementary material). The 14C ages were calibrated with the IntCal13 curve (Reimer et al., 2013) within a Bayesian age-depth modelling routine 'BACON' (Blaauw & Christen, 2011). All 13 cores, including the master profile, were analyzed for geochemistry on a wet-sediment basis using an Olympus Delta Professional ED-XRF mounted on the University of Liverpool Geotek Multi-Sensor Core Logger (MSCL). XRF is a common method in limnology (Davies et al., 2015) and, to lesser extent, in studies on peat profiles (e.g. Longman et al., 2019). Patterns in concentration of the atmospheric fallout pollutant Pb (Renberg et al., 2000) displayed a strongly repeatable signal. Profiles for conservative lithogenic elements, e.g. Rb, also showed strongly repeatable stratigraphic records. The master core was subsampled in 1-cm resolution, while the other 12 cores for beetle remains were subsampled according to their geochemical signals, resulting in 18 pooled samples of varying volume (see Figure S2).

2.4 Fossil beetle analysis

Fossil beetle preparation followed the methods described in detail by Elias (2010). Samples were wet sieved over 200 µm mesh size and the organic remains were soaked in paraffin oil and floated in water. Isolated flots were once more sieved at 200 µm and rinsed before being stored in ethanol (C_2H_5OH). Beetle remains were picked under a binocular light microscope with 10x magnification and were identified to family, genus and species level with the use of online databases (Kerbtier.de, Cassidae.uni.wroc.pl) and museum collections in United Kingdom (Plymouth City Museum and Oxford Museum of Natural History) and Czechia (Czech National Museum in Prague, the Central Bohemian Museum in Roztoky u Prahy and the Moravian Museum in Brno). A description of the complete beetle assemblage can be found in Schafstall et al. (2020b). Bark beetle (Scolytinae) remains consist of subfossil elytra, pronota, heads and legs. Species were classified as either primary or secondary bark beetle species, according to their ability to successfully attack and invade healthy trees (e.g. Martikainen et al., 1999). For each bark beetle taxon, the number of individuals per 100 ml of sediment sample was calculated in order to account for difference in sample sizes.

2.5 Pollen analysis

Pollen analysis of the 2016 master core was performed in continuous 1 cm resolution between 1-70 cm and in 2 cm intervals for the rest of the core, amounting to a total of 78 samples. Subsamples of 0.5 cm^3 were prepared with standard procedures of KOH-, acetolysis- and HF-treatment (Fægri and Iversen 1989). The samples were mounted in glycerin and a minimum of 500 terrestrial pollen grains were identified under a light microscope using a 400x magnification. Pollen identification was based on standard pollen keys (Punt 1976–2003; Beug 2004), microtopographic atlases (Reille 1992–1998), and a reference collection in the Institute of Botany, CAS, in Průhonice. Pollen data was plotted using the program Tilia (Grimm, 1990).

2.6 Macroscopic charcoal analysis

Charcoal analysis was performed on the 2016 master core. Macroscopic charcoal (> 180 µm) represents local fire events in the vicinity of the study site (Peters and Higuera, 2007; Higuera et al., 2007, 2010). Macroscopic charcoal was analyzed following a method adapted from Mooney and Tinner (2011). A known volume of sediment (0.5-1 cm^3) was disaggregated using 20 ml sodium hexametaphosphate (Calgon) with 10 ml potassium hydroxide (KOH) and left for a few hours. The sediment was washed gently through a 250 µm sieve, then either 1 or 2 ml of sodium hypochlorite was added to the sediment in water and left for the minimum time necessary to achieve a consistent bleaching effect up to a maximum time of overnight. The sediment was then washed gently through a 125 µm sieve to retain any fragmented particles. A light microscope and pipette were used to sort and remove any dark non-charcoal material, after which the petri dishes were photographed using a 12-megapixel digital camera and light table. The total concentrations and influx of macroscopic charcoal counts were calculated for each sample.

CharAnalysis software was used to detect the peaks in macroscopic charcoal records indicating local fire events (Higuera, 2009, 2010; Kelly et al., 2011). First, macroscopic concentrations (particles / cm^3) were interpolated to mean temporal sample resolution. Next, the charcoal record was separated into a low-frequency background component (BCHAR) and a peak component using the CharAnalysis software (Higuera, 2009). To determine the background component, smoothing with LOWESS regression within a 500-year moving-window was employed. The peak component was then calculated as residuals between interpolated charcoal records and BCHAR (Cpeak = CHAR-BCHAR) and evaluated using the 99th percentile of a Gaussian mixture model in order to separate fire events reflected by charcoal peaks from the background noise. The detected peaks were screened using a minimum-count peak ($p = 0.05$) test in CharAnalysis.

2.7 Data analysis

The pollen record from Diera Hollow was used to calculate a Disturbance Frequency (DF) Index (after Kuneš et al., 2019). First, each pollen found in each sample was assigned to a plant species following Beug (2004) and associated with a disturbance indicator value of that species based on the Whole-Community DF available for Central European flora (Herben et al., 2016). This DF is expressed as mean disturbance return time based on various disturbance processes including logging, cutting, mowing, herbivory, trampling, herbiciding, burning, wind-throws, soil erosion, ploughing, hoeing or burrowing. If the given pollen taxon covers several species, one of these species was assigned to it randomly (weighted by the present-day frequencies of these species). This process was repeated 100 times to provide mean disturbance indicator value represented by the given pollen grain. Then the mean disturbance frequency of the entire pollen sample is calculated as a mean of estimated disturbance frequency indicator values of all pollen grains in the sample. DF is expressed on a common logarithm scale and ranges from −2 (once in 100 years) to 0.78 (six times per year). Since we expect that bark beetle outbreaks modify plant communities and can lead to fire events due to deadwood accumulation, we assessed relationships between density of bark beetle remains and disturbance frequencies and fire events, respectively. We fitted a series of linear models linking responses (disturbance frequency index and macroscopic charcoal influx) to the total density of primary bark beetles (overall models) and densities of the three most abundant species (species-specific models). Since the reaction of plant communities and occurrence of potential fire events may be delayed in time behind the outbreaks, we evaluated immediate responses using the matched data from the same stratigraphic layers and also delayed responses using first-order lagged data (median lag of 12 years). All models were carefully checked for homogeneity of variances, normality, and temporal autocorrelation using diagnostic plots of residuals. Bark beetle densities and charcoal fluxes were log-transformed to fulfill the assumptions of linear models. No significant serial autocorrelation was detected. The analyses were performed in R (R Development Core Team, 2019) using the libraries ggplot2 (Wickham, 2016) and ncf (Bjornstad, 2020).

3. Results

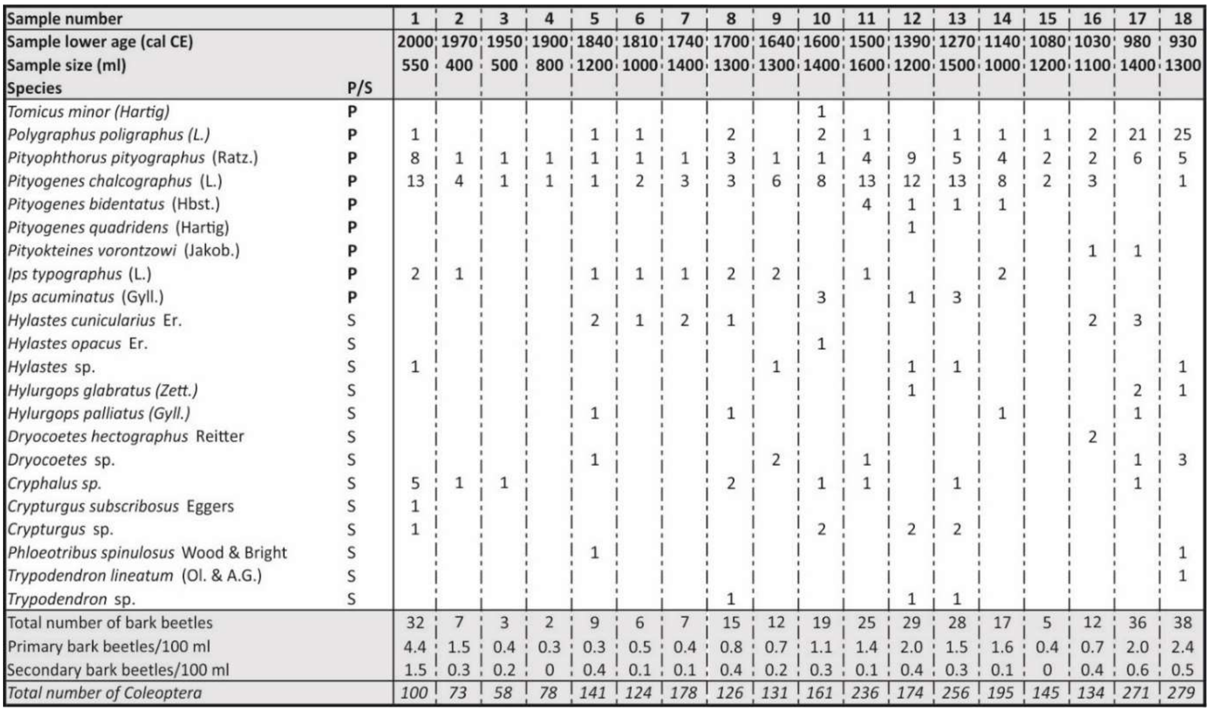
3.1 Primary bark beetles

A total of 302 individuals from 22 taxa of the subfamily of Scolytinae, all conifer bark beetles, were identified from the beetle assemblages from Diera Hollow (Table 1). Primary bark beetle remains (see Table 2 for a brief summary of the ecology of these species) were found in higher numbers than secondary bark beetle remains; secondary bark beetles reached maximum values of 1.5 individuals per 100 ml sample but were completely absent in some of the samples. The amount of primary bark beetles per 100 ml sediment ranged between 0.3 and 5.9, depending on the sample. Primary bark beetles were more numerous around AD 900 – 1000, AD 1300 – 1500 and in the top sample which has a basal age of ~ AD 2000.

Three taxa of primary bark beetles; *Polygraphus poligraphus* (L.), *Pityogenes chalcographus* (L.) and *Pityophthorus pityographus* (Ratz.) appear in numbers of five individuals or more in at least one of the 18 samples, while all other taxa have occurrences in low numbers of less than five individuals per sample (Table 1). The pollen and charcoal records from the 2016 master core extend from AD 590 until present, while the bark beetle record extends from AD 930 until present. For the bark beetle samples, the median between the minimum and maximum age of each sample (see Table 1) was taken to create single data points in order to better compare the bark beetle record with the other records.

The first distinctive peak in bark beetle remains (see Table S1; Figure 2) was found in samples 17 and 18 (AD 930 – 1030), with high numbers of *P. poligraphus*. Starting from sample 14 (AD 1140), but most prominently in sample 12 (AD 1390), a distinctive peak in the numbers of *P. chalcographus* and *P. pityographus* was found, although these values only exceed the standard deviation (SD) for *P. pityographus* in sample 12 (AD 1390). Finally, samples 1 and 2 contain high amounts of *P. chalcographus* and *P. pityographus*, with numbers several times exceeding the SD of *P. chalcographus* in sample 1 (AD 2000 – present).

Table 1 Counts of primary (P) and secondary (S) bark beetles (Scolytinae) from the samples of Diera Hollow. The number of P and S bark beetles per 100 ml sediment of each sample is displayed at the bottom of the table. The bottom row shows the total number of identified individuals from all Coleoptera families, per sample.



Sample number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Sample lower age (cal CE)		2000	1970	1950	1900	1840	1810	1740	1700	1640	1600	1500	1390	1270	1140	1080	1030	980	930
Sample size (ml)		550	400	500	800	1200	1000	1400	1300	1300	1400	1600	1200	1500	1000	1200	1100	1400	1300
Species	P/S																		
Tomicus minor (Hartig)	P										1								
Polygraphus poligraphus (L.)	P	1				1	1		2		2	1		1	1	1	2	21	25
Pityophthorus pityographus (Ratz.)	P	8	1	1	1	1	1	1	3	1	1	4	9	5	4	2	2	6	5
Pityogenes chalcographus (L.)	P	13	4	1	1	1	2	3	3	6	8	13	12	13	8	2	3		1
Pityogenes bidentatus (Hbst.)	P											4	1	1	1				
Pityogenes quadridens (Hartig)	P												1						
Pityokteines vorontzowi (Jakob.)	P																1	1	
Ips typographus (L.)	P	2	1			1	1	1	2	2		1			2				
Ips acuminatus (Gyll.)	P										3		1	3					
Hylastes cunicularius Er.	S					2	1	2	1								2	3	
Hylastes opacus Er.	S										1								
Hylastes sp.	S	1								1			1	1					1
Hylurgops glabratus (Zett.)	S												1					2	1
Hylurgops palliatus (Gyll.)	S					1			1						1			1	
Dryocoetes hectographus Reitter	S																2		
Dryocoetes sp.	S					1				2		1						1	3
Cryphalus sp.	S	5	1	1					2		1	1		1				1	
Crypturgus subscribosus Eggers	S	1																	
Crypturgus sp.	S	1									2		2	2					
Phloeotribus spinulosus Wood & Bright	S					1													1
Trypodendron lineatum (Ol. & A.G.)	S																		1
Trypodendron sp.	S								1				1	1					
Total number of bark beetles		32	7	3	2	9	6	7	15	12	19	25	29	28	17	5	12	36	38
Primary bark beetles/100 ml		4.4	1.5	0.4	0.3	0.3	0.5	0.4	0.8	0.7	1.1	1.4	2.0	1.5	1.6	0.4	0.7	2.0	2.4
Secondary bark beetles/100 ml		1.5	0.3	0.2	0	0.4	0.1	0.1	0.4	0.2	0.3	0.1	0.4	0.3	0.1	0	0.4	0.6	0.5
Total number of Coleoptera		*100*	*73*	*58*	*78*	*141*	*124*	*178*	*126*	*131*	*161*	*236*	*174*	*256*	*195*	*145*	*134*	*271*	*279*

Table 2 Description of the ecology of primary bark beetle species (invading healthy trees), identified at Diera Hollow. Bark beetle ecology after Pfeffer (1989).

Bark beetle species	Ecology
Ips typographus (L.)	Feeds mainly on Picea; can form outbreaks when large amounts of weakened wood (wind, snow, draught etc.) are available. Large outbreaks have occurred throughout Europe in the last decades.
Polygraphus poligraphus (L.)	Feeds mainly on Picea; attacks dense, depressed stands of trees. No severe outbreaks have been recorded, but it can be an important disturbance agent locally.
Pityogenes chalcographus (L.)	Feeds on *Picea*, as well as on other coniferous tree species (*Pinus, Abies, Larix*). Infestation of crown or branches is preferred but it also infests trunk parts. Outbreaks have been recorded, killing young trees at plantations and young stands.
Pityophthorus pityographus (Ratz.)	Feeds mainly on *Picea*, but also on other coniferous tree species (*Pinus, Abies, Larix*); only in the crown or branches. No severe outbreaks were recorded in any historical records.
Tomicus minor (Hartig)	Feeds on *Pinus*, attacking upper trunk part of weakened trees. Damaging mature trees by maturation feeding in fresh shoots.
Pityogenes bidentatus (Hbst.)	Feeds mainly on *Pinus*, attacking crowns and branches. Frequent species, but no significant damage to forest stands was recorded in any historical records.
Pityogenes quadridens (Hartig)	Feeds on *Pinus*, attacking crowns and branches. No significant damage to forest stands was ever recorded.
Ips acuminatus (Gyll.)	Feeds on *Pinus,* attacking upper trunk part of weakened trees, with severe outbreaks in dry periods. Large outbreaks have occurred in the last years.
Pityokteines vorontzowi (Jakob.)	Feeds on *Abies*. Responsible for fir dieback in southern and central Europe, together with other *Pityokteines* species.

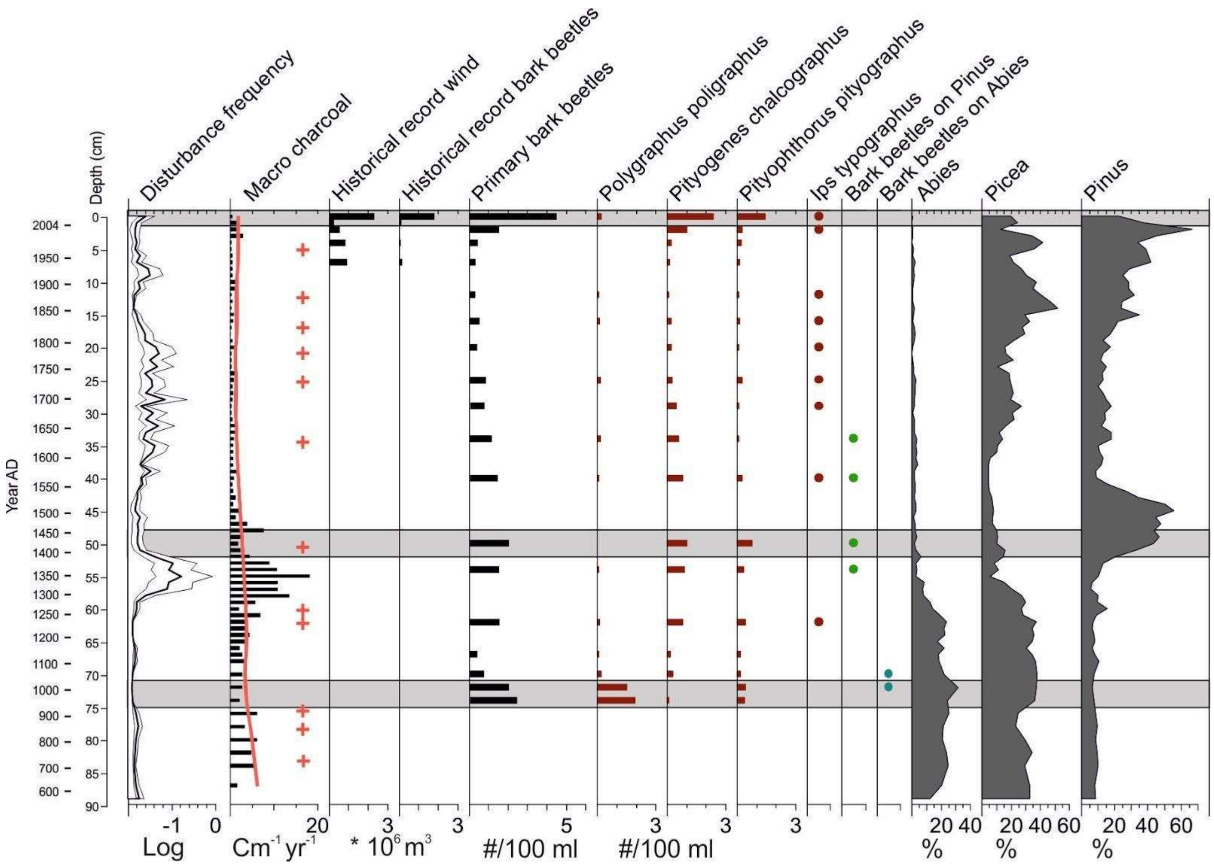


Fig 2 Summary figure showing fossil records from Diera Hollow. A disturbance frequency based on the composition of different plant taxa in the pollen record (log-transformed), displayed with its standard deviation; a macro charcoal influx (particles cm^{-2} $year^{-1}$), with fire events marked as pluses calculated from offsets from the background signal BCHAR (red line); historical records showing documented wind throws and bark beetle outbreaks ($10^6 m^3$ loss of wood); primary bark beetle remains (individuals per 100 ml; single occurrences) obtained from the same locality. Bark beetles feeding on *Picea* are *Polygraphus polygraphus*, *Pityogenes chalcographus*, *Pityophthorus pityographus* and *Ips typographus*. Bark beetles feeding on *Pinus* are *Tomicus minor*, *Pityogenes bidentatus*, *Pityogenes quadridens* and *Ips acuminatus*. Bark beetles feeding on *Abies* are *Pityokteines vorontzowi* (see also Table 2). Pollen abundances (% terrestrial pollen sum) of the conifer host trees *Picea, Pinus* and *Abies*. The pollen and charcoal record extend from AD 590 until present, while the bark beetle record extends from AD 930 until present. Depth and correlated ages are displayed on the left.

3.2 Changes in main tree taxa

Notable changes occur in the pollen record of main conifer tree taxa, namely *Picea, Pinus* and *Abies*. A peak in *Abies* pollen occurs around AD 1000, otherwise values remain relatively constant between AD 590 – 1250. Between AD 1300 – 1400, pollen values of *Abies* and *Picea* decreased significantly. Around AD 1400 a peak in the *Pinus* pollen curve occurs, which subsides ~ AD 1550. *Picea* pollen increased around AD 1600 while *Abies* pollen continued to decrease; *Pinus* pollen gradually started to increase from AD 1750. At AD 1850, *Picea* pollen values reached their second maximum while *Pinus* pollen simultaneously showed a brief decrease. From AD 1950, *Pinus* pollen values were as high as around AD 1500. *Abies* pollen are nearly absent by this time. More detailed data from the pollen record have been published in Schafstall et al. (2020b).

3.3 Disturbance events detected by Disturbance Frequency Index

The disturbance frequency index (DFI) shows continuously lower values before AD 1250. Between AD 1250–1400, high values of the DFI indicate disturbance of the vegetation surrounding the sample site. A second, more moderate period of vegetation disturbances occurs between AD 1550 – 1850. Between AD 1900 – 1950, a short disturbance event is recorded of similar magnitude as between AD 1550 – 1850.

3.4 Past fire events

Macroscopic charcoal influx values (particles cm^{-2} $year^{-1}$) are higher in the oldest part of the core (AD 560 – 1450) and drop notably after AD 1450. Between AD 560 – 870 values remain constantly above 4 particles cm^{-2} $year^{-1}$ on average, after which values remain lower except for short peaks at AD 950 and AD 1220. Notable increases in macroscopic charcoal record occur between AD 1260 – 1360, with the highest amount of macro-charcoal (18 particles cm^{-2} $year^{-1}$) around AD 1320. There is a decline in charcoal concentrations between AD 1370 – 1420, followed by another short peak around AD 1430. After this, the macroscopic charcoal concentrations decline notably below 2 particles cm^{-2} year^{-1} until ~AD 1970, when there is a moderate peak in the macroscopic charcoal record. CharAnalysis detected 12 significant peaks indicating fire events around AD 725, 850, 930, 1220, 1260, 1420, 1620, 1720, 1770, 1830, 1870 and 1960.

3.5 Comparison of bark beetles with disturbance frequency and fire events

We did not find any significant relationship between the total density of primary bark beetles and pollen-based disturbance frequency index ($F_{1,16}$ = 0.03, p = 0.855, r^2 < 0.01) and macroscopic charcoal fluxes ($F_{1,16}$ = 1.77, p = 0.202, r^2 = 0.1), respectively, using data from the same stratigraphic layers (immediate responses) (Table 3). Similarly, species-specific immediate response models of disturbance index ($F_{3,14}$ = 0.84, p = 0.494, r^2 = 0.15) and charcoal ($F_{3,14}$ = 1.23, p = 0.335, r^2 = 0.21) showed no significant relationship. However, models with time-lagged responses revealed significant relationships between the bark beetle densities and the charcoal influx (overall model: $F_{1,15}$ = 7.39, p = 0.016, r^2 = 0.33; species-specific model: $F_{3,13}$ = 7.07, p = 0.005, r^2 = 0.62). The amount of macroscopic charcoal particles increased with the total number of primary bark beetles in the previous stratigraphic layer (Figure 3a). Among the dominant bark beetle species, only *P. pityographus* showed significant relationship with the time-lagged charcoal influx (species-specific model in Table 3). The amounts of charcoal particles increased with the numbers of *P. pityographus* in the precedent layers (Figure 3b). The time-lagged response of the disturbance frequency was not significantly affected by either total density of bark beetles ($F_{1,15}$ = 0.01, p = 0.937, r^2 < 0.01) or density of dominant bark beetle species ($F_{3,13}$ = 1.4, p = 0.28, r^2 < 0.24).

Table 3 Summary of linear models testing for the immediate and time-lagged response of macroscopic charcoal influx and disturbance index to the density of all primary bark beetle species (overall model) and to densities of three dominant species (species-specific model). Estimates of model parameters (b) and their standard errors (se) are displayed along with test statistics (t) and associated probabilities (p). Results significant at α = 5% are highlighted.

	Immediate response						Time-lagged response					
	Charcoal flux			Disturbance index			Charcoal flux			Disturbance index		
Model/parameters	b (se)	t	p	b (se)	t	p	b (se)	t	p	b (se)	t	p
Overall model												
Density of all primary bark beetles	0.621 (0.343)	1.81	0.089	0.005 (0.035)	0.16	0.875	**0.771 (0.273)**	**2.82**	**0.013**	0.006 (0.046)	0.13	0.901
Species-specific model												
Density of *P. poligraphus*	0.233 (0.219)	1.07	0.304	0.004 (0.021)	0.22	0.833	0.254 (0.122)	2.08	0.058	0.004 (0.023)	0.18	0.858
Density of *P. chalcographus*	0.093 (0.287)	0.33	0.750	0.039 (0.027)	1.42	0.177	0.28 (0.169)	1.66	0.121	0.052 (0.032)	1.60	0.134
Density of *P. pityographus*	0.360 (0.408)	0.88	0.393	-0.023 (0.039)	-0.61	0.554	**0.744 (0.245)**	**3.03**	**0.010**	-0.047 (0.047)	-1.01	0.332

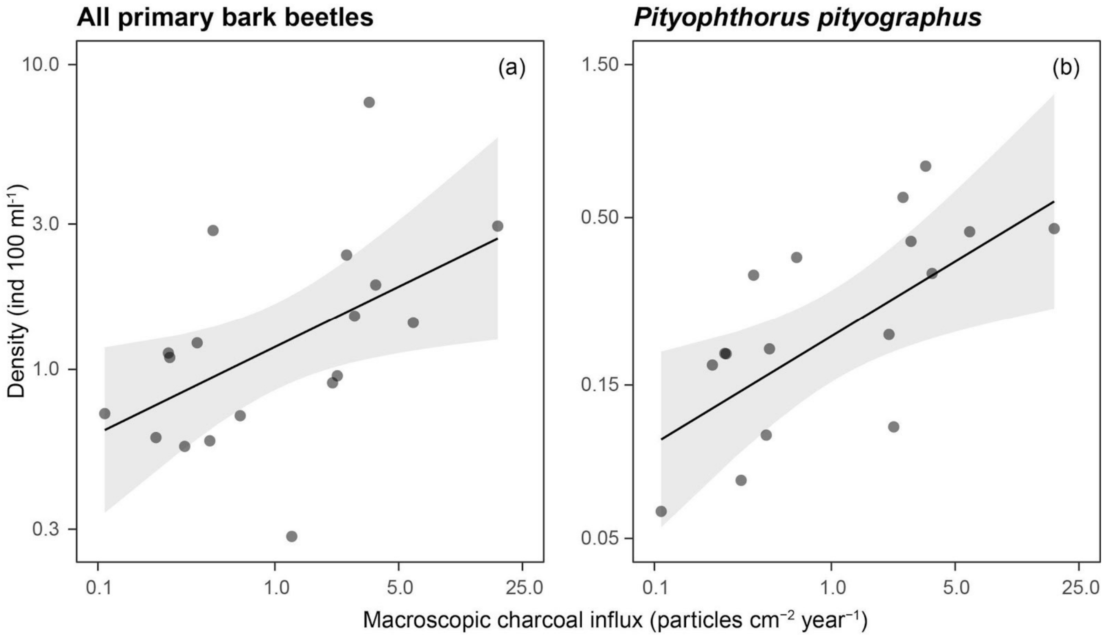


Figure 3 **Significant effect of the total bark beetle density (a – overall model) and density of *P. pityographus* (b – species-specific model) on the amount of macroscopic charcoal influx in a subsequent stratigraphic layer (first-order lagged response). Model-based estimates (lines) are displayed along with their 95% confidence intervals (gray bands). Dots represent observed values (a) and partial residuals (b), respectively. Note that the right plot (b) shows a partial relationship while keeping density of the remaining two dominant species constant at their mean values. For more details, see Table 2.**

4. Discussion

Here we present the first fossil beetle record from Europe which demonstrates that conifer bark beetles, when analyzed in large quantities, can be used as a reliable proxy to reconstruct past insect outbreaks. Previously, only one fossil site from North America recorded similar amounts of primary conifer bark beetle species (Elias et al., 1991; documented in Schafstall et al., 2020a). The well-documented large bark beetle outbreak in the High Tatras after AD 2004 was clearly recorded in the sediment record, providing means to assess bark beetle remains from older samples as indication of past outbreaks. Therefore, several peaks in the fossil bark beetle record during the last millennium suggest reoccurring bark beetle outbreaks in the area around the sample site.

4.1 The fossil bark beetle record and other records of past disturbance

Peaks in the numbers of bark beetle fossils as well as other proxies such as pollen and charcoal show a 1400-year long disturbance record for the High Tatra Mountains. The modern bark beetle outbreak which started after AD 2004 is apparent in the fossil bark beetle record, with a distinctive peak in numbers of *P. chalcographus* and *P. pityographus*. The post-2004 bark beetle outbreaks affected a large area between ca. 2007 and 2017 (Kunca et al., 2019, Potterf et al., 2019), including the area around Diera Hollow. Almost every year during this period, more than 1000 hectare of forest loss in the total area was contributed to bark beetle attacks (Havašová et al., 2017). *P. chalcographus* and *P. pityographus* appear in the same area and attack the same individual trees as *I. typographus*, whereas *P. chalcographus* maintains populations in much higher numbers than *I. typographus* (Jurc et al., 2006; Zubrik et al., 2008). Here, the distinctive peaks in fossil remains of *P. chalcographus* and *P. pityographus* clearly indicate the post-2004 outbreak in the area around the sample site.

Based on the proxy data for disturbance events, there appears to be a relationship between other types of disturbances such as fire between AD 1250 – 1400 and the higher numbers of *P. chalcographus* and *P. pityographus* fossils shortly thereafter, although only the number of *P. pityographus* remains exceeds their SD (see table S1). The disturbance frequency index (DFI) is extremely high during this time, and high values of macro charcoal suggest that forest fires occurred in the area during this period. The increase in macro charcoal and DFI coincides with the first evidence of human activity in the region, according to human-indicator pollen (Schafstall et al., 2020b). Directly after this period of high disturbance, several bark beetle species feeding on pine were identifed in the fossil record. As *P. chalcographu*s and *P. pityographus* colonize not only spruce but also other conifers, it is likely that the peak in remains of this species is related to an increase of pine trees around Diera Hollow following the major disturbance event(s) between AD 1250 – 1400. Based on the available data from bark beetles, charcoal and pollen, a significant relationship between bark beetle population densities and macro charcoal is evident. These results suggest a lagged response in local fire events, on average 20 years after increases in bark beetle populations (depending on the resolution of the bark beetle samples). The significant lagged correlation between the total primary bark beetle population and forest fires could have important implications. In a synthesis on the relationship between bark beetles and forest fires in North America by Jenkins et al. (2014), where forest fires are common in many mountain conifer forests, a 2.5 to 7.8-fold increase of coarse woody fuels was discussed to have been found approximately 20 years after an outbreak of *Dendroctonus ponderosae* (Page and Jenkins, 2007). The peak in remains of the primary bark beetle *P. poligraphus* around AD 930 – 1030 exceeded its SD significantly, although no increased DFI was found for this period. *P. poligraphus*, however, has been recorded to only cause major dieback of its host, *P. abies*, when trees are severely weakened (Kraemer, 1953). The macro charcoal record suggests that several fire events took place prior to the peaks in remains of *P. poligraphus* but as the beetle record only starts at AD 930 it remains uncertain if the increase in *P. poligraphus* remains occurred before, during or after the occurrence of local fires. It is plausible that the higher amounts of macroscopic charcoal prior to ca. AD 1250 are reflective of the early fire regime in the region, which ended with an extreme increase in local amounts of macro charcoal and high disturbances of the vegetation in the region between AD 1250 – 1400. The coincidence of these changes in fire events with human activity in the region is highly suggestive of human interference with or manipulation of the fire regime, possibly either by controlled burning or making changes to the vegetation (structure). However, as it was discussed that the pollen record and DFI likely reflect changes in a larger source area. Nevertheless, the 1000-year development of the forest around Diera Hollow should be considered with the influence of moderate human activity in the region since AD 1250.

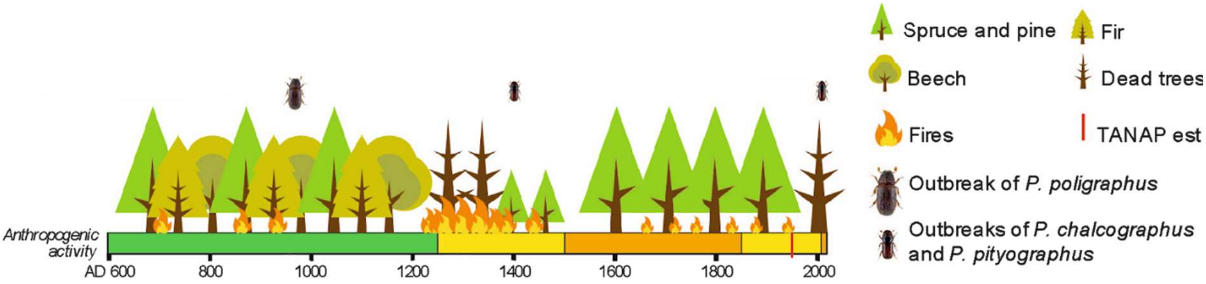


Figure 4 An overview of the development of forest structure, fire events and bark beetle outbreaks around fossil sample site Diera Hollow at the foothills of the High Tatra Mountains in Slovakia, compared to reconstructed anthropogenic activity in the region based on human-indicator pollen and historical records. Tatra National Park (TANAP) was established in 1949.

Between AD 1500 and AD 2000, the DFI and charcoal records suggest multiple disturbance events, however peaks in primary bark beetle remains are absent. Amounts of bark beetle fossils remain low despite several reconstructed fire events and an increased DFI of the vegetation between AD 1550 – 1800 and around AD 1930 (Figure 2). The area was under moderate anthropogenic pressure between AD 1500 ~ 1800, primarily under the Walachian colonization of the Slovakian uplands which led to herding intensification above the timberline and in forest glades (Gladkiewicz and Homza, 2003; Rączkowska, 2019 and references therein). Mining activities might have influenced the landscape since the 11th century and mining activity continued until the 20th century, but sources about these activities are mostly absent on the Slovak side of the mountains and Polish references show activity centers at a further distance from our sample site (Rączkowska, 2019). Historical records starting from AD 1900 (Figure 2), based on forest inventories (Koreň, 2006), describe several other disturbance events in the High Tatra Mountains due to wind throws. These include a large windstorm in

AD 1925 which also affected the area around the sample site (Koreň, 2006) and could be related to the peak in DFI around AD 1930. The largest ones occurred in 1912, 1941, 1981 and 2004, but not all affected the area around our sample site. Although the bark beetle outbreaks after the calamity of 2004 are by far the largest recorded for this area, also three previous bark beetle outbreaks were described in the historical records (Koreň, 2006). After the previously mentioned windthrow in 1925, substantial damage to trees by bark beetles was reported around Podbanské which is located more than 30 kilometers away on the western side of the mountain chain. Another bark beetle outbreak occurred in 1968 between Tatranská Javorina and Ždiar, approximately 10 kilometers from the fossil site and on the other side of the eastern mountain range. Even this distance appears to have been large enough for the bark beetle outbreak to be absent in our fossil record. A well-documented, more recent outbreak took place between 1993 - 1998 (Grodzki et al., 2010), again around Tatranská Javorina. Also this outbreak, during which approx. 60.000 m3 of trees were killed on the Slovak side of the National Park (Grodzki et al., 2010), was not apparent from the sediment record of Diera Hollow.

4.2 Quantifying bark beetle fossil remains to reconstruct past outbreaks

Diera Hollow provides a fossil beetle record with large amounts of bark beetles, suitable for quantitative analysis. Conifer bark beetles seem to preserve very well in acid peat bogs, which are likely the best sites for fossil beetle remains (e.g. Ellias, 2010). The distinctive peaks in numbers of *P. chalcographus* and *P. pityographus* around AD 2004 shows that it is possible to correlate peaks in numbers of bark beetle remains to historical outbreaks. Low numbers of *I. typographus* do not indicate any outbreak around AD 2004. An increase in the occurrences of *I. typographus* fossils from AD 1550 onward might suggest an increase in this conifer pest around the sample site, but due to low occurrences in the fossil record of 1 or 2 individuals per sample no correlation could be made. Both *I. typographus* and *P. chalcographus* have been recorded in great numbers from pheromone traps during outbreaks in various locations in central Europe; tens of thousands of specimens of *I. typographus* and hundreds of thousands of specimens of *P. chalcographus* are mentioned from various different sources, with exact numbers depending on the region (Niemeyer, 1992; Jurc et al., 2006; Zubrik et al., 2008). Although *P. chalcographus* generally exceeds *I. typographus* in numbers eight- to tenfold during outbreaks, it is remarkable that no peak in *I. typographus* remains was recorded around AD 2004. It could be that remains of *I. typographus* do not preserve in peat bogs often, just as they appear to be relatively rare in lake sediments (Kuosmanen et al., 2020). There are, however, indications that not only high densities of Norway spruce but also several other factors such as crown closure and stand age determine local concentrations of *I. typographus* populations (Schroeder 2012; Økland et al., 2016; Stereńczak et al., 2020), which would complicate any fossil signal. *P. chalcographus* (and, although less intensively studied in terms of outbreaks, *P. pityographus*) densities are primarily linked to Norway spruce stand density (Schroeder, 2012) and therefore, together with its apparent abundance in the fossil record, peaks in the fossil remains of these two species might be a more suitable proxy for conifer bark beetle outbreaks in Central Europe. Taking the three reconstructed bark beetle outbreaks into consideration, each outbreak appears to have taken place occurred under different relationships to other agents of disturbance. Changes in the landscape from AD 1250 onward possibly caused a change of bark beetle regimes from a closed spruce forest with *P. poligraphus* as dominant bark beetle species to a semi-open forest landscape dominated by *I. typographus, P. chalcographus* and *P. pityographus*. The high numbers of several tree-killing bark beetle species in the record of Diera Hollow show that also for the reconstruction of the conditions which caused past bark beetle outbreaks, it is beneficial to consider more beetle species than just the main disturbance agent *I. typographus*.

These results of a first quantitative bark beetle record for central Europe show that the use of large amounts of sediment (~2 liters per 10 cm profile) can lead to quantitative reconstructions from beetle remains (e.g. Whitehouse, 2004; Olsson and Lemdahl, 2009; Zhang and Elias, 2019). Just like other studies based on fossil beetle remains, bark beetle fossil remains provide a highly detailed but strictly local signal of past outbreaks and for more regional reconstructions several sites would need to be studied. The outbreaks in 1968 and

1993 - 1998 that occurred around 10 kilometers away from the sample site were not captured in the sediment record of the studied forest hollow, confirming that those outbreaks were too distant to generate a noticeable peak in the bark beetle record.

4.3 Bark beetle outbreaks and ecosystem services in temperate mountain forests

The 1000-year bark beetle record from this study is an important step in the development of new proxy records for long-term forest dynamics in Central Europe, adding to recent studies on vegetation development and fire events in this region (e.g. Jamrichová et al., 2017; Feurdean et al., 2017; Carter et al., 2018). Bark beetle remains were found in sediment records as old as Late Glacial (Schafstall et al., 2020a and references therein) and have likely been part of forest ecosystems for millions of years (Kirejtshuk et al., 2009). After the Slovakian government supported a large-scale salvage logging project to mitigate bark beetle outbreaks in the High Tatra Mountains after 2005 (Nikolov et al., 2014; Havašová et al., 2017), controversy remains about the long-term effects of these management actions (Vanička et al., 2020) and long-term negative effects such as the delay of natural regeneration on the affected plots (Michalová et al., 2017), and the effects on water circulation by an increase in forest roads (Fidelus-Orzechowska et al., 2018). Currently there is an increase in studies that argue for the positive role of primary bark beetles as keystone species in forest dynamics in central Europe, as they create new gaps in the vegetation which support biodiversity (e.g. Müller et al., 2008). The relevance of suppressing bark beetle outbreaks in consumption forest is foremost clear (e.g. Toth et al., 2020), but previous assumptions that bark beetle attacks negatively impact ecosystem services appear to be untrue in many studied cases, as was found in particular in studies on the long-term effect of large disturbances on forest biomass (Seedre et al., 2020), forest hydrology (Kopáček et al., 2020) and water quality (Beudert et al., 2014). While most arguments about bark beetle attacks as a negative effect on ecosystem services are currently contradicted by other studies, the public perception and the perception of policy makers on bark beetle outbreaks remains generally negative (Werner et al., 2006; Müller, 2011; Mikusiński and Niedziałkowski, 2020). It has become increasingly important to educate the general public as well as policy makers about the social-ecological implications of bark beetle outbreaks (e.g. Morris et al., 2018). This study contributes to the conception that bark beetle outbreaks, even in their unprecedented magnitude, are acting as a natural disturbance agent in temperate conifer mountain forest (e.g. Kulakowski, 2016). On a longer time scale, such bark beetle outbreaks would likely be one of the drivers to direct these ecosystems to a new stable state, more tolerant to climate change.

5 Conclusions

This study presents the first fossil record with high numbers of conifer bark beetle remains in mountain spruce forests in Central Europe. Large amounts of subfossil conifer bark beetle remains from a 1000-year long peat record from a forest hollow in the High Tatra Mountains, Slovakia, were compared with past disturbance events derived from a pollen record and charcoal record from the same site. It was possible to identify the large bark beetle outbreak which started in this region after a windstorm in 2004, as high numbers of the primary bark beetles *Pityogenes chalcographus* and *Pityophthorus pityographus* were found in the top sample of the core. Between AD 1140 – 1500 elevated numbers of *P. chalcographus* and *P. pityographus* might indicate outbreaks on pine trees during a long period of succession after a large disturbance. High occurrences of *Polygraphus poligraphus* around AD 930 are likely indicators of an outbreak of this species, although no changes to the vegetation structure were recorded during this period. Main disturbance agent *Ips typographus* was only found in very low numbers (1 or 2 individuals per sample) and no increase in numbers was found around AD 2004. Although outbreaks of *P. chalcographus* and *P. pityographus* do not cause major mortality of mature spruce trees, their high abundance and direct relation to densities of host threes would make these two species a more evident fossil proxy for past bark beetle outbreaks in central Europe than *I. typographus*. A lagged correlation of approximately 20 years between bark beetle densities and macro charcoal densities highlights the role of bark beetles in the natural disturbance regime of this region. Negative effects of bark beetle outbreaks on forest ecosystem services appear to be less evident on a longer time scale. Our study shows that in the High Tatra Mountains, bark beetle outbreaks were a natural part of forest dynamics which was altered after the increase of anthropogenic activities in the region. On a longer time scale, bark beetle outbreaks might lead temperate conifer ecosystems into a new stable state which could be more resilient to current climate.

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Table S1 Values for the three primary conifer bark beetle species *Polygraphus poligraphus*, *Pityogenes chalcographus* and *Pityophthorus pityographus* (individuals/100 ml) which occurred in numbers of five or more in at least one of the samples in the fossil beetle record of Diera

Hollow. The medians of sample ages are shown. The Z-score is a measure for the number of standard deviations above or below the mean. Z-scores higher than 1 are displayed in bold.

Sample	Age (AD)	*P. Poligraphus*		*P. chalcographus*		*P. pityographus*	
		#/100 ml	Z-score	#/100 ml	Z-score	#/100 ml	Z-score
1	2009	0.181818	-0.1386	2.363636	**3.3174**	1.454545	**3.5337**
2	1985	0	-0.4858	1	0.8574	0.25	-0.1814
3	1960	0	-0.4858	0.2	-0.5858	0.2	-0.3356
4	1925	0	-0.4858	0.125	-0.7211	0.125	-0.5669
5	1870	0.083333	-0.3267	0.083333	-0.7963	0.083333	-0.6954
6	1825	0.1	-0.2949	0.2	-0.5858	0.1	-0.644
7	1775	0	-0.4858	0.214286	-0.5601	0.071429	-0.7321
8	1720	0.153846	-0.192	0.230769	-0.5303	0.230769	-0.2407
9	1670	0	-0.4858	0.461538	-0.114	0.076923	-0.7152
10	1620	0.142857	-0.213	0.571429	0.0842	0.071429	-0.7321
11	1550	0.0625	-0.3665	0.8125	0.5191	0.25	-0.1814
12	1445	0	-0.4858	1	0.8574	0.75	**1.3608**
13	1330	0.066667	-0.3585	0.866667	0.6168	0.333333	0.0757
14	1205	0.1	-0.2949	0.8	0.4966	0.4	0.2813
15	1095	0.083333	-0.3267	0.166667	-0.646	0.166667	-0.4384
16	1055	0.181818	-0.1386	0.272727	-0.4546	0.181818	-0.3916
17	1005	1.5	**2.3787**	0	-0.9467	0.428571	0.3694
18	955	1.923077	**3.1866**	0.076923	-0.8079	0.384615	0.2338
Mean		*0.254403*		*0.524749*		*0.308802*	
SD		*0.523646*		*0.554322*		*0.324229*	

3.3 Reconstructions based on insect remains from lake sediments

3.3.1 Postglacial succession of caddisfly (Trichoptera) assemblages in a central European montane lake.

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Authors' contributions

The study was planned by DV and NS. NS and DV mounted Trichoptera larvae remains; photographing of Trichoptera remains was performed by DV. Analysis of ecological properties of species was performed by PC, NS and DV. RCC provided the age-depth model of the site and geochemistry data. Figures were prepared by DV and NS. DV and NS contributed equally to the preparation of the manuscript, while all co-authors commented and contributed.

Extended summary

Introduction

The Bohemian Forest lakes, situated along the Czech-German-Austrian border, were strongly affected by atmospheric acidification between the 1950s and the late 1980s (Fott et al. 1994). The subsequent chemical recovery of the lake water should precede and enable a biological recovery, including caddisfly (Insecta: Trichoptera) communities. Nevertheless, local data from the pre-acidification period and detailed knowledge of the history of the lakes are missing, making an evaluation of lake recovery very difficult. By assessing the fossil content of the lake sediment column, a reconstruction of abiotic and biotic factors of the lake can show changes in the lake through time and when these changes took place. Trichoptera larva remains have been used to reconstruct water quality (Hering et al. 2004; Savić et al. 2013), bottom substrate (Beisel et al. 1998), macrophyte presence (Buczyńska et al. 2017) and recovery from environmental stress (Bradt et al. 1999). With this study, we aim to reconstruct long-term lake conditions of a Bohemian Forest lake by identifying Trichoptera larva remains and attributing ecological properties to identified species. This is, to our knowledge, the first paleoecological study on Trichoptera larvae in central Europe.

Methodology

Prašilské Lake is a moraine-dammed glacial lake and is located in the Bohemian Forest at an altitude of 1079 m a.s.l. Three overlapping cores of 1.5 m each were collected from the lake, as well as an additional 0.43 m core of unconsolidated deposits from the sediment-water interface. From all cores the geochemistry was measured (micro-X-Ray Fluorescence scan, micro-XRF) and selected samples from the cores were used for dating (^{14}C, ^{210}Pb and ^{137}Cs radioisotopes) after which Bayesian age-depth modelling 'BACON' was used to create an age-depth model for the entire profile. The long cores were subsampled in 0.5 cm resolution while the gravity core was subsampled in 1 cm resolution, resulting in samples of 1.5 - 5 ml and 5 - 20 ml in volume. Erosional layers, visible as dark colored bands, were targeted and otherwise samples were selected in high resolution, resulting in 318 selected samples. Caddisfly larva remains were picked using a 15x binocular microscope, dehydrated in ethanol and mounted in Euparal to permanent slides. For identification we focused on frontoclypeal apotomes, which are used in European identification keys (Waringer and Graf, 2011), and used identification keys and a larva reference collection from Bohemian Forest lakes and streams.

Results

Age-depth modeling dated the oldest sediments of Prašilské Lake to 11,400 cal yr. BP. Apart from the organic bands, samples were sparse in macro remains. The largest erosional band in the sediment showed clear signs of reworking and macro remains from these samples were excluded from the results. In total, 58 individuals from 8 different taxa were identified. Specimens which could not be identified to species level were contributed to a morphotype, belonging to a certain taxon. Four zones were established based on the climatological subdivision of the Holocene and the sediment lithology: 11,400 – 8300 cal yr. BP (early Holocene); 8300 – 7600 cal yr. BP (multiple erosion events); 7600 – 4200 cal yr. BP (middle Holocene); 4200 cal yr. BP – present (late Holocene). Based on the low amounts of individuals, only quantitative analyses could be made. All except one species of Trichoptera are currently present in Prašilské Lake or in one of the three streams feeding into the lake, while the other species (*Holocentropus dubius*) is currently found in another lake in the Bohemian Forest and the Bayerischer Wald on the German side; lakes Laka and Grosser Arbersee. Most of the identified species are eurytopic, but many are frequently found in peat bogs and were described as acid-tolerant.

Discussion

Qualitative analysis of the occurrences of the identified Trichoptera species confirms the past occurrence of several species in Prašilské Lake which were thought to be newly discovered in this lake after the 1980s (Soldán et al. 2012). Other glacial lakes, where these species occurred previously, have a much denser biotope of macrophytes in their littoral zone than Prašilské Lake currently has (Soldán et al. 2012; Ungermanová et al., 2014). After the zone with organic bands from multiple erosional events, the middle Holocene zone was the richest in both individuals and number of species. In contrast, the late Holocene sediment zone is sparse in Trichoptera remains. However, no species turnover or introduction of new species was found in this zone. Apart from single occurrences of species which might indicate diversification of the lake substrate during the middle Holocene, the Trichoptera record shows foremost the continuous presence of acid-tolerant species throughout the Holocene. These results suggest that Prašilské Lake has been a dystrophic, moderately acid lake from its early development and throughout the Holocene.

Implications

Trichoptera larva remains are common in lake deposits with abundant organic content and provide additional information about lake water properties and substrate, which makes them suitable as additional proxy to e.g. chironomids and diatoms in paleo-reconstructions. Despite limited data, the results from this study show that also with regards to studies on lake acidification, long-term perspectives are of importance. Any research which argues to manipulate the glacial lakes on the Czech-German border to become less acidic (e.g. Ungermanová et al. 2014; Vrba et al. 2016).), should consider that these novel results show that such efforts would likely not return these lakes to their original state. It has to be considered that any invertebrate species which have reportedly disappeared from these lakes in the last decades, did not disappear because of the lake's acidification pH but was perhaps affected by other environmental factors. It would be advised to compare the Bohemian glacial lakes to other acidic dystrophic glacial lakes (e.g. (Chvojka, 1992), to decide best practices for restoring the pre-industrial state of these lakes.

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ORIGINAL ARTICLE

Postglacial succession of caddisfly (Trichoptera) assemblages in a central European montane lake

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Abstract

The Bohemian Forest lakes, situated along the Czech-German-Austrian border, were strongly affected by atmospheric acidification between the 1950s and the late 1980s. The subsequent chemical recovery of the lake water should precede and enable a biological recovery, including changes in caddisfly (Insecta: Trichoptera) assemblages. Nevertheless, local pre-acidification data and detailed knowledge of the lake district history are missing, making evaluation of lake recovery difficult. We performed high-resolution analysis of caddisfly remains in a 2.2 m long sediment profile from Prášilské Lake covering the complete history of the lake-catchment evolution. Caddisfly larvae are good indicators of environmental conditions and their subfossil remains are well preserved in unconsolidated waterlaid sediments. A total of 10 caddisfly morpho-taxa were found providing a record from 11,400 cal. yr. BP to the present. With the exception of *Athripsodes aterrimus*, all identified species are currently present in the Bohemian Forest glacial lakes or their inflow streams but not all of them are documented in Prášilské Lake. The caddisfly fauna consisted of acid-resistant, acid-tolerant and eurytopic species since the Early Holocene. Based on our results, the acid, dystrophic state of Prášilské Lake has been occurring since the lake formation. We conclude that the first signs of natural acidification appeared not later than during the Holocene onset in the Bohemian Forest region. Furthermore, we did not detect any abrupt changes in the species composition connected to the period of anthropogenic acidification during the twentieth century. This study provides for the first time a record of postglacial succession of caddisfly assemblages in a central European mountain lake.

Keywords Natural acidification · Holocene · Palaeolimnology · Macrozoobenthos · Lake sediment · Erosion events · Bohemian Forest

Introduction

During the last decades, many freshwater bodies across the Northern Hemisphere have experienced anthropogenic acidification (e.g. Mylona 1996; Clair et al. 2007; Jia and Gao 2017). This process, caused by high inputs of acidic or acidifying compounds to the atmosphere and their subsequent transport, also resulted in chemical changes in groundwater and soil (Norton et al. 2013), as well as substantial changes in terrestrial and aquatic ecosystems, including reduction of biodiversity and local species extinctions (e.g. Beamish 1976; Fott et al. 1994; Bobbink et al. 1998). In geologically sensitive regions, the negative effect of decreased pH is usually associated with acidification-induced oligotrophication, low phosphorus availability, lack of food resources for secondary producers, and ionic aluminium toxicity (Vrba et al. 2015; Stuchlík et al. 2017). However, levels of acidification stress

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and acidification recovery rate are always site-specific, depending on the ability of an ecosystem to neutralize the flux of acidity (Stuchlík et al. 2017). In addition to the acidification caused by atmospheric pollution, the process of natural acidification and phosphorus depletion plays a crucial role in longer time scales (Kuneš et al. 2011; Boyle et al. 2013). pH history reconstructions from many Northern Hemisphere lakes show more alkaline conditions after the last local deglaciation (e.g. Engstrom et al. 2000). In the low- and mid-altitude temperate regions with bedrock formed from metamorphic and crystalline rocks, the first signs of acidification begun to manifest since the Early Holocene (Birks et al. 2000; Norton et al. 2011). According to the mineral-depletion hypothesis (Salisbury 1922; Boyle 2007), this shift can be explained by leaching of the calcium phosphate mineral apatite from granitic till soils or windblown material (loess) during the postglacial period(s). For alternative acidifying mechanisms, such as direct climate impacts and successional vegetation cover changes, only a lesser importance is assumed (Boyle et al. 2013).

Among organisms sensitive to acidification in water environment, several groups have an advantage of good preservation in waterlogged anoxic environments, allowing tracking of acidification history using fossil assemblages. Especially diatom (Bacillariophyta) and cladoceran (Crustacea: Branchiopoda) remains are widely used for pH reconstructions and gained importance in the field of palaeoecology (e.g. Smol 2008). Also, insect remains are often abundant and well-preserved in Quaternary lacustrine and fluvial sediments, but their bioindication potential has been little used in acidification-focused studies (Elias 2010). Especially caddisflies (Insecta: Trichoptera) can provide a potentially important proxy, as their recent ecology and pH preferences are, compared to the other water invertebrates, relatively well known (Williams 1988; Fjellheim and Raddum 1990; Braukmann and Biss 2004; Graf et al. 2008; Schartau et al. 2008). Besides studies related to recovery from anthropogenic acidification (e.g. Larsen et al. 1996; Langheinrich et al. 2002; Ross et al. 2008), current caddisfly assemblages are also used for bioindication of water quality and hydromorphological degradation (Hering et al. 2004; Savić et al. 2013), bottom substrate (Beisel et al. 1998), macrophyte presence (Buczyńska et al. 2017), and recovery from environmental stress (Bradt et al. 1999). Williams (1988) acknowledged their value in palaeoecological studies, as subfossil Trichoptera are abundant in limnic and fluvial sediments. Subfossil caddis larvae remains consist especially of chitinous head sclerites, thoracic sclerites, and disarticulated leg segments (Williams 1988; Elias 2010). Caddisfly cases or retreats can be also preserved in the sediments but usually in low numbers (Williams 1988). For identification, froclypeal apotome (frotoclypeus), one of the head sclerites, is the most valuable. Caddisfly frontoclypeal apotomes differ based on shapes and textures, including differences in colour pattern, muscle scar pattern and setal distribution (Elias 2010; Waringer and Graf 2011). Although the presence of caddisfly larvae remains was occasionally reported from Quaternary sediments (e.g. Elias and Wilkinson 1983; Solem et al. 1997), few comprehensive palaeoecological studies using caddisflies have been conducted in Europe. The first quantitative study based on well-dated record was published by Solem and Birks (2000) showing climate-related Late Glacial and Early Holocene caddisfly succession in Lake Kråkenes, Norway. Later, one Danish and several English studies on riverine deposits resulted in detailed reconstructions of the flow environment of former river channels and the adoption of subfossil caddisfly larvae remains in paleo-flow reconstructions (Wiberg-Larsen et al. 2001; Greenwood et al. 2003, 2006; Ponel et al. 2007; Howard et al. 2009). These studies demonstrate that subfossil Trichoptera larvae are still an underused valuable palaeoecological tool and can be applied in studies in other regions as well. Moreover, no study has yet utilized caddisfly remains to reconstruct the history of natural or anthropogenic acidity.

Among lake districts affected by strong anthropogenic acidification, the Bohemian Forest, a Czech Republic-Germany-Austria border area with geologically sensitive bedrock (mica-schist, gneiss, granite), has been intensively studied during the last decades (Vrba et al. 2015 and references therein). Three glacial lakes on the German side (Großer Arbersee, Kleiner Arbersee, Rachelsee) and five lakes on the Czech side (Černé Lake, Čertovo Lake, Laka Lake, Plešné Lake, Prášilské Lake) are distributed over the Bohemian Forest (Fig. 1) and protected within the Šumava National Park, the Šumava Landscape Protected Area, and the Bayerischer Wald National Park. Their atmospheric acidification started presumably in the 1950s and peaked in the late 1970s and first half of the 1980s, when surface water pH decreased below 5 (Fott et al. 1994). Moreover, the total aluminium concentrations at the most affected localities were ~1 mg.l^{-1} and elevated terrestrial export of toxic ionic aluminium and lake water oligotrophication resulted in drastic changes in biota (e.g. Fott et al. 1994; Vrba et al. 2000; Soldán et al. 2012). Despite a decline in sulphur and nitrogen deposition and rapid improvement in water chemistry of all lakes in the last 30 years, biological recovery has been relatively slow (Vrba et al. 2016). There is also a long, albeit fragmented, history of macrozoobenthos research in the Bohemian Forest lakes (Soldán et al. 2012) and the first mention of caddisfly larvae from Černé Lake can be found in Frič (1872). The recovering lakes are a subject of regular monitoring since 1984, including aquatic insect larvae sampling (e.g. Ungermanová et al. 2014; Vrba et al. 2016). Currently, a total of 46 species of Trichoptera is known from these lakes and their inflow streams and outlets (Soldán et al. 2012). Although the signs of biological recovery (re-appearance of indigenous

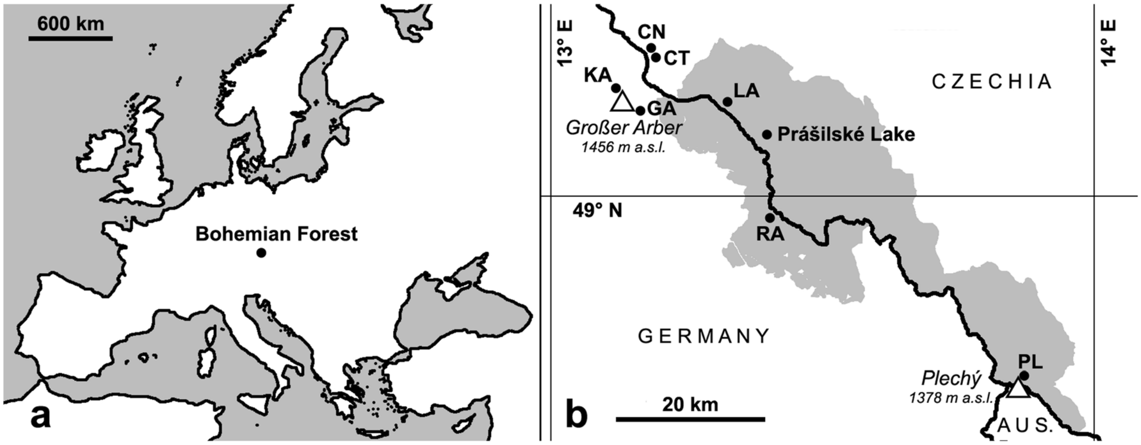


Fig. 1 Location of the Bohemian Forest in Europe (**a**). Location of the study site (Prášilské Lake) within the Bohemian Forest lake district (**b**). Area of Šumava National Park, Czechia, and Bayerischer Wald National Park, Germany, is shown in grey. Depicted are the tallest mountains of the two national parks, as well as all eight glacial lakes. LA – Laka Lake, CT – Čertovo Lake, CN – Černé Lake, KA – Kleiner Arbersee, GA – Großer Arbersee, RA – Rachelsee, PL – Plešné Lake

species, decline in eurytopic and acid-tolerant species, or colonisation of vagile species) are obvious in the lake biota, including macrozoobenthos (Vrba et al. 2016), the long-term history of the lakes and their pre-acidification states are almost unknown. Thus, these gaps in knowledge make it difficult to interpret the currently observed changes in invertebrate assemblages. In this study, we reconstruct a postglacial caddisfly succession in one of the Bohemian Forest lakes – Prášilské Lake – using their subfossil remains. Here we aim: (i) to demonstrate the pre-acidification/preindustrial caddisfly species composition and its comparison with the species composition of the currently recovering lake; and (ii) to assess potential signs of natural acidification during the lake evolution.

Material and methods

Study site

Prášilské Lake (49.075° N, 13.400° E) is a moraine-dammed glacial lake in the Bohemian Forest (Šumava NP), Czech Republic, and is situated at an altitude of 1079 m a.s.l. (Fig. 1). The total surface area is 4.2 ha and the basin comprises a steep littoral zone that deepens rapidly to a maximum depth of 17 m. At the nearest meteorological station Churáňov (49.068°N, 13.615°E, 1122 m a.s.l.), the mean annual rainfall is 1090 mm, the mean January temperature −4.1 °C, the mean July temperature 12.9 °C, and the number of frost days is 165 (during the climatic period 1961–1990). Currently, three mountain streams drain a lake catchment of 65 ha that is dominated by Norway spruce (*Picea abies*) forest (Šobr and Janský 2016). According to published literature (Vrba et al. 2000; Soldán et al. 2012 and references therein), Prášilské Lake used to be a humic brown-water lake with more or less neutral pH before the onset of anthropogenic acidification. Heavy atmospheric pollution, resulting in acidification of the lake, occurred between 1950 and 1980 and the current pH is approximately 5.0–5.3 pH (Vrba et al. 2000; Soldán et al. 2012). The low water pH levels in this lake may explain the poor composition of the littoral vegetation, which consists of *Carex rostrata* and two species of *Sphagnum* (Soldán et al. 2012). Compared to other Bohemian Forest lakes, Prašilské Lake contains only moderate concentrations of dissolved aluminium (Kopáček et al. 1999). This may be the reason why two sensitive crustacean species (*Daphnia longispina* (O. F. Müller, 1776) and *Cyclops abyssorum* G. O. Sars, 1863) have survived in this lake to present, while they became extinct in all other sites (with exception of Großer Arbersee) during the peak of anthropogenic acidification and accompanied rise of ionic forms of aluminium (Kohout and Fott 2006; Kopáček et al. 2009). There is no documented evidence of any fish population in the lake since at least the mid-nineteenth century when the lake was first studied, and it has been speculated that the site is too difficult to reach by fish (Vrba et al. 2000). Prášilské Lake has been subject of long-term ecological studies on the recovery of acidified Bohemian Forest lakes (e.g. Fott et al. 1994; Ungermanová et al. 2014; Vrba et al. 2016).

Sediment record and age-depth modelling

In August 2015, a 2.19 m sediment profile (1480–1699 cm below lake water surface) was collected in three 1.5 m long overlapping cores (PRA15–1-2, PRA15–2-1 and PRA15–2-2) using a Russian peat corer of 0.075 × 1.5 m chamber and using a floating platform in the central part of the lake basin (49.0752925° N, 13.4000039° E). A gravity corer (Boyle 1995) was used to recover unconsolidated deposits including the sediment-water interface. The retrieved gravity core (PRA15-GC-2) was 0.43 m long and 0.1 m in diameter. For sedimentological interpretation and correlation of the cores, the whole profile including its overlapping parts was scanned with micro X-Ray Fluorescence (Olympus Delta Professional µXRF) and line-scan photographed at high-resolution (15 µm) under uniform lighting using the University of Liverpool Geotek Multi-Sensor Core Logger (MSCL). For obtaining chronological control, the cores were dated using Accelerator Mass Spectrometry (AMS) ^{14}C dating, ^{210}Pb and ^{137}Cs radioisotope dating, and a Bayesian age-depth modelling routine 'BACON' (see Carter et al. 2018a for additional details). The ages are reported in calibrated years before present (cal. yr. BP; calibration sensu Reimer et al. 2013), where 'present' refers to 1950 AD. In this study, we also present the rubidium (Rb) concentrations measured by µXRF, which is interpreted as a proxy record for detrital sediment supply recording changes in erosion and transport of allochthonous inorganic matter from the catchment to the lake.

Sediment subsampling and caddisfly analysis

The long cores from Prášilské Lake were used for a multi-proxy study (see Carter et al. 2018a, 2018b) and subsampled in 0.5 cm resolution, while core PRA15-GC-2 was subsampled in 1 cm resolution. During the subsampling, several thin (2–0.1 cm) grey and dark brown units containing various plant and animal macro-remains were identified. These erosional layers were targeted and the adjacent samples above and below were selected for analysis of the caddisfly remains. Finally, most of the samples from non-overlapping parts of the long cores and the gravity core were analysed. A total of 318 sediment samples with wet volume of 1.5–5 mL for the long cores and 5–20 mL for the gravity core were processed. The samples were sieved over 100 µm mesh size to retain all macro-fossils. Caddisfly larvae remains were picked using a stereoscopic microscope at 15x magnification, dehydrated in 90% ethanol, and mounted in Euparal to prepare permanent slides. To avoid an overestimation of individuals, we focused only on frontoclypeal apotomes. Frontoclypei were identified using a reference collection of Trichoptera larvae from Bohemian Forest lakes and streams, and the identification key by Waringer and Graf (2011). Conventional identification keys to caddisfly larvae are only partially useful since they use combination of many characters located on different parts of the body. Therefore, the direct comparison with recent identified larvae was essential. Where identification to species level was not possible, morphotypes were established for the frontoclypei. Ecological characteristics of the individual caddisfly species based on Wallace et al. (1990), Braukmann and Biss (2004), Graf et al. (2008), Schartau et al. (2008), and personal observations were used to derive ecological properties of the identified taxa. According to the latest agreements on the subdivision of the Holocene epoch (Walker et al. 2012) and sediment lithology, we divided our stratigraphic record into 4 zones - the Early Holocene (11,400–8300 cal. yr. BP), a multiple-erosion event (8300–7600 cal. yr. BP), the Middle Holocene (7600–4200 cal. yr. BP) and the Late Holocene (4200 cal. yr. BP – present). The multiple-erosion event represents a site-specific transitional unit covering the proposed Early–Middle Holocene Boundary at 8200 cal. yr. BP (Walker et al. 2012).

Results

Chronology and lithology

The age-depth model (Table 1, Fig. 2) dates the oldest sediments of Prášilské Lake to 11,400 cal. yr. BP. The whole profile consists of a brown organic gyttja, except for the basal 0.09 m of sandy sediment at the base of PRA15–2-2. In addition, the long cores were characterized by the presence of thin grey and dark brown units contrasting strongly with the lighter brown colour of the gyttja. Most of these unites contained increased concentrations of inorganic material and plant and insect macro-remains. Because of very low thickness (< 2 mm) of some units, we used the Rb curve to track these event laminations interpreted as erosion layers instead of their visual description (Figs. 2 and 3).

Thin erosional units (bands) occurred in an irregular interval at depths of 16.46, 16.38, 16.05, 15.94, 15.87, 15.79, 15.73, 15.39, and 15.03 m. Only two of them, 15.87 and 15.72, had a thickness over 0.01 m. Moreover, the largest band of bright brown/greyish erosional sediment was found between 16.215–16.355 m. It contained abundant macro-remains, only the uppermost 8 mm (16.215–16.223 cm) was clayey and poor in remnants (> 100 µm) of subfossil organisms. Radiocarbon dates below and above this distinctive 0.14 m thick unit show a relatively long deposition time from 8300 to 7600 cal. yr. BP. Besides increased inorganic content in the erosional units, the Rb curve demonstrates gradually decreasing values (from 60 to 10 ppm) during the transition from sandy to more organic sediment in the basal part of the profile and a peak (50 ppm) in the uppermost part of PRA15–2-2 (Figs. 2 and 3).

Trichoptera record

Altogether, 58 individuals from 10 taxa were found in the profile (Figs. 3 and 4). An overview of the species occurring in Prášilské Lake and its inflow streams during the last century (1918/1919–2015) along with the taxa identified from the lake sediment samples is summarized in Table 2. In some cases, trichopteran frontoclypei could not be identified to species level and were named

Table 1 Results of AMS radiocarbon dating

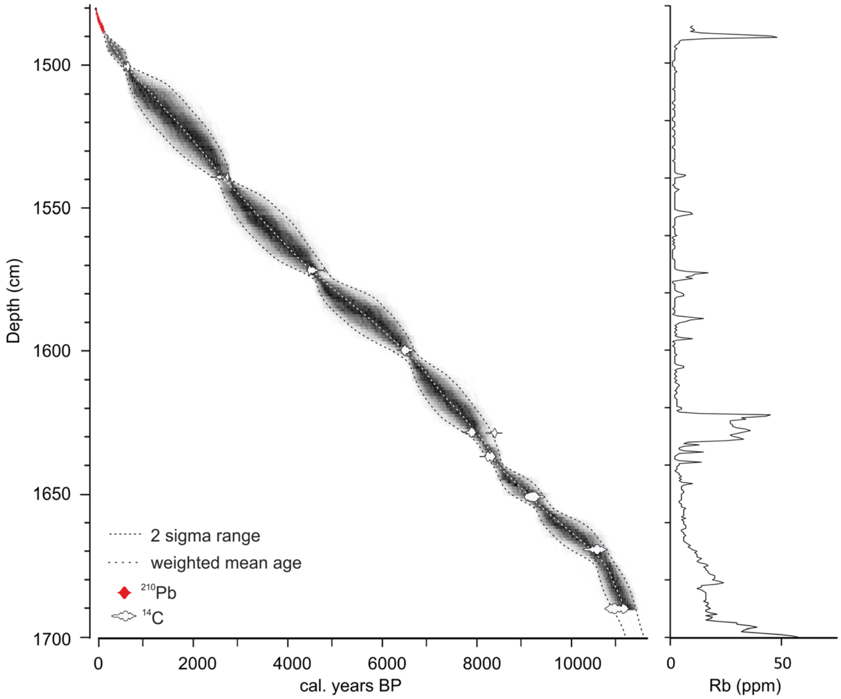
Depth (cm)	Core code	Laboratory code	^{14}C age (a BP)	Calibrated age (cal. a BP, 2σ range)	Mean calibrated age (cal. a BP)	Material dated
1500.5–1501	Pra-15-2-1	Poz-84783	590 ± 30	494–711	602	Bulk
1539–1539.5	Pra-15-2-1	Poz-81580	2,545 ± 30	2,422–2782	2,631	*Picea* needle
1628.5–1629	Pra-15-2-1	Poz-87722	7,055 ± 40	7,763–8317	8,009	*Picea* needle
1571.5–1572	Pra-15-2-2	Poz-81582	4,040 ± 35	4,223–4812	4,506	*Picea* needles
1599.5–1600	Pra-15-2-2	Poz-81583	5,700 ± 40	6,198–6677	6,469	*Picea* needle
1628.5–1629	Pra-15-2-2	Poz-80182	7,550 ± 40	7,763–8317	8,009	*Picea* needles
1637–1637.5	Pra-15-2-2	Poz-87724	7,460 ± 40[a]	8,209–8497	8,371	*Picea* needles
1651–1651.5	Pra-15-2-2	Poz-84781	8,210 ± 50	8,852–9449	9,191	*Picea* needle
1669.5–1670	Pra-15-2-2	Poz-81780	9,330 ± 60	10,027–10,749	10,441	*Picea* bud scales, *Betula* leaf and seed
1690–1690.5	Pra-15-2-2	Poz-80183	9,620 ± 60	10,877–11,367	11,147	*Picea* seed

[a] Date excluded by Bacon model

according to the taxa to which the remnants were likely to belong. Therefore, we established 4 morphotypes. Two distinct taxa of the genus *Limnephilus* were recognized – *L. rhombicus*-type (frontoclypeus pale with a dark brown longitudinal band broadened anteriorly) and *L. coenosus*-type (frontoclypeus uniformly dark brown without a pale area in the posterior angle). A phryganeid morphotype *Agrypnia – Phryganea* includes *Agrypnia* spp. and *Phryganea* spp., and a psychomyiid morphotype *Lype – Tinodes* could be represented by species with an almost concolorous frontoclypeus (e.g. *Lype phaeopa* and *Tinodes waeneri*) (Fig. 4). In addition, we documented presence of 6 species from 5 families: *Athripsodes aterrimus* (Leptoceridae), *Cyrnus trimaculatus* and *Holocentropus dubius* (Polycentropodidae), *Molanna nigra* (Molannidae), *Oligotricha striata* (Phryganeidae), and *Philopotamus ludificatus* (Philopotamidae).

Ecological evaluation of the caddisfly assemblages is presented in Table 3. Individual taxa include species widely distributed in lentic waters (*Agrypnia – Phryganea*, *Holocentropus dubius*, *Limnephilus coenosus*-type, *Molanna nigra*, *Oligotricha striata*), as well as in both lentic and lotic waters (*Athripsodes aterrimus*, *Cyrnus trimaculatus*, *Limnephilus rhombicus*-type, and *Lype – Tinodes*). Only *Philopotamus ludificatus* is a characteristic inhabitant of streams. Among these taxa, almost all basic functional-feeding groups are represented, although passive filter feeders, shredders, and predators are predominant. Most of the

Fig. 2 Bayesian age-depth model and rubidium (Rb) concentrations for Prášilské Lake sediment profile (core drives PRA15-GC-2, PRA15–1-2, PRA15–2-1, and PRA15–2-2)



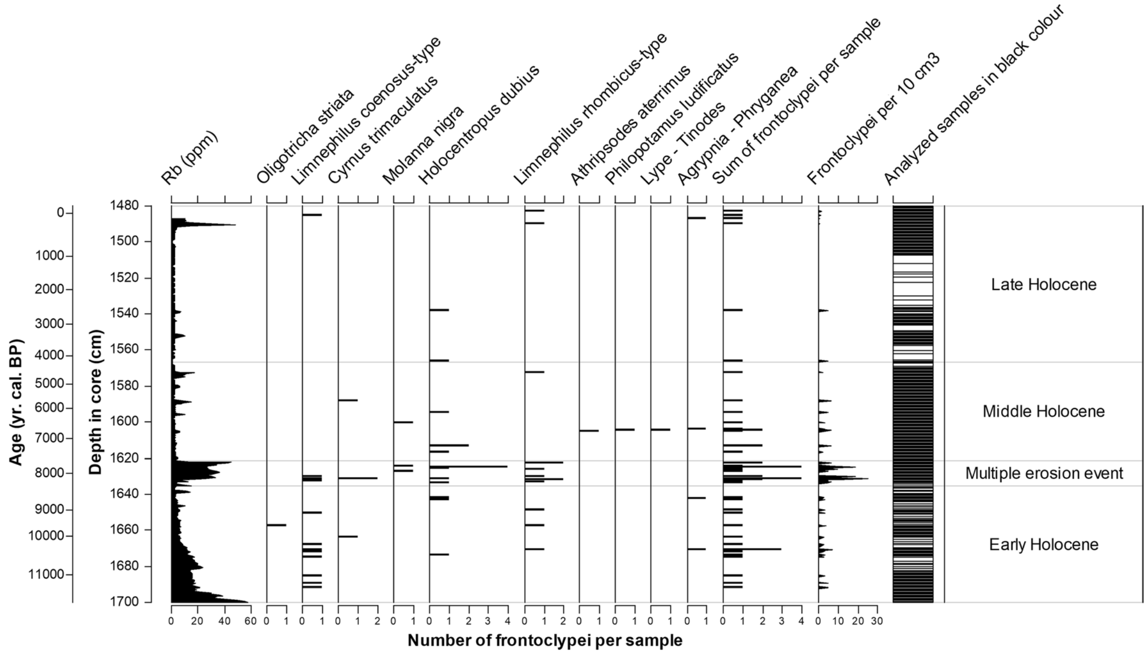


Fig. 3 Changes in caddisfly assemblages in Prášilské Lake through time. The core runs from the top of the sediment at 1480 cm water depth to the sandy substrate at 1699 cm. Increases in rubidium (Rb) demonstrate periods of erosional activity in the lake catchment. The four zones were added according to the division of the Holocene epoch (Walker et al. 2012), with an additional zone represented by a multiple erosion event between the depth of 1634.5 cm and 1621.5 cm (8300–7600 cal. yr. BP)

documented taxa use a wide range of food items. Similarly, the substrate preferences are diverse, ranging from species which preferably occur in fine mud or sand to species which depend on stable substrates like stones and water

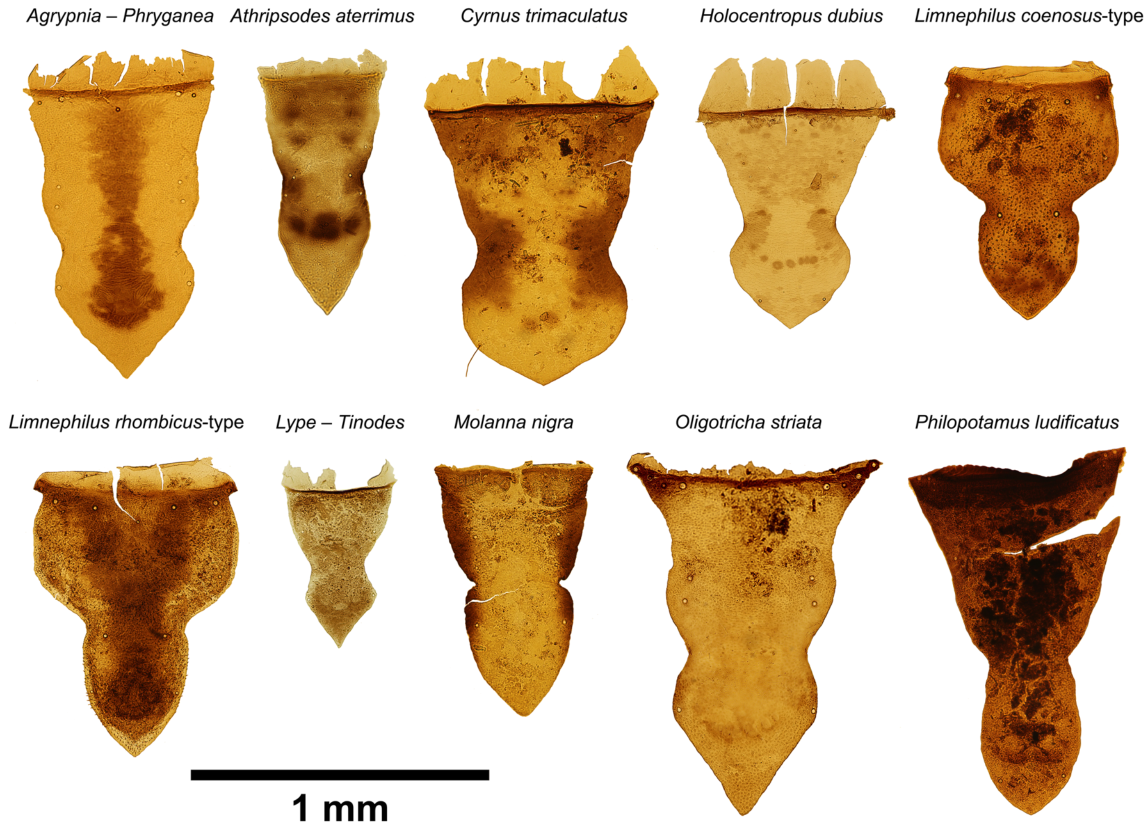


Fig. 4 Frontoclypeal apotomes of all caddisfly taxa found in this study

Table 2 Occurrences of caddisfly larvae (+) documented in Prášilské Lake during the Early Holocene (11,400–8300 cal. yr. BP), the multiple erosion event (MEE, 8300–7600 cal. yr. BP), the Middle Holocene (7600–4200 cal. yr. BP), and the Late Holocene (4200 cal. yr. BP – recent)

	Early Holocene (11,400 cal. yr. BP – MEE)	Multiple erosion event	Middle Holocene (MEE – 4,200 cal. yr. BP)	Late Holocene (4,200 cal. yr. BP – recent)	1918/1919–2015 – lake (modern monitoring)	1918/1919–2015 – inflows (modern monitoring)
Family: **Rhyacophilidae**						
Phyacophila glareosa McLachlan, 1867						+
Rhyacophila praemorsa McLachlan, 1879						+
Family: **Philopotamidae**						
Philopotamus ludificatus McLachlan, 1878			+			+
Family: **Polycentropodidae**						
Cyrnus trimaculatus (Curtis, 1834)	+	+	+			
Holocentropus dubius (Rambur, 1842)	+	+	+	+	+[a]	
Plectrocnemia conspersa (Curtis, 1834)					+	+
Plectrocnemia geniculata McLachlan, 1871						+
Family: **Psychomyiidae**						
Lype – Tinodes			+			
Family: **Phryganeidae**						
Agrypnia varia (Fabricius, 1793)					+	
Agrypnia – Phryganea	+		+	+		
Oligotricha striata (Linnaeus, 1758)	+				+	
Phryganea bipunctata Retzius, 1783					+	
Family: **Apataniidae**						
Apatania fimbriata (Pictet, 1834)						+
Family: **Limnephilidae**						
Drusus annulatus (Stephens, 1837)						+
Drusus discolor (Rambur, 1842)						+
Limnephilus centralis Curtis, 1834					+	
Limnephilus coenosus Curtis, 1834					+[a]	
Limnephilus coenosus-type	+	+	+	+		
Limnephilus lunatus Curtis, 1834					+	
Limnephilus rhombicus (Linnaeus, 1758)					+	
Limnephilus rhombicus-type	+	+	+	+		
Chaetopteryx villosa (Fabricius, 1798)					+	+
Pseudopsilopteryx zimmeri (McLachlan, 1876)						+
Psilopteryx psorosa bohemosaxonica Mey et Botosaneanu, 1985						+
Parachiona picicornis (Pictet, 1834)						+
Family: **Molannidae**						
Molanna nigra (Zetterstedt, 1840)		+	+		+	
Family: **Leptoceridae**						
Athripsodes aterrimus (Stephens, 1836)			+			

Modern data (1918/1919–2015) were compiled by Soldán et al. (2012) and supplemented by 2 additional species ([a]) observed by J. Petruželová (pers. comm.)

Table 3 Caddisfly taxa and morpho-taxa documented in the sediment record from Prášilské Lake and their feeding strategies and habitat, substrate and pH preferences. For the morpho-taxa which most likely belong to a particular species ([a]), we present ecological characteristics of a such species

Taxon	Functional feeding group	Habitat	Substrate	Sensitivity to acid water	References
Agrypnia – Phryganea	gat, pre, shr	L	alg, mph, pel, pom, woo	–	Graf et al. (2008)
Athripsodes aterrimus (Stephens, 1836)	gat, pre, shr	L, S	mph, pel, psa	IN	Fjellheim and Raddum (1990); Graf et al. (2008); Schartau et al. (2008)
Cyrnus trimaculatus (Curtis, 1834)	pff, pre	L, S	mal, mil, mph	IN	Fjellheim and Raddum (1990); Graf et al. (2008)
Holocentropus dubius (Rambur, 1842)	pff, pre	L	mph	IN	Fjellheim and Raddum (1990); Graf et al. (2008); Schartau et al. (2008)
[a]*Limnephilus coenosus* Curtis, 1834	gra, pre, shr	L	pel, mph, pom, psa	AR	Zamora-Muñoz and Svensson (1996); Krno et al. (2006); Graf et al. (2008)
[a]*Limnephilus rhombicus* (Linnaeus, 1758)	gra, pre, shr	L, S	pel, mph, pom, psa	AR	Fjellheim and Raddum (1990); Braukmann and Biss (2004); Graf et al. (2008)
[a]*Lype phaeopa* (Stephens, 1836)	gra, xyl	L, S	woo	AS?	Graf et al. (2008)
Molanna nigra (Zetterstedt, 1840)	gat, pre	L	pel, psa	IN?	Graf et al. (2008); Soldán et al. (2012)
Oligotricha striata (Linnaeus, 1758)	gat, pre, shr	L	mal, mph, pel, pom, psa	AT	Wallace et al. (1990); Braukmann and Biss (2004); Graf et al. (2008)
Philopotamus ludificatus McLachlan, 1878	pff	S	mal, mil	AS	Braukmann and Biss (2004); Graf et al. (2008)
[a]*Tinodes waeneri* (Linnaeus, 1758)	gat, gra, pff, pre	L, S	mal, mil	IN	Fjellheim and Raddum (1990); Graf et al. (2008); Ings et al. (2017)

Functional feeding groups: gat – gatherer/collector, gra – grazer and scraper, pff – passive filter feeder, pre – predator, shr – shredder, xyl – xylophage

Substrate preference: alg – algae, mal – stones and bedrock, mil – coarse gravel (2–20 cm), mph – macrophytes and mosses, pel – mud, pom – coarse and fine particulate organic matter, psa – sand, woo – woody debris. Habitat: L – lake (littoral and/or sublittoral zone), S – stream

Sensitivity to acidification: AR – acid resistant (pH < 5.5), AS – moderately acid sensitive (pH around 6.5–7.0), AT – acid tolerant (pH 6.5–5.5 and sometimes bellow), IN – indifferent (occurrence across wide range of pH including values < 5.5)

macrophytes. On the other hand, a categorization to pH sensitivity groups is more uniform showing presence of acid-resistant, acid-tolerant, and pH indifferent caddisflies. The only exception is the single finding of pH sensitive *Philopotamus ludificatus*, an inhabitant of non-acidified streams (the specimen probably originates from any of the lake inflow streams).

To evaluate changes in caddisfly species composition in time, 4 zones based on the climatological subdivision of the Holocene and sediment lithology were established (Fig. 3). The first zone (1699–1631 cm; 11,400–8300 cal. yr. BP; Early Holocene) covers the development of the lake shortly after its formation and initially contains remains of *Limnephilus coenosus*-type after which *Holocentropus dubius*, *Limnephilus rhombicus*-type, *Agrypnia – Phryganea*, *Cyrnus trimaculatus*, and *Oligotricha striata* occurred. The second zone (1634.5–1621.5 cm; 8300–7600 cal. yr. BP; multiple erosion event) covers the large erosion band accompanied by peaks in Rb concentration. This zone contains the highest numbers and volumetric abundances of Trichoptera remains (up to 27 frontoclypei per 10 cm^3). The assemblage consists of relatively abundant *Limnephilus rhombicus*-type and *Holocentropus dubius*, and less abundant *Cyrnus trimaculatus*, *Limnephilus coenosus*-type, and *Molanna nigra.* In the third zone (1621.5–1567 cm; 7600–4200 cal. yr. BP; Middle Holocene), we found frontoclypeal apotomes of *Holocentropus dubius*, and single evidence of *Athripsodes aterrimus*, *Agrypnia – Phryganea*, *Cyrnus trimaculatus, Limnephilus rhombicus*-type, *Molanna nigra*, *Philopotamus ludificatus*, and *Lype – Tinodes*. The last zone (1567–1480 cm; 4200 cal. yr. BP – present; Late Holocene) is characterized by a very low volumetric abundance of caddisfly remains (0–5 frontoclypei per 10 cm^3). Only two specimens of *Holocentropus dubius* were documented between the depths 1621.5 cm and 1483.5 cm. The top part of this zone (1483.5–1480 cm; 1960–2015 AD) contains *Agrypnia – Phryganea*, *Limnephilus coenosus*-type, and *Limnephilus rhombicus-type*. The most abundant taxa in the whole profile were *Holocentropus dubius* (31%), *Limnephilus coenosus*-type (24%), and *L. rhombicus*-type (24%). The remaining taxa were less represented (<7%) (Fig. 3).

Discussion

The subfossil Trichoptera larvae assemblages from Prášilské Lake include most of the species which were found in the lake during the irregular environmental monitoring since 1918/1919 (Soldán et al. 2012 and references therein; see Table 2). Only *Chaetopteryx villosa* and *Plectrocnemia conspersa*, common species in streams, rivers and small upland lakes (Wallace et al. 1990; Andersen and Tysse 2008), currently inhabiting all Bohemian Forest lakes and/or their inflow streams (Soldán et al. 2012), were not found in our samples. We also have not found any evidence of *Limnephilus centralis* and *Limnephilus lunatus*, two species recorded in the first half of the twentieth century (Šámal 1920; Novák 1996). Both morphotypes of the genus *Limnephilus* presented in this study, *L. coenosus*-type and *L. rhombicus*-type, may include more species with the same frontoclypeal colour pattern because the identification of living larvae to species level is based on a combination of different morphological characters including characters on soft body parts (Waringer and Graf 2011). However, since the species *L. rhombicus* and *L. coenosus* are much more common in the Bohemian Forest lakes (Soldán et al. 2012), it is highly likely that the remains identified as *L. rhombicus*-type and *L. coenosus*-type, respectively, correspond with these two species. Similarly, *Agrypnia varia* and *Phryganea bipunctata* were not found with certainty, but we assume that these species are included within the *Agrypnia – Phryganea* morphotype. Nevertheless, for these identifications, it has to be taken into regard that they might concern species which are rare or absent in the recent Bohemian Forest lakes. On the other hand, several taxa, which were not reported from Prášilské Lake at present, were found in the sedimentary archive – *Athripsodes aterrimus, Cyrnus trimaculatus*, *Lype – Tinodes* morphotype, and *Philopotamus ludificatus*. In the latter case, however, it is worth mentioning that the species is known from the lake inflow streams. It cannot be ruled out that in the past a small portion of the caddisfly remains could be transported from these inflow streams to the lake and deposited in the sediments. Nevertheless, the majority of frontoclypeal sclerites cannot have been transported far from the larval habitat. We assume this because of low discharge of the recent inflows and very small proportion of stream Diptera remains found in the same sediment samples (D. Vondrák, unpublished data). The caddisfly stratigraphic record (Fig. 3) should not be interpreted to represent complete species composition or precise concentration of individuals through time. Due to the low number of remains/individuals in the lake sediment we are not able to assess detailed changes in volumetric or relative abundances. Our results are of a qualitative nature. Therefore, we focus on interpreting the ecological preferences of the individual indicator species.

Ecological characteristics of individual species found in the sediment record are summarized in Table 3. *Holocentropus dubius*, a polycentropodid species and the most dominant taxon in our sediment samples, generally occurs in the littoral zone with macrovegetation (Graf et al. 2008) and is also known from dystrophic (peaty) mountain lakes (Chvojka 1992). Despite its frequent occurrence in Prášilské Lake in the past, it has not been recorded there during the recent monitoring (1918/1919–2015) until its first observation in 2007 (J. Petruželová, pers. comm). In the Bohemian Forest lakes, stable populations of *H. dubius* are only known from Laka Lake and Großer Arbersee (Soldán et al. 2012; Ungermanová et al. 2014), two sites with well-developed littoral macrovegetation (Fig. 1). The other dominant taxa (<20%) in the sedimentary record are the two morphotypes of genus *Limnephilus* – *L. coenosus*-type and *L. rhombicus*-type. *L. rhombicus* is a eurytopic species known from a variety of standing and slow-flowing waters including acidic peaty waters (Wallace et al. 1990). It is widely distributed in the Bohemian Forest (K. Novák, unpublished data) and it was recorded from all glacial lakes with the exception of Rachelsee (Soldán et al. 2012). *L. coenosus* is a common species in pools on peat bogs (Waringer and Graf 2011) and in small, strongly acidified lakes (Krno et al. 2006). It is also well established in the Bohemian Forest, above all in peat bogs (Novák 1996). The phryganeid taxon *Agrypnia – Phryganea* could include not only *Agrypnia varia* and *Phryganea bipunctata*, but also *A. obsoleta* (McLachlan, 1865) and *P. grandis* Linnaeus, 1758 since all species are known from the glacial lakes in this area (Novák 1996; Soldán et al. 2012). *Agrypnia varia* and *P. bipunctata* occupy the same ecological niche – littoral zone with macrophytes. *Oligotricha striata* is a common species in pools, especially with acidic peaty water (Wallace 1991). This species is known from all present Bohemian Forest lakes, except of Černé and Čertovo lakes (Fig. 1), and also from peatbog pools in the region (Novák 1996; Soldán et al. 2012). The larvae of *Molanna nigra* prefer a psammopelal habitat (sand or clay) of mid-montane and lowland lakes (Graf et al. 2008). *Molanna nigra* is a species with boreomontane distribution and is known from northern Europe (Graf et al. 2008) and also from Siberia (Ivanov 2011). In central Europe, it has isolated populations in the Bohemian Forest glacial lakes at altitudes up to 1079 m (recently known only from Prášilské Lake, Čertovo Lake, and Großer Arbersee; Fig. 1) (Soldán et al. 2012). Our records show the species to be present in Prášilské Lake since at least 8000 cal. yr. BP, i.e. around the complex multiple erosion episode. *Cyrnus trimaculatus* is a widely distributed species in flowing as well as in stagnant waters with macrophytes and stony substrate (Graf et al. 2008). It was recorded in historical records from Černé Lake and Großer Arbersee (Klapálek 1903), but more recent records are missing. Larvae of *Philopotamus ludificatus* prefer the epirhithral zone of mountain and submountain streams (Graf et al. 2008). The species is also known from streams in the Bohemian Forest including inflow streams of Prášilské Lake and Laka Lake (Novák 1996; Soldán et al. 2012). *Athripsodes aterrimus* occurs in lakes and pools as well as slow flowing rivers among water plants and on psammopelal habitats (Wallace et al. 1990; Graf et al. 2008). This widely distributed European species occurs also in small pools in the Bohemian Forest at altitudes of ca. 1000 m a.s.l. (P. Chvojka, unpublished data), but it was not found in any of the glacial lakes recently (Soldán et al. 2012). The *Lype – Tinodes* morphotype includes species with an almost concolorous frontoclypeus, e.g. *L. phaeopa* and *T. waeneri*. Both species occur in stagnant and slow flowing waters primarily in lower altitudes. Larvae of *L. phaeopa* live on logs and woody debris while *T. waeneri* prefers stony substrata (Graf et al. 2008). None of the species of Psychomyiidae were recorded from the Bohemian Forest lakes during recent investigations (Soldán et al. 2012), only *L. phaeopa* was found in Großer Arbersee in historical records (Klapálek 1903).

As pH fluctuates annually, seasonally and even daily, the occurring caddisflies are good indicators of the longer-term acidity status of water bodies (Graf et al. 2008). Most of the taxa we identified occur in waters with low pH – only *Philopotamus ludificatus* is moderately sensitive to acidic conditions (Braukmann and Biss 2004; Schartau et al. 2008) – and display a wide range of feeding strategies (Table 3). Some of the species are eurytopic and/or their substrate preferences are ambiguous. In addition, the littoral zone of Prášilské Lake at present is a diverse mosaic of microhabitats and has probably taken this similar form since formation of the lake. Therefore, it is not possible to reconstruct the pattern of changes in the littoral zone substrate through time from our limited caddisfly record. Nevertheless, all dominant taxa found in the sediment core (*Holocentropus dubius*, *Limnephilus* spp., *Agrypnia – Phryganea*) inhabit dystrophic water bodies with *Sphagnum* spp. (Graf et al. 2008).

The Early-Holocene caddisfly assemblages (Fig. 3) indicate that the littoral zone of Prášilské lake was partially overgrown by aquatic vegetation (including *Sphagnum* spp.), in combination with muddy and/or sandy substrate. A very similar modern Trichoptera taxocoenoses were found in Laka Lake and Großer Arbersee in this region (Soldán et al. 2012), and at Nižné Rakytovské Lake, a small, dystrophic montane lake (1320 m a.s.l.) further afield in the High Tatra Mts. (Chvojka 1992). Changes between organic and minerogenic sedimentary units usually reflect the alternating stability of catchment hillslopes. During the second phase of the lake evolution (Fig. 3), a series of erosion events occurred between 8300 and 7600 cal. yr. BP. This increased transport of allochthonous material documented by the sharp rise in Rb content, may also be reflected in a removal of water insect remains from the shallow to deeper parts of the lake basin. As a result, the highest concentration of frontoclypeal sclerites was recorded in this stratigraphic zone. *Molanna nigra* indicate the presence of muddy and sandy substrate but a distinct peak of phytophilous taxa (*H. dubius*, *L. coenosus*-type, *L. rhombicus*-type) suggest a high amount of available plant debris during the same period. This combination of substrates is also in agreement with the ecology of *Cyrnus trimaculatus* (Table 3). The timing of this zone roughly coincides with the establishment of Norway spruce as the most dominant forest canopy taxa in the lake catchment (Carter et al. 2018a), highest biomass burning (Carter et al. 2018b), and the so-called 8.2 ka cooling event (e.g. Tinner and Lotter 2001). However, the series of erosion events in our record lasted around 600 years, while global environmental responses to this climatic event are thought to have lasted no longer than 160 years (Thomas et al. 2007), thus these erosion events cannot be readily linked to the 8.2 ka cooling. In the Middle Holocene, the Trichoptera assemblages were more diverse (8 taxa recorded) and suggest a continuous presence of a more varied littoral zone consisting of macrophytes, mud, sand or gravel. During the Late Holocene, the caddisfly remains were almost absent in the profile implying less favourable conditions for the larvae. The sporadic presence of only one species, *Holocentropus dubius*, was documented until the twentieth century when *Agrypnia – Phryganea* and both *Limnephilus* morphotypes reappeared again in the record. A low population density could be the cause that the remains did not reach the coring site in the central part of the lake basin in detectable concentrations. However, the period of caddisfly decline begun at the end of the Middle Holocene and approximately coincides with a local European beech (*Fagus sylvatica*) expansion into the Norway spruce dominated forest and a dramatic decrease in biomass burning circa 6500–500 cal. yr. BP (Carter et al. 2018b). Related changes in leaf litter characteristics (Albers et al. 2004) might have supported near-bottom oxygen depletion. Unfortunately, this lack of subfossil remains therefore does not allow the reconstruction of the pre-acidification trichopteran fauna. It can only be assumed that *H. dubius* was likely to be represented as one of the dominant species. The small increase in number of species and volumetric abundance in the sediment record during the last century (the uppermost part of the Late Holocene zone; Fig. 3) is probably not related to atmospheric acidification and can be explained by other factors. Historical records show that strong gales during the period 1868–1870 and subsequent active logging destroyed large parts of the forest and increased erosion in the immediate vicinity of Prášilské Lake (Čada et al. 2016). Moreover, the single outflow of the lake was dammed in 1883, raising the lake water level by 2.5 m (Švambera 1914). Both events could have changed the representation of bottom substrate types, oxygen concentration near the bottom or certain hydrological conditions (e.g. water residence time, mixing regime). The pioneer investigations by Šámal (1920) and Novák (1996) document presence of *C. villosa*, *M. nigra*, *O. striata* and members of genus *Limnephilus* between 1910s and 1950s. For the same period, we found an evidence of *Agrypnia – Phryganea* and both *Limnephilus* morphotypes. This is practically the same assemblage as recorded later in the recovering lake (Soldán et al. 2012).

The subfossil Trichoptera assemblages suggest that Prášilské Lake has been a dystrophic, moderately acid lake from its early development and throughout the Holocene. The species composition shows many similarities to the modern-day ones of Laka and Großer Arbersee lakes (see Soldán et al. 2012). Therefore, the process of natural acidification affected lake water chemistry shortly after the lake formation near the Younger Dryas – Holocene boundary. This is consistent with the timing of Early Holocene lake acidification observed at Kråkenes Lake in Norway (Solem and Birks 2000; Boyle et al. 2013). In the case of Prášilské Lake, however, we are not able to confirm significantly different Late-glacial assemblages. An unexpected absence of a Late-glacial sedimentary record at the study site was confirmed by repeated drilling. This suggests that the onset of lacustrine sedimentation in Prášilské Lake is younger than in other Bohemian Forest lakes. Namely for Černé Lake (Michler 2001), Großer Arbersee (Michler 2000), Plešné Lake (Pražáková et al. 2006), Rachelsee (Carter et al. 2018a) and two former lakes (Vočadlová et al. 2015; Kletetschka et al. 2018) the presence of several meters thick Late-glacial sediments is well documented. This asynchrony between timing of local deglaciation (Mentlík et al. 2013) and sedimentation onset in Prášilské Lake may result from a lag time necessary to seal a permeable moraine. Nevertheless, the anticipated Early Holocene onset of natural acidification is supported by evidence from a closely located site, Plešné Lake (Fig. 1), presented by Pražáková et al. (2006) and Kopáček et al. (2009). Their results imply a forest soil development and a subsequent rise in soil organic acids' input to the lake water following the Holocene climatic warming. Both processes are interpreted as key factors leading to dissolved (organically-bound) aluminium increase, pH decrease, oligotrophication, and change in zooplankton species composition. Therefore, we assume that the Early Holocene climatic shift and subsequent changes in vegetation cover triggered natural acidification in the Bohemian Forest region. A future investigation of Late-glacial and Early Holocene sedimentary records might provide further insights into natural acidification history of central European mountain ranges with metamorphic and crystalline bedrock.

Conclusions

Here we present, to our knowledge, the first continuous post-glacial records of subfossil caddisfly succession in a mountain lake in central Europe. The results demonstrate signs of natural acidity in the Bohemian Forest region since the Late Pleistocene-Holocene transition. The Prášilské Lake record is characterized by resident caddisfly fauna dominated by species tolerant to low pH (*Holocentropus dubius, Limnephilus coenosus*, *L. rhombicus*). Based on our results and the scarce observations from the first half of the twentieth century, we conclude that no evidence of a dramatic change in original caddisfly taxocoenoses as a result of the strong anthropogenic acidification was found. The suggested naturally acidic state of the humic lake ameliorated the negative effect of changes in water chemistry on macrozoobenthos community. Our results can be used as a baseline for assessment of biological recovery level of the study lake in future conservation policies and management. Sediments of glacial lakes represent crucial natural archives of local post-glacial environmental history that should be intensively studied. Despite its potential, caddisflies have received less attention from Quaternary palaeoecologists than many other microfossil groups. Our study underlines the importance of caddisfly remains as one of the valuable biological proxies in palaeolimnological research.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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4. Discussion

The results from this thesis have profoundly increased the number of fossil insect records in central Europe (section 4.1), to some extend filling a data gap in fossil insect records in central Europe (Elias, 2006; 2010). Analysis of the current published data on fossil conifer bark beetle records in the Northern Hemisphere (Chapter 3.2.1; article II) shows that the sparsity of fossil bark beetle data most likely results from different aims of focus of previous fossil studies, but also suggests that these data have been collected by a limited number of researchers, each with their preferred geographical region of study. Fossil insect records from Šumava in the Czech Republic and the High Tatra Mountains in Slovakia contribute to our knowledge of past Coleoptera and Trichoptera communities in montane regions of Central Europe and enhanced our knowledge of past conifer bark beetle communities. The record from Diera Hollow in the High Tatra Mountains (chapter 3.1.1, article I) reveals important details about the ecological succession and development of the local site and surrounding area. The results show that mixed beech-fir-spruce forest existed at elevations up to 1000 meters, and are contradictory to common knowledge about this region which states that beech (*Fagus*) did not occur in this part of the Tatra Mountains during the last 3000 years (Rybníčková and Rybníček, 2006). Furthermore, the changes in the fossil beetle record through time show how the floral and faunal communities at the foothills of the High Tatra Mountains were influenced by anthropogenic activities since the Middle Ages (AD 1250) which is much earlier than is recorded from historical records (Gladkiewicz and Homza, 2003). The results of this study give insight in how early historical anthropogenic pressure influenced local faunal communities, with the appearance of taxa living on dung and in open landscapes and ultimately decreasing the biodiversity of the forest beetle community. Diera Hollow is the first site in central Europe from which abundant conifer bark beetle fossils are published (chapter 3.2.2, article III) and correlations between increases in bark beetle remains and other proxies of disturbance, like charcoal, give important insights in how bark beetle outbreaks are a part of forest dynamics, at present and in the past. Finally, a study on insect remains from a 2.2 m long sediment record from Prašilske Lake in Šumava (chapter 3.3.1; Article IV), shows that information about the development of the physical properties such as acidity of the lake, from the onset of the Holocene until present, could be retrieved despite the low number of insect fossils. As the novel results from these two sites in central Europe reveal detailed environmental reconstructions which are useful to the wider research community, expanding the number of studies on fossil insect assemblages in this region is recommended. The most important findings of this thesis are discussed in more detail below.

4.1 An expansion of fossil insect records in central Europe

The data review on sites with conifer bark beetles, conducted for this thesis (Chapter 3.2.1; article II) highlights that existing sites with fossil bark beetle remains are concentrated in western Europe and the western United States, and in general contain only few individual bark beetle fossils. Reasons for the geographical inequality in site location are debatable (e.g. lack of suitable sites in certain regions, different research focus), however it is noticeable that many paleoentomological studies were executed not far from the institutions of the expert Quaternary entomologists. For instance, the sites described in Elias (1985) are located in the Front Range near Boulder University, Colorado, where Scott Elias was based). Quaternary entomology remains a popular study in the United Kingdom but is maintained by a limited number of people (e.g. Mansell et al., 2014; Buckland et al., 2018) and did not expand further into Europe as was initially the case (e.g. Lemdahl, 1991; Coope et al., 1998). After the initial peak in research on fossil beetle remains in the 1980's and 1990's, Quaternary entomology is now considered by many to be an 'old' tool in paleo-reconstructions (Elias, 2010) and not as well established in paleo-research as palynology due to the limited distribution and abundance of existing records. The time and dedication needed to develop identification skills required for paleoentomological studies must be an important reason for this; paleoentomology is a specialty on its own. Nevertheless, efforts to spark interest in Quaternary entomology continue and are currently supported by databases which provide access to all published fossil insect records (Buckland and Buckland, 2006; Kuzmina, 2014; Williams et al., 2018). With the new studies presented in this thesis, the number of sites with fossil beetle remains in central Europe has increased considerably. Previously, only one site from the Czech Republic was published (Sálková et al., 2015), and no sites with fossil insect assemblages from Slovakia were published. The few existing sites with fossil insect records appear to have focused on either Late Glacial climate (e.g. Lemdahl, 1991) or archeology (e.g. Sálková et al., 2015). Currently, research focus in paleoecology is concentrated on reconstructing past environments in order to create ecological baselines to compare with changes in our present-day natural environment. It is widely advocated by paleoecologists to use paleoecology to support research on ecological baselines, ecological thresholds and conservation biology (Willis and Birks, 2006; Froyd and Willis, 2008; Lindbladh et al., 2013). By increasing the number of paleoecological studies in central Europe, opportunities for fossil beetle reconstructions to be included in local studies would further increase. The influence of changing environmental conditions under climate change, can be better understood by reconstructing changes in forest beetle communities and in particular bark beetles and other saproxylic beetles (Lindbladh et al., 2013). The results from this thesis refute the assumption that bark beetle fossils are practically absent in lake sediments (Morris et al., 2015). Lake sediments from Šumava in the Czech Republic (Laka Lake, Kuosmanen et al., 2020; Prašilske Lake, unpublished data) contained remains of bark beetles throughout the record, however only in low amounts. The study on fossil insect remains from Diera Hollow in the High Tatra Mountains in Slovakia increased our knowledge on the role of natural disturbances, and the influence of anthropogenic disturbances, in Norway spruce mountain forest (article I and III, section 4.2). Results from Trichoptera remains from Prašilské Lake also revealed new information which contradicts assumptions about long-term acidification of the glacial lakes in this region (article IV, section 4.3).

4.2 Long term environmental changes reconstructed from insects

Although Prašilské Lake provided a long sediment record, covering the complete Holocene epoch, fossil insect remains were concentrated only in the few organic bands in the sediments, which resulted in a low abundance of fossil insect remains (Schafstall, unpublished data). Lakes have proven to be less appropriate localities for finding large quantities of insect macro remains (Elias., 2010), although there are examples where smaller lakes with extremely organic sediments yielded enough insect remains for a detailed long-term environmental reconstruction (e.g. Ponel et al., 2011). In the published studies on terrestrial insect remains from lake sediments, the sampled layers of organic material were larger and provided a ‘snapshot’ of the insect community during a certain time period (e.g. Ashworth and Brophy, 1972; Lemdahl, 2000). Elias describes in Advances in Quaternary Entomology (2010) how parts of the lake shore where sediment gathers, such as the inlet or outflow of lakes, would be preferred locations to core for macro remains of terrestrial insects. Most other paleoecological proxies like pollen and chironomids are however best collected from the center of a lake (Aaby and Digerfeldt, 1986; Elias, 2010), so that terrestrial insect remains often have to be collected from a separate core. Long-term environmental records from peat archives are more common and produced detailed descriptions of changes in beetle communities during the Holocene (e.g. Whitehouse, 2004; Olsson and Lemdahl, 2010). Other studies have combined the results from shorter sections from various sites, to reconstruct long term changes in a wider area. Such studies could capture in high detail changing climate during the Late Glacial (Coope et al., 1998) as well as changes in the landscape during the Holocene (e.g. Whitehouse and Smith, 2010).

Trichoptera larval remains from Prašilské Lake provided a low-resolution environmental reconstruction of the lake (chapter 3.3.1; Article IV). Here it was demonstrated that the chemical properties of the lake remained largely unchanged throughout the Holocene and that current acidic conditions of Prašilské Lake were not primarily caused by acidification during the last century, as they were assumed previously (Vrba et al., 2016; Stuchlík et al., 2017). However, not much more information could be gained from this sparse macrofossil record, even though previous studies reveal much more detailed reconstructions based on fossil Trichoptera remains (Birks et al., 2000; Howard et al., 2009). Nevertheless, reconstructions of past environmental changes on a longer time scale can often be improved with data based on fossil insect remains. In the case of limited insect remains, the best practice is to combine one or more insect groups with as many other fossil types as possible (e.g. Birks et al., 2000; Sher et al., 2005).

4.3 Natural and anthropogenic disturbances

The mountain spruce forest surrounding Diera Hollow has been influenced by various natural and anthropogenic disturbances, many of which could be reconstructed from the fossil beetle records (chapters 3.1.1 and 3.2.2: Articles I & III). In these studies, established methodology such as the flotation technique to isolate beetle remains from organic sediments (Kenward, 1974; Elias, 2010) was used, but also some less conventional methods such as the large amount of sediment retrieved from 12 parallel cores to provide enough beetle remains for a detailed reconstruction. However, efforts were made to confidently correlate these sediment cores and this was achieved by wiggle-matching the geochemical signals obtained from micro-XRF scans (Croudace et al., 2006). This is a method common in paleolimnology and has occasionally been used in studies on peat bogs (Longman et al., 2019), but to our knowledge never to correlate such a great number of cores. As this method proved successful, it should be highlighted as an alternative methodology to take bulk sediment from protected peat bogs instead of digging trenches (e.g. Forbes et al., 2019). Correlated by their geochemical signal, a temporal resolution of 50 – 100 years could be confidently established for the fossil beetle samples. Consequently, the beetle record could be correlated in higher resolution to a pollen record from the same site. In general, a beetle community responds to changes in vegetation composition around the site and suggests that fossil beetle records can be used to confirm presence of plant taxa based on their ecological preferences (e.g. Olsson and Lemdahl, 2010; Ponel et al., 2011). But most important, long-term and abrupt changes recorded in the beetle community can be connected to the changes in the vegetation surrounding the sampling site.

Some controversy remains about whether the beetle record and the pollen record have the same source area, mainly because of the appearance of plant taxa in the pollen record which are considered extraneous. Although it is acknowledged that the source area of pollen in small forest hollows is less than 100 meters from the sample site (Overballe-Petersen and Bradshaw, 2011), the source area would likely increase if the surrounding forest became less dense (Sugita, 2007). The presence of (low amounts of) pollen from agricultural crops in the pollen record is an indication of increasing landscape openness as agricultural activities likely took place at some distance from the site (Article I). The source area for beetle remains the same under variable canopy cover, and only beetles carried by water inflows might originate from further than 400 m from the sample site (Elias, 2010). A second taxon considered to be extraneous is *Fagus*, as the occurrence of this tree was not historically recorded at higher elevations in this region (Rybníčková and Rybníček, 2006). However, *Fagus* pollen were present in high numbers before the influx of agricultural pollen and the presence of the leaf-mining weevil *Orchestes fagi*, almost exclusively living on beech, supports the past presence of beech trees in the direct vicinity of Diera Hollow.

Spruce-beech-fir forest was present around the sample site from at least AD 590, which transgressed into forest dominated by spruce and pine from AD 1200. It is likely that these changes were at least partially driven by increasing anthropogenic impact on the study area, as the pollen record shows an influx of agricultural indicator pollen (Behre, 1981). Additionally, a disturbance frequency index (Kuneš et al., 2019), based on the pollen record, and a charcoal record from the same site (Article III) suggest that the area around the sample site became heavily disturbed between AD 1250 – 1400. After this long-term event, the pollen record shows a period of almost 200 years of succession by pine and birch. As discussed by Feurdean et al. (2017), fire events appear to have played a significant role in forest dynamics in the Carpathian Mountains. The fire record from Diera Hollow (Article III) shows higher fire intensity before the large disturbance event (AD 1250) (BCHAR, figure 2), but a lower magnitude of local fires afterwards (AD 1400 onwards). This might be due to changes in the vegetation composition as Norway spruce (*Picea abies*), which became the dominant tree species after the large disturbance event, was found to be related to a reduction in wildfires (Ohlson et al., 2011, Carter et al., 2018b). More straightforward, changes in the fire regime could have been caused by changes in climate (as described further on in this section), anthropogenic activity or a combination of both. The fire events prior to the large disturbance events could be anthropogenic as well, as it was found that anthropogenic fire events in mountain areas in the Czech Republic have occurred before the onset of agricultural activities in the region (Novák et al., 2010). The beetle record becomes more diverse between AD 1250 – 1600, showing co-occurrence of forest species and species living in more open terrain. The intermediate disturbance hypothesis (Wilkinson, 1999) explains this phenomenon; species from different ecological niches can co-occur or occur in proximity of each other, all within close proximity of the sample site. Low occurrences of dung beetles between AD 1200 – 1600 suggest that the sample site was in close proximity of an animal route, where animals were guided to pasture grounds higher up the mountain (as previously hypothesized by Zámečniková (2008)). Between ca. AD 1600 – 1800, intermediate disturbance is registered as values of Poaceae pollen increase. After AD 1800, the area becomes partially abandoned (Olah et al., 2009). The decline in population in the region and the establishment of Tatra National Park in AD 1949, combined with active afforestation, led to an increase of forests in the region. The establishment of Tatra National Park and the start of active forest management could also be derived from the fossil beetle record. Dung beetles were no longer found in the fossil record and several species living in the understory of forests (re)appeared. The initial forest composition, however, was not restored.

Climate must have had an important influence on the changing forest structure as well, but its influence on the landscape surrounding the sample site remains ambiguous. Multiproxy data from lakes on the Polish side of the High Tatra Mountains (Gąsiorowski and Sienkiewicz, 2010) as well as data from lakes on the Slovakian side of the mountains (Bitušik et al., 2009) were used to reconstruct biotic responses to the Little Ice Age in high detail. The Little Ice Age (LIA) was a relatively long (AD 1220 – 1925) and climatically unstable period in this region. Kłapyta et al. (2016) argue that, based on these data, the first half of this period (AD 1220 – 1540) was cold and dry while the second part (AD 1540 – 1925) was cold and wet. While temperatures were derived from fossil diatom and chironomid assemblages (Bitušik et al., 2009; Gąsiorowski and Sienkiewicz, 2010), showing various cold adapted alpine species, a low precipitation rate was derived from the fact that recorded sedimentation rates during the first part of the LIA were extremely low. The second part of the LIA is characterized by high sedimentation rates and recorded rises in the water table of lakes such as Štrbské Pleso around AD 1500 (Rybníčková and Rybníček, 2006). An increase in the waterside vegetation such as Cyperaceae at Diera Hollow after AD 1500 (Article I) could be an indication of a rise in the water table. However, no increased sedimentation rate was measured at Diera Hollow after AD 1500. The hypothesized dryer period between AD 1220 – 1500 might have been the cause of the recorded decline of beech trees around the site, as beech is vulnerable to periods of drought (Bolte et al., 2007). Dryer conditions from AD 1220 could also have led to the large disturbance event with increased fire activity between AD 1250 – 1400.

A second unconventional method in Quaternary entomology, which was applied in the first study from Diera Hollow (Article I), was to derive a diversity index from the different fossil beetle assemblages through time. Several indexes exist and all are used in ecology (Pielou, 1967), in particular Simpson's diversity index (Simpson, 1949) and the Shannon diversity index (Shannon and Weaver, 1949). Although both indexes are used in paleoecology (e.g. Birks et al., 2016), the Shannon index was preferred as it puts less weight on the most abundant species in an assemblage (Pielou, 1967). A Shannon diversity index based on the beetle assemblages shows that from AD 1600, the overall beetle diversity steadily declines. Even though no historical records exist of any settlement in the direct vicinity of the sample site, proxies for disturbance and anthropogenic activity in the region coincide with the decline in diversity of the local beetle community. It appears that between AD 1600 – 1950, the fossil beetle assemblage consisted increasingly of species which appear in the forest hollow and less in its surroundings, except for large amounts of bark beetles (Scolytinae). Mechanisms which would explain this observation could not be identified, however.

Conifer bark beetle remains were numerous in the record from Diera Hollow and quantitative reconstructions of primary bark beetles were compared to other proxies for disturbance; a disturbance frequency index (DFI) derived from pollen data (Kuneš et al., 2019) and a macro charcoal record, both from the same sample site (Article III). The Z-score (number of standard deviations from the mean) of the minimum number of individuals (MNI) over the 18 samples (calculated for each species to keep a standard for the magnitude of possible peaks), indicated a peak of *Pityogenes chalcographus* and *Pityophthorus pityographus* remains in the uppermost sample. This peak coincides with the largest disturbance event ever recorded in the High Tatra Mountains (Koreň, 2006; Fleischer et al., 2017). In November 2004, an autumnal gale uprooted and destroyed large parts of the southern slope of the Eastern High Tatra Mountains (Nikolov et al., 2014), Subsequent outbreaks of the conifer pest *Ips typographus* on the remaining trees contributed to a total of 2.5 million m^3 loss of forest in the entire region (Koreň, 2006). Just like in the records from Šumava (Article II) where outbreaks of *I. typographus* occurred as well, fossils of this main conifer pest were found but only in low numbers. However, *P. chalcographus* and *P. pityographus* outbreaks usually coincide with *I.*

typographus outbreaks as they attack the same host trees but reach a much higher population density. During outbreaks, *P. chalcographus* often reaches population levels times which are ten times higher than *I. typographus* (Zubrik et al., 2008). Additionally, a peak in *P. chalcographus* and *P. pityographus* remains was found between AD 1250 – 1450, likely colonizing the young pine trees which appeared on the site after the large disturbance event. Prior to this event, large numbers of *Polygraphus poligraphus* indicate an outbreak of this species between AD 930 – 1030. This earliest outbreak appears not to have influenced the vegetation composition but might be related to a fire event prior, which could have weakened stands of spruce trees (Ehnstrom et al., 1995). Even though *P. chalcographus* and *P. pityographus* invade healthy pine trees as well, all four primary bark beetle species prefer Norway source as host tree (Pfeffer, 1989). The above findings suggest that it is possible to detect bark beetle outbreaks if the whole bark beetle community is regarded rather than only the main pest agent, something that was previously chiefly acknowledged by Morris et al. (2015). It should be considered that *Ips typographus* outbreaks could be a relatively new phenomenon, enhanced by anthropogenic influence (e.g. Pfeffer and Skuhravy, 1995). Although bark beetle outbreaks were a natural component of conifer forest dynamics, mechanisms appear to have differed from the current ones. To confirm if any bark beetle outbreaks occurred which were not recorded in the fossil beetle record, a comparison with historical records was made (Koreň, 2006). In these records, which date back to the late 19th century, only few bark beetle outbreaks are mentioned. One smaller outbreak, which occurred in 1968 around Tatranská Javorina and about 10 kilometers away from the sample site on the other side of the mountain range, did not result in rises in bark beetle remains. This supports the assumption that bark beetle outbreaks would have to happen in the direct vicinity of a forest hollow to be captured in the fossil record as beetle records only capture a local signal of 400 meters around the sample site (Smith et al., 2010). On a longer time scale, the changes in abundance of various primary bark beetle species through time possibly indicate how a decrease in forest density around Diera Hollow caused a shift to conifer forest with *I. typographus* and its smaller relatives *P. chalcographus* and *P. pityographus* as the main conifer pests. The fossil beetle assemblage from Diera Hollow, combined with other proxies such as pollen, provides important information about the development of the site through time, natural and anthropogenic disturbances around the site and the effect of these disturbances on the local beetle community. Such datasets could also be used for restoration and conservation practices (Froyd and Willis, 2008; Lindbladh et al., 2013). The time-lagged correlation between primary bark beetle densities and macroscopic charcoal concentrations (Article III) demonstrates the complexity of disturbance regimes in Central Europe, but also underlines the role of primary bark beetles as natural component of such disturbance regimes. The argued negative influence of bark beetle outbreaks on forest ecosystem services such as overall biomass and water quality in the last decades (e.g. Morris et al., 2018) appears to be non-existent or quickly diminishing within a few years or decades in many cases, according to more recent studies (Beudert et al., 2014; Kopáček et al., 2020; Seedre et al., 2020). The results from this doctoral thesis highlight the role of bark beetles as natural component in the disturbance regimes of Central Europe. Long-term records of fire events, bark beetle outbreaks and other disturbance agents which can be indirectly reconstructed from organic sediments, would be useful in reconstructing past disturbance events in several national parks in central Europe which are currently discussing strategies on dealing with bark beetle outbreaks, such as Šumava National Park (Zyval et al., 2016), Białowieża National Park (Grodzki, 2016) and many more.

4.4 Limitations of this research

The main limitation in Quaternary entomology, and to the results of this thesis, is the amount of time it requires to reproduce a complete insect record. In general, it is considered that a minimum of 50-100 individuals per sample is required in order to make quantitative reconstructions based on insect remains (e.g. Elias, 2010). The identification of each species, consecutively, takes substantial amounts of time. Furthermore, as the study on fossil insects is not well-developed in central Europe; most of the paleoenvironmental studies on fossil Coleoptera were conducted by, or in collaboration with expert researchers from northwest Europe (e.g. Lemdahl, 1991; Walkling and Coope., 1996; Jost-Stauffer et al., 2001). As the subject of Quaternary entomology is uncommon in central Europe, there is less knowledge available among entomologists on this topic and it proved a challenge to find experts on beetle families who were willing to assist with the confirmation of identifications made by the author. As a great amount of time had to be invested in reaching out to expert entomologists and to convince them of the value of Quaternary entomology, only the beetle assemblages from the site Diera Hollow could be fully identified. Consequently, these results could not be compared to any other record from the same region. It would be worth to investigate if the observed pattern in beetle diversity is recurrent in other regions in central Europe and if so, if anthropogenic activity is related to the recorded decrease in diversity in other regions of central Europe. This is also the case for the recorded bark beetle outbreaks from Diera Hollow which are currently, as far as we know, unique in its kind.

The limited knowledge on some beetle species in the High Tatra Mountains formed an important limitation in these studies as well, as less detailed reconstructions could be made based on the presence of these species. Therefore, this thesis advocates for the expansion of knowledge on the distribution and biology of insect species in central Europe. By actively sharing distribution data with database websites such as Biolib (Zicha, 1999 – 2020) and GBIF (GBIF, 2018), our knowledge on central European insect species would improve greatly. With the prospect of having more data available from central European beetle species, it might be worth to expand the MCR database (Atkinson et al., 1987) further eastwards and make temperature reconstructions possible for central Europe, such as was done with great success for western Europe by Coope et al. (1998). Insects form an important part of biodiversity and by studying their ecology and distribution patterns in greater detail, especially in environmentally sensitive areas such as mountain ranges, research on the conservation of biodiversity could be supported.

4.5 Future studies

The research on the identification of fossil insect pests, and discovery of possible ways to utilize these fossil types, are slowly advancing (e.g. Girona et al., 2018). Results from this thesis provide important clues about strategies in site selection and key species in the reconstruction of bark beetle outbreaks. In the assumption that bark beetle remains are not rare in fossil sediments, inundated depressions in the direct vicinity (<400 m) of a past bark beetle outbreak could be targeted for subsequent studies in Central Europe. Reconstruction of past bark beetle outbreaks, the environmental conditions under which these past outbreaks took place and any effects they caused on the vegetation and environment, could inform policy makers further on how to assess current bark beetle outbreaks. As such, it would as well be worth to reassess studies on primary bark beetle remains in North America (Morris et al., 2015). With the newly discovered techniques for palaeoentomology, such as the use of the Shannon diversity index on fossil beetle assemblages, it would be worth to expand the number of studies in central Europe. There is great variety in the forests and their vegetation composition across Central Europe and fossil beetle records could aid in reconstructing the forest dynamics in other regions, as well as in reconstructing the anthropogenic influence on these forests through time. Finally, as the DNA of most of the destructive bark beetle species is well known (e.g. Avtzis et al., 2012), it would also be worth exploring the possibilities of identifying past bark beetle outbreaks by their DNA signature in the sediment. Ancient sedimentary DNA (sedaDNA) has been a topic of studies since the 1980's but recently, it is considered that our knowledge about sedaDNA has increased far enough so that new studies with these techniques can significantly contribute to Quaternary studies (Brown and Barnes, 2015; Edwards, 2020). By comparing fossil bark beetle records with bark beetle sedaDNA, signals in the sedaDNA could be calibrated against another record.This would be approciate in order to document the relative differences in estimated bark beetle biomass through time and amounts of associated sedaDNA (Edwards, 2020). In conclusion, the results from this thesis have sparked interest in expanding paleoentomological studies in central Europe, as well as to develop new techniques to identify past bark beetle outbreaks.

5. Conclusions

Quaternary entomology is an established field which has shown the use of fossil insect remains in different types of environmental reconstructions. Recently, the reconstruction of past disturbance events has gained importance as the magnitude and frequency of natural disturbances such as windstorms, droughts, forest fires and insect outbreaks during the last decades is unprecedented. The fossil beetle record from Diera Hollow in the High Tatra Mountains provides detailed information about the development of this landscape from AD 930, highlighting the natural and anthropogenic factors controlling landscape transition in this region. Results from this thesis show that long-term landscape dynamics, as well as natural and anthropogenic disturbances therein, can be reconstructed from fossil insect assemblages in central Europe. Tentative techniques such as core wiggle-matching by their geochemical signals, measuring beetle diversity with diversity indexes, and peak detection of bark beetle remains by using the standard deviation of the minimum number of individuals (MNI) have provided reliable results and set a precedent for further studies in this region. The abundant fossil bark beetle record allowed for reconstruction of past bark beetle outbreaks around the sample site, a research objective that has the potential to advance further after this study as new data would inform policy makers about the past environmental conditions during which past bark beetle outbreaks took place, and the effect on the environment from these past outbreaks. The studies in this PhD thesis are the first advances in Quaternary entomology in central Europe, a region which is likely very suitable for further research in this field, and successfully demonstrate how the application of subfossil insect remains can aid in the reconstruction of former landscapes and past natural, and anthropogenic disturbances.

6. Literature

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7. Supplementary material

Supplementary materials are included in the electronic version of this PhD thesis and comprise the supplementary data of the three publications presented, whereas the first two articles contain supplementary data. These consist of the following:

7.1 Article I (chapter 3.1)

- Supplemental data A: Sites used in this review
- Supplemental data B: Featured bark beetle species and their host trees
- Supplemental data C: All data
- Supplemental data D: References

This data is also available as an interactive spreadsheet, through the link https://www.researchgate.net/publication/342048459_Bark_beetle_database_Schafstall_et_al_2020xlsx

7.2 Article II (chapter 3.2)

- Table S1: Radiocarbon dates
- Table S2: List of identified beetle taxa
- Figure S1: XRF curves: Pb signal
- Figure S2: XRF curves: Fe signal
- Figure S3: XRF curves: Rb signal
- Figure S4: Example of XRF curve wiggle matching between cores and subsampling
- Figure S5: Partitioning of beetle ecological group to the Shannon index on the beetle assemblages of Diera Hollow