

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

4

5 Nick Schafstall^{1*}, Nicki Whitehouse^{2,3}, Niina Kuosmanen^{1,4}, Helena Svobodová- Svitavská⁵,
6 Mélanie Saulnier¹, Richard Chiverrell⁶, Peter Fleischer^{7,8}, Petr Kuneš⁹, Jennifer Clear¹⁰

7

8 *1. Dept. of forest ecology, Czech University of Life Sciences, Kamycka 129, 165 00 Praha-Suchdol, Czechia;*
9 *nick.schafstall@gmail.com; kuosmanen.niina@gmail.com; melanie.saulnier14@gmail.com*

10 *2. Dept. Of Archaeology, School of Humanities, University of Glasgow, 1 University Gardens, Glasgow G12 8QQ,*
11 *United Kingdom; nicki.whitehouse@glasgow.ac.uk*

12 *3. School of Geography, Earth and Environmental Sciences, Plymouth University, Drake Circus, Plymouth,*
13 *Devon, PL4 8AA, United Kingdom*

14 *4. Department of Geosciences and Geography, Faculty of Science, P.O. Box 64 (Gustaf Hällströmin katu 2)*
15 *FI-00014 University of Helsinki, Finland*

16 *5. Laboratory of paleoecology, Institute of Botany, Czech Academy of Sciences, Zámek 1, 252 43 Průhonice ,*
17 *Czechia; helena.svitavska@ibot.cas.cz*

18 *6. Dept. of Geography and Planning, University of Liverpool, Roxby Building, Liverpool, L69 7ZT, United Kingdom*
19 *R.C.Chiverrell@liverpool.ac.uk*

20 *7. Faculty of Forestry, Technical University in Zvolen, Ul. T. G. Masaryka 24, 960 01 Zvolen, Slovakia*
21 *p.fleischersr@gmail.com*

22 *8. State Forest of TANAP, Tatranská Lomnica 64, 059 60 Vysoké Tatry-Tatranská Lomnica, Slovakia*

23 *9. Dept. of Botany, Charles University, Benátská 433/2, 128 01 Praha 2, Czechia*
24 *petr.kunes@natur.cuni.cz*

25 *10. Dept. of Geography, Hope University, Hope Park, Liverpool L16 9JD, United Kingdom*
26 *clearj@hope.ac.uk*

27

28 * Corresponding author email:

29 nick.schafstall@gmail.com

30

31 **Abstract**

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

53

54 Key words: Coleoptera; nature conservation; biodiversity; human impact; Central Europe;
55 climate change.

56

57 **1. Introduction**

58 Montane biomes are diverse multi-functional environments with a variety of habitats
59 often occupied by specific, endemic animal and plant communities constrained by
60 environmental conditions (Kessler and Kluge, 2008; Dimitrov et al., 2012; Amori et al., 2019).
61 Humans have progressively modified these ecosystems by altering land-use to their
62 requirements, resulting in the decline of many plant and animal species. The establishment
63 of national parks during the 20th century serves to preserve the remaining biodiversity in
64 remote mountain areas, yet these montane forests are increasingly impacted by extreme
65 climate events and their ecosystems are changing rapidly (McCain and Colwell, 2011; Elsen
66 and Tingly, 2015). In particular, the frequency of extreme events disturbing forest
67 ecosystems, such as drought and windstorms, have increased significantly in North America
68 and Europe during the last 50 years (Schelhaas et al., 2003; Allen et al., 2010). However,
69 historical recordings of disturbance agents are rare in some regions (Schelhaas et al., 2003).
70 Paleoecological reconstructions can be used to understand the long-term effects of changing
71 climate and anthropogenic pressure on the landscape structure and the flora and fauna in
72 montane regions (La Sorte and Jetz, 2010; McCain and Colwell, 2011). In the last decades it
73 has become apparent that linking paleoecology with conservation management is key to
74 understand the effects of current conservation efforts (Froyd and Willis, 2008). Ecological
75 data on longer time scales allow for a better reconstruction of natural variability in a
76 landscape and give clearer results about ecological thresholds and resilience within a natural
77 system. Furthermore, by addressing ecological data on longer time scales it can be argued if
78 the current disturbance events in montane forests are unprecedented (Froyd and Willis,
79 2008; Kidwell, 2015).

80

81 Fossil pollen and botanical macrofossils are the most commonly used proxies for
82 reconstructing paleoenvironment and vegetation structure (e.g. Magyari et al., 2012).
83 Subfossil beetle (Coleoptera) remains are a valuable additional proxy to pollen as these can
84 often be identified to species level and provide detailed information about past beetle
85 habitats (e.g. van Geel et al., 1989). Many beetle species live in specific niche environments

86 because of their preferences for certain temperature and moisture levels, landscape
87 openness and host plants (Elias, 2010). Local communities (< 400 m; Smith et al., 2010) are
88 the source area for beetle remains at fossil sites. In previous studies, the comparison of
89 fossil beetle assemblages with modern beetle communities provided valuable information
90 about the timing and drivers of local beetle taxa extinctions (e.g. Whitehouse, 2006).
91 Therefore, fossil beetle records provide not only detailed information to reconstruct
92 landscape composition through time, but also contribute to solve issues in conservation and
93 management (e.g. Buckland and Kenward, 1973; Gustavsson et al., 2009). Lindbladh et al.
94 (2013) highlight fossil beetle remains as an underused, yet valuable proxy in forested
95 landscape reconstructions as fossil beetles can contribute to the reconstruction of forest
96 composition, (relative) amounts of old trees and coarse woody debris, and to reconstruct
97 natural disturbances. Even insect outbreaks could potentially be quantified from fossil beetle
98 remains.

99

100 Central Europe has a diverse landscape with high flora and fauna species diversity,
101 and is currently under pressure from intensive land use (Turnock, 2002). The High Tatra
102 Mountains are located on the border between Slovakia and Poland and are part of the
103 Western Carpathian range, the highest range of the Carpathian Mountains. The area is a
104 prominent UNESCO biosphere reserve with species such as brown bear (*Ursus arctos*),
105 Eurasian lynx (*Lynx lynx*) and wolf (*Canis lupus*), and many endemic plant and animal
106 species ([unesco.org](https://www.unesco.org)). In the last decades, extreme events such as windthrows and droughts
107 have increased significantly in this region (e.g. Fleischer et al., 2017). Consequently, the
108 Tatra Mountains are an ideal region to investigate long-term (millennial) changes in the local
109 flora and fauna, based on pollen and beetle remains. In this study, we aim to 1) Reconstruct
110 changes in diversity of the local forest beetle community and 2) Identify the drivers behind
111 changes in beetle community and vegetation diversity. Understanding the drivers behind
112 species composition and diversity change over the last 1000 years can be used as a

113 potential analogue to help understand the response and resilience of these ecosystems to
114 future climate and anthropogenic changes.

115

116 **2. Methods**

117 *2.1 Site area*

118 Diera Hollow is a small forest hollow of 30 m x 80 m in size and located at 982 m
119 a.s.l. on a former end moraine of the High Tatra Mountains near the village Tatranská
120 Lomnica, Slovakia (49.09885° N, 20.15814° E; Figure 1). The region has a sub-continental
121 climate with an average minimum temperature of -5.3 °C and an average maximum
122 temperature of 15.4 °C. The mean annual rainfall is 830 mm (Tatranská Lomnica weather
123 station, 830 m a.s.l.). Forest hollows are waterlogged anoxic peat depressions within a forest
124 canopy. Due to their small to moderate size (~100 – 2000 m²) their sediments reflect a local
125 environmental signal. The pollen signal is representative of the vegetation recorded within a
126 radius approximately 100 m of the site (Overballe-Petersen and Bradshaw, 2011), and
127 comparable to the source area radius of 400 m for beetle remains (Smith et al., 2010). The
128 site was heavily damaged by the autumnal storm Alžbeta in 2004 and is currently
129 surrounded by pine (*Pinus*), spruce (*Picea abies*), larch (*Larix decidua*), birch (*Betula*) and
130 bilberry (*Vaccinium myrtillus*). Seedlings of birch, bedstraw (*Galium* sp.), rosebay willowherb
131 (*Epilobium angustifolium*) and sedges (*Carex* spp.) are present at the site. Prior to the
132 windstorm in 2004, the area surrounding the study site was densely forested, with spruce as
133 the dominant species.

134

135 *2.2 Field methods*

136 A master sediment core was extracted from Diera Hollow in 2016, with a 5 x 50 cm
137 D-section corer (Jowsey, 1965; Aaby and Digerfeldt, 1986). To provide the volumes of
138 material required for analysis of fossil beetles, a further 12 proximal sediment cores were
139 sampled in 2017 using a gridded system, with a 10 x 50 cm D-section corer. To minimize the
140 disturbance of the sampling site inside the nature reserve, sampling was performed by

141 collecting multiple parallel cores instead of digging trenches, a sampling method often used
142 in paleoentomological studies (e.g. Forbes et al., 2020). Cores measured between 50 cm
143 and 78 cm in total length due to variable moraine deposits and bedrock. The master core (88
144 cm in length) was radiocarbon dated and analyzed for geochemistry (Energy-Dispersive X-
145 Ray Fluorescence: ED-XRF), subfossil beetles and pollen, while the additional cores were
146 analyzed for beetle remains.

147

148 *2.3 Chronology, geochemistry and core correlation*

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

158

159 All 13 cores, including the master profile, were analyzed for geochemistry on a wet-
160 sediment basis using an Olympus Delta Professional ED-XRF mounted on the University of
161 Liverpool Geotek Multi-Sensor Core Logger (MSCL). XRF core scanning is a non-
162 destructive, rapid approach for quantifying elemental concentrations in a sediment core
163 (Croudace et al., 2006) and has been used frequently in paleolimnological studies (Davies et
164 al., 2015) and, to lesser extent, studies on peat cores (Poto et al., 2015; Longman et al.,
165 2019). Patterns in geochemistry were comparable between the master profile and the 12
166 proximal cores; patterns in concentration of the atmospheric fallout pollutant Pb (Renburg et
167 al., 2000) displayed a strongly repeatable signal. Profiles for conservative lithogenic
168 elements, e.g. Rb, also showed strongly repeatable stratigraphic records. The strong

169 matches between the cores (Figures S1 – S4) facilitated the transfer of the age-depth model
170 between cores and provided a basis for subsampling the 12 cores. These cores were pooled
171 into 18 samples with total volumes 400 – 1600 ml, with narrower 1 – 4 cm intervals to
172 provide greater detail for the last 100 years (400 – 500 ml) and the remainder in 4 – 7 cm
173 depth intervals (800 – 1600 ml). Details on the subsampling can be found in figure S4.

174

175 *2.4 Fossil beetle analysis*

176 Fossil beetle preparation of the 18 samples followed the methods described in detail
177 by Elias (2010). Samples were wet sieved at 250 µm and the organic remains were soaked
178 in paraffin oil and floated in water. Isolated floats were sieved and rinsed before being stored
179 in ethanol (C₂H₅OH). Beetle remains were picked under a binocular light microscope with
180 10x magnification and were identified to family, genus and species level with the use of
181 online databases (Kerbtier.de, Cassidae.uni.wroc.pl) and museum collections in United
182 Kingdom (Plymouth City Museum and Oxford Museum of National History) and Czechia
183 (Czech National Museum in Prague, Regional Museum Rožtoky u Prahy and the Moravian
184 Museum in Brno). The minimum number of individuals (MNI) was calculated by adding up all
185 elytra, heads and dorsal plates(pronota) identified as Coleoptera.

186

187 *2.5 Ecological attributes*

188 Specific ecological attributes of beetle genera and species were derived from
189 literature through online databases; BugsCEP (Buckland and Buckland, 2006) and Biomap
190 (2019), which contained full species descriptions. According to their ecological preferences,
191 species or genera were divided into 20 functional groups to facilitate interpretation.
192 Functional groups are personal interpretations used to summarize the ecology of beetle taxa
193 and can vary to certain degree according to the type of study they are used for (e.g.
194 archaeological vs. paleoecological). The functional groups in this study are based on
195 previous work from the United Kingdom (e.g. Whitehouse, 2004). Many beetle species can
196 be found in more than one type of landscape, and the ecology of taxa is as well often

197 constrained by their feeding strategies. Unless beetle taxa were clearly eurytopic, the most
198 dominant ecological feature was chosen for each beetle taxon: Eurytopic (appearing in a
199 wide variety of biotopes); Aquatic (living at least partially in water bodies); Aquatic standing
200 water (living in stagnant bodies of water); Aquatic running water (living in flowing water
201 bodies); Marsh/wetland (hygrophilous species living in marshes or wetlands); Bank
202 vegetation (living on vegetation at the banks of water bodies); Hygrophilous (living in a
203 variety of biotopes, with a high humidity as common factor); Heathland/moorland (living in
204 moderately wet, open landscape); Meadow (living in open landscape, often feeding on
205 meadow vegetation); Disturbed/arable (living on disturbed soils, often disturbed by
206 anthropogenic activities); Foul/dung (living in dung and rotting vegetation or other materials);
207 Dung (only living in dung); Dry decomposer (fungivore in dry environments); Wet
208 decomposer (mostly fungivores; found in moist places); Shaded woodland (living in shaded
209 woodland but in the understory); Trees (living on trees); Deciduous trees (living on
210 deciduous trees); Coniferous trees (living on coniferous trees); Deadwood (living in dying
211 trees and decaying wood) and Conifer pest (colonizing healthy trees). The category Conifer
212 pest was added as large quantities of conifer bark beetles (Curculionidae: Scolytinae) were
213 found and these could provide additional information about past disturbances. Beetle data
214 was displayed using the program Tilia (Grimm, 1990), zonation was performed by D-chord
215 cluster analysis (see section 2.7).

216

217 *2.6 Pollen analysis*

218 Pollen analysis of the 2016 master core was performed in continuous 1 cm resolution
219 between 1 – 70 cm and in 2 cm interval for the rest of the core, amounting to a total of 78
220 samples. Subsamples of 0.5 cm³ were prepared with standard procedures of KOH-,
221 acetolysis- and HF-treatment (Fægri and Iversen, 1989). The samples were mounted in
222 glycerine and a minimum of 500 terrestrial pollen grains were identified under a light
223 microscope using a 400x magnification. Pollen identification was based on standard pollen
224 keys (Punt 1976, 2003; Beug, 2004), microtopographic atlases (Reille, 1992 – 1998), and a

225 reference collection in the Institute of Botany, CAS, Průhonice. Pollen data was plotted using
226 the program C2 (Juggins, 2003). The full pollen dataset can be accessed upon personal
227 request to the authors and will be published elsewhere.

228

229 *2.7 Statistical analysis*

230 Shannon's diversity index (Shannon and Weaver, 1949) takes both the number of
231 individuals and the number of taxa into account, by calculating the natural log from the
232 proportion of an individual species of the total sum of individuals. This diversity index is used
233 commonly in ecology as well as archeology and paleoecology (Pielou, 1967; Liu et al.,
234 2015). Both beetle diversity and pollen diversity were plotted against time to compare forest
235 beetle community dynamics with forest vegetation dynamics.

236

237 To emphasize changes in the terrestrial beetle community, aquatic species were
238 excluded from the following analyses; 266 out of 313 taxa remained. Raw counts were
239 converted to percentages to account for differences in total sum of individuals per sample
240 (Legendre and Legendre, 2012). The square-chord method (Overpeck et al., 1985) was
241 used to calculate dissimilarities between all samples. A hierarchical cluster analysis was
242 then performed on the resulting square-chord dissimilarity (SQD) matrix to identify patterns
243 in the beetle assemblages. Ward's minimum variance criterion (Ward, 1963) was used to
244 implement the hierarchical clustering, to define beetle zones. This technique produces
245 compact, equal-sized dendrograms by minimizing the total within-cluster variance (Mirkin,
246 2005). Furthermore, a PCA (Gabriel, 1971) was performed on the samples according to their
247 dissimilarity matrix, to explore which components (species) attributed most to the variance
248 throughout the section. All statistical analyses were performed using the statistical software
249 R (R core team, 2018) and different packages: vegan (Oksanen et al., 2019), usedist
250 (Bittinger, 2017), factoextra (Kassambara and Mundt, 2017), ggplot2 (Wickham, 2016), dplyr
251 (Wickham et al., 2019) and tidyverse (Wickham, 2017).

252

253 3. Results

254 3.1 Beetle assemblages

255 A total of 2860 individuals were identified from 313 taxa and 38 families (Table S2).
256 The number of individuals per sample ranged between 58 and 279 (Table S2, Figure 3). In
257 figure 3, depths are according to core 11, which matched best with the master core from
258 2016 and was used to correlate all other cores to (see Figure S1 – S4). The beetle record
259 was divided into five distinctive zones according to the hierarchical cluster analysis (Figure
260 4): Zone 1 (930 – 1080 CE), Zone 2 (1080 – 1500 CE), Zone 3 (1500 – 1740 CE), Zone 4
261 (1740 – 1950 CE) and Zone 5 (1950 CE – present).

262

263 Zone 1 (930 – 1080 CE) has a high abundance of aquatic species (21.8 – 24.4%).
264 Especially species living in standing water (e.g. the diving beetle *Hydroporus tristis* and the
265 water scavenger beetle *Anacaena lutescens*) were found but also species living in running
266 water such as *Limnius perrisi*, which feeds on moss from stones in mountain streams (Koch,
267 1989a; 1989b). Marsh/wetland species (4.4 – 6 %) consist mostly of species in the families
268 Carabidae and Staphylinidae. Species living on or hunting within bank vegetation (6.8 – 10.1
269 %) consist primarily of *Cyphon* spp. and *Stenus* spp (Koch, 1989b). Species living in rotting
270 materials (Foul/dung; 9 – 12.2 %) primarily consist of a variety of rove beetles, among which
271 many species of the subfamily Aleocharinae. This zone contains a high proportion of species
272 living on deciduous trees (6 – 10 %) which consists almost entirely of the species
273 *Rhynchaenus fagi*, a leaf-mining weevil which colonizes beech trees (Koch, 1989a). The
274 proportion of conifer pests is high in this zone as well (6 – 11.5 %), consisting mostly of the
275 species *Polygraphus poligraphus*, a species which attacks depressed stands of spruce
276 (Pfeffer, 1989). Species living in meadows or glades, such as *Eusphalerum alpinum*, which
277 visit flowers in mountain meadows (Koch, 1989a), are also abundant (5.9 – 10.5 %).
278 *Arpedium quadrum*, a predator in heathlands and alluvial meadows and an indicator of
279 heathland/moorland (Koch, 1989a), is the most abundant species (5.3 %) from the remaining
280 ecological groups.

281

282 In Zone 2 (1080 – 1500 CE), common species are *Stenus* spp. (16.1 %), *A. quadrum*
283 (9 %), *Pityogenes chalcographus* (7.5 %), *Pityophthorus pityographus* (5.8 %), *Cyphon* spp.
284 (4.7 %) and *Eusphalerum anale* (3.1 %). The proportion of aquatic beetles declines while
285 marsh/wetland species such as *Trechus* spp. and *Olophrum piceum* increase (Koch, 1989a).
286 Bank species (primarily *Stenus* spp. and *Cyphon* spp.) increase significantly. *Pit.*
287 *chalcographus* and *P. pityographus* replace *P. poligraphus* as abundant conifer pests
288 (Pfeffer, 1989), but species indicative for shaded woodland, deciduous trees and deadwood
289 species all decline to values below 4 %. Dung species, such as *Aphodius abdominalis*
290 (Koch, 1989b), start to appear in this zone. In the upper part of Zone 2, species living in
291 meadows (such as *Eusphalerum* spp.) increase to 15.3 %.

292

293 Zone 3 (1500 – 1740 CE) shows a shift in dominant species: *Cyphon* spp. (8.7 %),
294 *Anotylus tetracarinatus* (6.9 %), *Stenus* spp. (5.5 %), *Pit. chalcographus* (5 %), *Gabrius*
295 *pennatus* (4.3 %), *Enochrus quadripunctatus* (3.8 %), *A. quadrum* (3.1 %), and *Platystethus*
296 *arenarius* (3.1 %). *A. tetracarinatus*, *G. pennatus* and *P. arenarius* are found in dung or other
297 rotting substances (Koch, 1989a) while *E. quadripunctatus* is an aquatic generalist (Koch,
298 1989a). Heathland/moorland species and meadow species decrease in number. Different
299 classes related to woodland do not change significantly in this zone but shaded woodland
300 species such as *Molops piceus* increase slightly to 5.4 % (Koch, 1989a). Dung species
301 (Koch 1989a, 1989b), such as *Aphodius* spp., *Onthophagus* cf. *joannae* and *Sphaeridium*
302 *lunatum/scarabaeoides*, increase to about 5 % of the total beetle assemblage.

303

304 Zone 4 (1740 – 1950 CE) contains mainly dominant species connected to the
305 inundated site and its (bank) vegetation: *Cyphon* spp. (18.1 %), *Hydroporus erythrocephalus*
306 (living in a wide range of still water habitats (Koch 1989a; 4.9 %), *Phyllotreta* spp. (4.2 %), *A.*
307 *lutescens* (3.9 %), *E. quadripunctatus* (3.5 %), *Donacia* spp. (3.5 %) and *Coelostoma*
308 *orbiculare* (3.4 %). *Cyphon* spp., *Phyllotreta* spp. and *Donacia* spp. feed on bank vegetation

309 while the other taxa are all aquatic (Koch 1989a, 1989b, 1992). This zone contains a lower
310 amount of species living in running water (0.7 – 2.6 %) as well as lower amounts of conifer
311 pests (2.6 – 4.1 %). Heathland/moorland species decline even further. Sample 6 in this zone
312 (1780 CE) has the highest proportion of dung species (e.g. *Aphodius* spp., *Onthophagus* cf.
313 *joannae* and *Sphaeridium lunatum/scarabaeoides*; 7.4 %) of all samples.

314

315 Zone 5 (1950 CE – present) has the lowest number of individuals recorded. Aquatic
316 species decline rapidly (down to 5 %) and aquatic beetles living in running water are absent.
317 Marsh species remain between 8.6 – 15.3 % but bank vegetation species decline to levels
318 similar to Zone 2 and 3 (13.8 – 16.7 %). Meadow species and species living in
319 disturbed/arable areas remain consistent. Foul/dung species increase (27.8 %) and dung
320 species are absent between 1970 CE and present. Shaded woodland species such as
321 *Anoplotrupus stercorosus* (Koch, 1989b) increase in the bottom sample of this zone (6.9 %)
322 while conifer pests (e.g. *Pit. chalcographus*) (24%) and species living in deadwood (8 %)
323 peak between 2000 CE – present. Conifer pest *Pit. chalcographus* reaches high values of 13
324 % of the total assemblage in this zone.

325

326 3.2 Pollen assemblages

327 In order to compare the changes in the beetle community to changes in the
328 vegetation, the zonation of the pollen diagram (Figure 5) follows the zonation used for beetle
329 communities. Zone 1 (< 1080 CE) is dominated by pollen from *Picea*, *Abies* and *Fagus*, with
330 *Pinus* contributing to 10 % of the total pollen sum. Zone 2 (1080 – 1500 CE) consists of two
331 phases: in the first phase there is a maximum of *Abies* and *Picea* pollen, which decline
332 around 1350 CE. Maximum values of *Fagus* pollen occur between 1250 – 1350 CE.
333 Between 1250 – 1500 CE, there are peaks in Poaceae and Cyperaceae, after which *Pinus*
334 pollen increase considerably and *Betula* pollen starts to increase. In contrast, *Fagus* pollen
335 decrease. From 1250 CE, there are notable increases in human indicator taxa, including
336 cultivated plants such as *Secale cereale* and *Triticum avellana* and plants growing on open

337 mineral soil connected to human settlements such *Plantago lanceolata* (Behre, 1981;
338 Gaillard, 2013). The green alga *Botryococcus neglectus*, indicative for oligotrophic or
339 mesotrophic reservoirs (Komárek and Fott, 1983), increases around 1250 CE. In Zone 3
340 (1500 – 1740 CE), the peak in *Pinus* pollen is followed by a peak in *Betula* pollen. When the
341 *Betula* pollen peak declines around 1600 CE, *Picea* and Cyperaceae pollen increase, while
342 *Abies* and *Fagus* pollen continue to decrease. *Quercus* and *Corylus* pollen also increase in
343 Zone 3. In Zone 4 (1740 – 1950 CE) *Picea* pollen values reach their second maximum, while
344 *Pinus* pollen gradually increases. Green alga *B. neglectus* decreases to very low values.
345 From 1950 CE (Zone 5), *Pinus* pollen values are as high as in Zone 2. There is also a
346 decrease recorded in Cyperaceae and human indicator pollen taxa.

347

348 3.3 Beetle and vegetation diversity

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

357

358 3.4 Patterns in beetle diversity

359 The PCA biplot (Figure 7) shows the 10 beetle taxa that contribute most to the total
360 variance. The first principal component (PC1) explains 34.3 % of the variance whereas the
361 second rotated factors PC2 contribute to 17.9 %. PC1 has the highest loadings from *Cyphon*
362 spp. (bank species, positive loadings), *Stenus* spp. and *A. quadrum* (marsh/wetland and
363 heathland species, respectively, negative loadings). PC2 has the highest loadings of *Pit.*
364 *chalcographus* (forest pest, positive loadings), *P. poligraphus*, *E. alpinum* and *R. fagi* (forest

365 pest, meadow species and deciduous tree indicator, respectively, negative loadings). The
366 oldest samples (930 – 1030 CE) are located within the negative portion of PC2; younger
367 samples are located in the positive portion of PC2. The positive portion of PC1 groups the
368 other, with highest values for samples from Zone 4 (1740 – 1900 CE). Samples from Zone 2
369 (1080 – 1390 CE) and Zone 5 (1950 – 2000 CE) overlap in the PCA biplot.

370

371 **4. Discussion**

372 *4.1. Forest diversity and ecosystem dynamics over the last millennium*

373 A variety of functional beetle communities enabled the reconstruction of past
374 changes in forest composition and biodiversity at Diera Hollow. The high abundances of
375 tree/forest beetle taxa are indicative of a closed forest ecosystem (Robinson, 1991, 2000;
376 Smith et al., 2010), with Norway spruce as the dominant species at the site over the past
377 1000 years. However, despite relatively consistent dominant forest cover, different beetle
378 communities have succeeded one another, many of which can be related to changes in the
379 local vegetation.

380

381 *4.1.1. Montane spruce-dominated forest (930 – 1080 CE)*

382 At the beginning of the last millennium, the dominance of forest/tree beetle taxa
383 suggests a predominantly forested environment. Dominant species *R. fagi* and *P.*
384 *poligraphus* indicate the presence of beech and spruce trees at the site, respectively (Koch,
385 1992; Pfeffer, 1989). Low abundances of *Pityokteines vorontzowi* indicate the presence of fir
386 trees (Pfeffer, 1989). This is further supported by the pollen record with the presence of
387 *Abies*, *Picea* and *Fagus* pollen. The dominance of dytiscid *H. tristis*, together with an
388 abundance of other diving beetles typically living in peaty pools (Koch, 1989a), suggests that
389 the site was a shallow peat bog. The high abundance of the species *A. quadrum* and *Stenus*
390 spp. suggest that the banks of the peat bog were not densely covered with vegetation
391 (Brundin, 1934; Koch 1989a). Besides, a variety of species populating open areas was
392 present, such as *Eusphalerum* spp. living on flowers in (alpine) meadows (Koch, 1989a), but

393 also *Silpha tristis*, known to feed on carrion (Koch, 1989a), *Limonium aeneoniger* living at
394 forest edges (Laibner, 2000) and various species of flea beetles living on herbs in open
395 areas (e.g. *Chaetocnema* sp.; Koch, 1989b).

396

397 4.1.2. Increased beetle diversity associated with landscape openness and floristic diversity 398 (1080 – 1500 CE)

399 From around 1250 CE, increasing changes in the species composition of the beetle
400 community indicate landscape openness and an increase in human activity in the region.
401 Beetle diversity appears to be closely linked to floristic diversity in this period, with an
402 increase of taxa living in open landscapes (Figure 4). There is a decline in species living on
403 deadwood (e.g. *Rhizophagus* spp. and *Anobium* sp.) and shaded woodland species (e.g.
404 ground beetle *Pterostichus foveolatus*; Koch, 1989a), suggesting a decline of old-growth
405 forest directly around the forest hollow. *R. fagi* indicates that beech trees remain present but
406 in low numbers. Several taxa living in forest clearings or at open water edges (e.g.
407 *Eusphalerum* spp. and *A. quadrum*) increase to become the dominant taxa and are
408 indicative of landscape openness (Koch, 1989a). Additionally, the presence of *Hydrobius*
409 *fuscipes* indicates that the peat bog was sun-exposed at this time (Fossen et al., 2016). The
410 increased presence of conifer pests; *Pit. chalcographus* and *P. pityographus* between 1430
411 – 1500 CE to 7.5 % of the total beetle assemblage, indicates an abundance of their primary
412 host, Norway spruce (Pfeffer, 1989). However, the pollen record shows lower amounts of
413 *Picea* pollen, suggesting a lower presence of trees. As these bark beetle species are known
414 to colonize thin branches or otherwise young trees, the high presence of these species might
415 have delayed the establishment of mature spruce trees around the site. The presence of *Ips*
416 *acuminatus* and *Pityogenes quadridens* colonizing *Pinus* spp. (Pfeffer, 1989) coincides with
417 an increase in *Pinus* pollen values, suggesting that pine became the dominant tree species
418 at Diera Hollow during this time. The increase of dung beetles living on dung from sheep,
419 cattle and horses (*P. arenarius*, *S. lunatum/scarabaeoides*, *Onthophagus* cf. *joannae*,
420 *Aphodius mixtus*, *A. rufipes*, *A. prodromus*; Koch, 1989b) from 1500 CE suggests an

421 increase in herding activities. Since both *S. lunatum/ scarabaeoides* and *O. joannae* prefer
422 horse, cattle or sheep dung (Koch 1989b), it is likely that the increase of dung beetles near
423 the site was caused by the presence of dung from domesticated animals. However, values
424 of dung beetles between 0.4 and 5 % does not suggest pasturing (Robinson, 1991, 2000)
425 and therefore, the site was likely located near routes where cattle and sheep were herded to
426 alpine meadows higher up in the mountains (as hypothesized by Zámečnicková, 2008).

427

428 4.1.3. Mixed deciduous-coniferous forest with patchy landscape openness (1500 – 1740 CE)

429 From 1500 CE onward *Cyphon* spp., *Donacia* spp. and *Phyllotreta* spp., all known to
430 live on bank vegetation (Koch, 1989b; 1992), start to increase and become the dominant
431 taxa. An increase in species living on bank vegetation around 1700 CE coincides with a
432 pronounced increase of Cyperaceae, the general food source for these species. The
433 presence of high amounts of *Quercus* pollen suggests an increase in light availability (e.g.
434 Annighöfer et al., 2015). Therefore, it is likely that the landscape openness increased during
435 this time. Low occurrences of the weevil *R. fagi* together with *Fagus* pollen indicate that
436 beech trees remained present near to the site until the end of the 19th century. The
437 presence of *A. stercorosus*, which is found in semi-humid deciduous and mixed forest (Koch,
438 1989b), confirms the occurrence of deciduous trees around the site, while the presence of
439 conifer pests and species living on conifer trees (e.g. *Polydrusus pallidus*; Koch, 1992)
440 suggests that conifer trees were still present. As dung beetle species continue to occur in the
441 record, the area likely remained impacted by herding activities.

442

443 4.1.4. Semi-natural closed forest and decline in beetle diversity (1740 CE – present)

444 Conifer pests and shaded woodland taxa start to increase from approximately 1800
445 CE, suggesting that the vicinity of Diera Hollow became dominated by Spruce-Pine forest
446 during this time. This process coincides with human abandonment of the region in the 19th
447 century (Olah et al., 2009). Tatra National park was established in 1949 CE and the effects
448 of forest management such as reforestation in the area are visible in the beetle record with

449 shaded woodland species increasing and dung beetles no longer present. Although the PCA
450 biplot (Figure 6) shows that samples after 1950 CE are mostly similar to samples between
451 1080 – 1500 cal CE (Zone 4), many forest beetle species did not reappear, and the original
452 Spruce-Fir-Beech woodland was not restored. The decline in beetle diversity according to
453 the Shannon Index started around 1500 CE and continued before a rapid decrease from
454 1950 CE. Partitioning of the Shannon Index for different functional groups (see Figure S6)
455 shows that from 1500 CE, the diversity of the beetle assemblages becomes increasingly
456 driven by aquatic taxa. The rapid decline of beetle diversity between 1950 – 2017 CE could
457 be attributed to the infilling or drying out of Diera Hollow, due to the sharp decline of the total
458 amount of aquatic species and the disappearance of species living in running water. Decline
459 of the alga *B. neglectus* from ~1750 CE is also an indication that the pool was decreasing in
460 size (Jankovská and Komárek, 1982). Apart from the slow infilling of the basin, both climatic
461 and anthropogenic changes could have contributed to the drying out of Diera Hollow. During
462 the period 1881–2008, the average annual precipitation in Slovakia decreased by 3.4%
463 (Ministry of Environment of the Slovak Republic, 2005). However, it has been argued that
464 forest plantations can have a negative effect on forest hydrology and affect surface water
465 generation and groundwater recharge, as young forests demand large amounts of water in
466 order to grow (van Dijk and Keenan, 2007).

467

468 *4.2. Drivers behind changes in the local beetle community and vegetation*

469 Climatic conditions, especially moisture fluctuations, are likely to have played a
470 significant role in the changes in the local vegetation and beetle community. In a study on
471 the Little Ice Age in the High Tatra Mountains (Niedźwiedź, 2004), the highest decrease in
472 temperature and increase in moisture was identified between 1575 – 1676 CE. An increase
473 in pollen from cultivated plants co-occurs with appearances of beetle species living on
474 animal dung from 1250 CE onwards (Figure 2) suggesting farming in the surrounding area.
475 Moreover, an increase in vegetation and beetle diversity associated with landscape
476 openness can be correlated to regional human activity. Even though limited sources are

477 available, one describes a village called Maklar or Matrei. This was a settlement for livestock
478 herders that was inhabited until 1360 CE (Greb, 1934). From 1400 CE onward, several wars
479 resulted in abandonment of a large part of the region (Cichocki, 2003; Pavercsik, 2003),
480 enabling forest succession (Figure 2, Figure 4). As soon as the region became more stable
481 from ~1500 CE, human recolonization started. Many settlements were founded as mining
482 communities in search for ore and metals, similar to villages in nearby mountain ranges
483 (Jambrich, 2007). A well-recorded example of recolonization in the area itself is Ždiar,
484 located ten kilometres north of Diera Hollow at an altitude of 850 m a.s.l. and founded in the
485 16th century (Hreško et al., 2015). Socio-economic activities in the village were mainly
486 related to agriculture, farming, logging and charcoal burning, activities which had a
487 pronounced effect on the surrounding landscape (Rączkowska, 2019). As the onset of
488 increased anthropogenic activities around 1500 CE coincides with the changing patterns in
489 beetle diversity compared to vegetation diversity (Figure 6), it is plausible that the decline in
490 local beetle diversity was related to anthropogenic activity. However, as there are no
491 archaeological evidence or historical documents of human settlement in the vicinity of the
492 sampling site, these indications should be considered with caution.

493

494 4.3. Implications for nature conservation

495 This study recorded several saproxylic beetles (European Red List, Nieto and
496 Alexander, 2010), as well as the rare species *Dapsa denticollis* and *Graphoderus zonatus*.
497 The cryptic endomychid *D. denticollis* has been collected in xerothermic grassland and forest
498 steppe habitats in eastern and south-eastern Europe (Franc and Hemala, 2013) and a single
499 individual was found in sample 16 (1080 CE). *G. zonatus* is a large diving beetle which
500 inhabits peaty pools (Koch, 1989a) and was found in samples up to 1840 CE. This species is
501 currently rare in many regions in Europe due to a decline of its habitat (Knoblauch and
502 Gander, 2019). The identified saproxylic species in our study were only identified
503 sporadically and no trend in their occurrence was found. A study by Majzlan (2015) confirms
504 that all identified saproxylic species are currently found within 5 – 10 kilometres from the

505 sampling site Diera Hollow. However, several of the beetle species identified in this study
506 have a mostly unknown ecology and distribution. This especially concerns species with a
507 strictly montane habitat, living in or near peat bogs and marshes (e.g. the leaf beetle
508 *Chrysolina lichenis*; Burakowski et al., 1990). It gives reason to look beyond the
509 standardized red-list saproxylic species (Nieto and Alexander, 2010) and consider the beetle
510 community as a whole. At Diera Hollow, not only beetle taxa indicative for (old-growth) forest
511 changed drastically over the last millennium but also taxa living in the forest hollow. Our
512 findings suggest that the current forest ecosystem and forest beetle species composition
513 remain affected by changes in the landscape that started centuries ago, possibly by the
514 legacy of previous human impact in the area as was found in other European montane
515 regions (e.g. Valsecchi et al., 2010). As argued by Froyd and Willis (2018), the identification
516 of these past baselines and ecological thresholds would contribute to the conservation of
517 insects and other groups of plants and animals in Tatra National Park. Based on our results,
518 we recommend stakeholders of the national park to 1) look further back in time than only a
519 few hundreds of years when considering restoration strategies (e.g. before 1080 CE), 2)
520 include insect diversity in the targets and monitoring of restoration efforts; and 3) include
521 forest hollows and other inundated depressions in conservation strategies for the national
522 park.

523

524 **5. Conclusions**

525 The fossil beetle and pollen record from Diera Hollow suggest that changes in the
526 local beetle and vegetation record were linked to regional changes, most likely driven by
527 anthropogenic activity. The site developed from a semi-closed to closed montane Spruce-
528 Fir-Beech forest at 930 CE, to a more open landscape from 1080 CE onward. Human
529 activities in the region were first recorded in the beetle and pollen record around 1250 CE.
530 From around 1740 CE, human abandonment of the region and subsequently, the
531 establishment of Tatra National Park in 1949 CE resulted in the reestablishment of a closed
532 woodland, but of a different composition than the ancient woodland. While climate was an

533 important driver behind changes in the vegetation and beetle community, anthropogenic
534 activity likely played a significant role in determining the beetle and floristic diversity during
535 the past millennium. Our results suggest that diversity indices such as the Shannon Index
536 can be used to assess ecological thresholds of local flora and fauna through time. Based on
537 our findings, initiatives to restore the original landscape of this region should compare with
538 the situation before 1080 CE. Furthermore, we recommend including beetles and other
539 insect communities in the monitoring of restoration efforts of flora and fauna biodiversity in
540 montane nature reserves as they could contribute to understanding the baselines and
541 ecological thresholds in these regions. Due to the recorded historical presence of rare beetle
542 species connected to peat bogs, we also advise to include mountain peat bogs in studies on
543 biodiversity and nature conservation.

544

545 **6. Acknowledgments**

546 The curators of the visited insect collections (Jan Friedman of Plymouth City
547 Museum, Darren Mann of the Oxford Museum of Natural History, Lukas Sekerka of the
548 National Museum in Prague, Petr Baňář of the Moravian Museum in Brno and Oldřich
549 Hovorka of Muzeum Roztoky u Prahy) are thanked for providing access to their collections.
550 Secondly, many experts on different beetle families helped to confirm identification and for
551 some families, the ecology of species: Robert Angus, Emmanuel Arriaga Varela, Max
552 Barclay, Stanislav Benedikt, Jan Bezděk, Jens Esser, Martin Fikáček, Jiří Hajek, Oldřich
553 Hovorka, Paweł Jałoszynski, Aslak Kappel, Miloš Knížek, Igor Orloff, Darren Mann, David
554 Sommer and Jan Ružička. Pavol Minarčák from the Tatra Museum in Poprad is thanked for
555 providing information about historical events in the region.

556

557 NS, NK, HSS and JLC (PI) were supported by the Czech Science Foundation (16-
558 23183Y). NS was as well supported by the Czech University of Life Sciences (IGA
559 A_19_04). HSS was further supported by a long-term project of the Czech Academy of
560 Sciences (RVO 67985939).

561

562

563 **7. References**

564 Aaby, B., Digerfeldt, G., 1986. Sampling techniques for lakes and bogs, in: Berglund, B.E.,
565 (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley, N.Y., pp. 181 –
566 194.

567

568 Allen, C.D., Macalady, A.K., Chenchouni, H., et al., 2010. A global overview of drought and
569 heat-induced tree mortality reveals emerging climate change risks for forests. Forest
570 Ecology and Management, 259, 660 – 684. <https://doi.org/10.1016/j.foreco.2009.09.001>

571

572 Amori, G., Boitani, L., Milana, G., et al., 2019. Endemism and diversity in European montane
573 mammals: macro-ecological patterns. Biological Journal of the Linnean Society, 128(1), 225
574 – 237. <https://doi.org/10.1093/biolinnean/blz081>

575

576 Annighöfer, P., Beckschäfer, P., Vor, T., et al., 2015. Regeneration patterns of European oak
577 species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment
578 and neighborhood. PLoS ONE 10, e0134935. <https://doi.org/10.1371/journal.pone.0134935>

579

580 Behre, K-E, 1981. The interpretation of anthropogenic indicators in pollen diagrams. Pollen
581 Spores 23, 225 – 245.

582

583 Beug, H.J., 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende
584 Gebiete (Guide to the Pollen Analysis for Central Europe and the adjacent Areas). Pfeil,
585 München.

586

587 Biomap, 2019. Biodiversity Map of Polish Biodiversity Information Network (PoIBIN).
588 <https://baza.biomap.pl/about.php>

589

590 Bittinger, K., 2017. usedist: Distance Matrix Utilities. R package version 0.1.0.
591
592 Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an
593 autoregressive gamma process. *Bayesian Anal.* 6, 457 – 474. <https://doi.org/10.1214/11->
594 BA618
595
596 Brundin, L., 1934. *Die Coleopteren des Torneträskgebietes. Ein Beitrag zur Ökologie und*
597 *Geschichte der Käferwelt in Schwedisch-Lappland.* Lund.
598
599 Buckland, P.C., Kenward, H.K., 1973. Thorne moor – Palaeo-ecological study of a Bronze
600 Age site. *Nature* 241(5389), 405 – 406. <https://doi.org/10.1038/241405a0>
601
602 Buckland, P.I., Buckland, P.C., 2006. BugsCEP Coleopteran Ecology Package. IGBP
603 PAGES/World Data Center for Paleoclimatology Data Contribution Series # 2006-116.
604 NOAA/NCDC Paleoclimatology Program, Boulder CO, USA. <https://bugscep.com>
605
606 Burakowski, B., Mroczkowski, M. and Stefańska, J., 1990. Chrząszcze – Coleoptera.
607 Stonkowate – Chrysomelidae, część 1. Katalog Fauny Polski, XXIII, 16, Warszawa. [In
608 Polish].
609
610 Christen, J.A., Perez, S.E., 2009. A new robust statistical model for radiocarbon data.
611 *Radiocarbon* 51(3), 1047 – 1059. <https://doi.org/10.1017/S003382220003410X>
612
613 Cichocki, W., 2003. Animate nature and relationship between man and environment [in
614 Polish], in: Gładkiewicz, R., Homza, M. (Eds.), *Terra Scepusiensis*, Lewoca-Wroclaw, pp. 89
615 – 102.
616

617 Croudace, I.W., Rindby, A. and Rothwell, R.G, 2008. ITRAX: Description and Evaluation of a
618 New Multi-function X-ray Core Scanner. Geological Society, London, Special Publications,
619 267, 51 – 63.
620

621 Davies, S., Lamb, H. and Roberts, S., 2015. Micro-XRF Core Scanning in Palaeolimnology:
622 Recent Developments. In: Croudace, I., Rothwell, R. (eds) Micro-XRF Studies of Sediment
623 Cores. Developments in Paleoenvironmental Research, vol 17. Springer, Dordrecht
624

625 Dimitrov, D., Nogués-Bravo, D., Scharff, N., 2012. Why Do Tropical Mountains Support
626 Exceptionally High Biodiversity? The Eastern Arc Mountains and the Drivers
627 of *Saintpaulia* Diversity. PLOS ONE 7(11), e48908.
628 <https://doi.org/10.1371/journal.pone.0048908>
629

630 Elias, S.A., 2010. Advances in Quaternary Entomology. Elsevier, Amsterdam. ISBN:
631 9780444534248
632

633 Elsen, P.R., Tingley, M.J., 2015. Global mountain topography and the fate of
634 montane species under climate change. Nature Climate Change 5(8), 772–U192.
635 <https://doi.org/10.1038/nclimate2656>
636

637 Faegri, K., Iversen, J., 1989. Textbook of pollen analysis. Wiley and Sons, Chichester.
638

639 Forbes, V., Ledger, P.M., Cretu, D. et al., 2019. A Sub-centennial, Little Ice Age Climate
640 Reconstruction Using Beetle Subfossil Data from Nunalleq, Southwestern Alaska.
641 Quaternary International. <https://doi.org/10.1016/j.quaint.2019.07.011>
642

643 Fossen, E.I., Ekrem, T., Nilsson, A.N., et al., 2016. Species delimitation in northern
644 European water scavenger beetles of the genus *Hydrobius* (Coleoptera, Hydrophilidae).
645 *ZooKeys* 564, 71 – 120. <https://doi.org/10.3897/zookeys.564.6558>

646

647 Franc, V. and Hemala, V., 2014. Remarkable record of *Dapsa denticollis* (Coleoptera:
648 Endomychidae) in northern Slovakia. *Natura Tutelae, Liptovský Mikuláš: Slovenské múzeum*
649 *ochrany prírody a jaskyniarstva v Liptovskom Mikuláši* 18(2), 175 – 178. ISSN 1336-7609

650

651 Froyd, C.A. and Willis, K.J., 2008. Emerging issues in biodiversity & conservation
652 management: The need for a palaeoecological perspective. *Quaternary Science Reviews*
653 27, 1723 – 1732.

654

655 Gabriel, K.R., 1971. The Biplot Graphical Display of Matrices with Applications to Principal
656 Component Analysis. *Biometrika* 58(3), 453 – 467. <https://www.jstor.org/stable/2334381>

657

658 Gaillard, M.-J., 2013. Archaeological applications. In: Elias, S.A. (ed.), *The Encyclopedia of*
659 *Quaternary Science* 3, p. 880 – 904, Elsevier, Amsterdam.

660

661 Greb, 1934. Makklar, Matlatren in der Zips. *Karpathenland*, no. 7, p. 3 – 5; 39 – 44.

662

663 Grimm, E.C., 1990. TILIA and TILIA*GRAPH. PC spreadsheet and graphics software for
664 pollen data. *INQUA Working Group on Data-Handling Methods Newsletter* 4, 5e7.

665

666 Gustavsson, G., Lemdahl, G., Gaillard, M.-J., 2009. Abrupt forest ecosystem change in SW
667 Sweden during the late Holocene. *The Holocene* 19(5), 691 – 702.

668 <https://doi.org/10.1177/0959683609105293>

669

670 Hreško, J., Petrovič, F., Mišovičová, R., 2015. Mountain landscape archetypes of the
671 Western Carpathians (Slovakia). *Biodivers Conserv* 24, 3269 – 3283.

672 <https://doi.org/10.1007/s10531-015-0969-6>

673

674 Jambrich, M., 2007. Historical and current overview of negative anthropogenic impacts on
675 eastern part of Low Tatras. *Oecologia Montana* 16, 10 – 12. ISSN: 2644–4682
676

677 Jankovská, V. and Komárek, J., 1982. Das Vorkommen einiger Chlorokokkalalgen in
678 böhmischen Spätglazial und Postglazial. *Folia geobot. phytotax.* 17, 165.
679

680 Jowsey, P.C., 1965. An improved peat sampler. *New Phytologist* 65, 245 – 248.
681 <https://doi.org/10.1111/j.1469-8137.1966.tb06356.x>
682

683 Juggins, S., 2003. UserGuide C2, Software for Ecological and Palaeoecological
684 DataAnalysisand Visualisation, User Guide Version 1.3. Department of Geography,
685 Newcastle.
686

687 Kassambara, A., Mundt, F., 2017. factoextra: Extract and Visualize the Results of
688 Multivariate Data Analyses. R package version 1.0.5.
689

690 Kessler, M., Kluge, J., 2008. Diversity and endemism in tropical montane forests – From
691 patterns to processes, in: Gradstein, S.R., Homeier, J., Gansert, D. (Eds.), *Tropical montane*
692 *cloud forests – patterns and processes in a biodiversity hotspot*, Biodiversity and Ecology
693 Series 2, Univ. Göttingen, Göttingen.
694

695 Kidwell, S.M., 2015. Biology in the Anthropocene: Challenges and insights from young fossil
696 records. *PNAS* 112(16), 4922 – 4929.
697

698 Knoblauch, A., Gander, A., 2019. Distribution of a residual population of the Dytiscid
699 *Graphoderus bilineatus* (de Geer, 1774) in the Grande Cariçaie nature reserves,
700 Switzerland. *Alpine Entomology* 3, 83 – 91. <https://doi.org/10.3897/alpento.3.30417>
701

702 Koch, K., 1989a. Die Käfer Mitteleuropas, Ökologie 1. Goecke and Evers, Krefeld.
703
704 Koch, K., 1989b. Die Käfer Mitteleuropas, Ökologie 2. Goecke and Evers, Krefeld.
705
706 Koch, K., 1992. Die Käfer Mitteleuropas, Ökologie 3. Goecke and Evers, Krefeld.
707
708 Komárek, J. and Fott, B., 1985. Chlorophyceae (Grünalgen), Ordnung Chlorococcales.
709 Nordic Journal of Botany 5(1), 111.
710
711 Laibner, S. 2000. Elateridae of the Czech and Slovak Republics. Kabourek, Zlin.
712
713 La Sorte, F.A., Jetz, W., 2010. Projected range contractions of montane biodiversity under
714 global warming. Proceedings of the Royal Society B-Biological Sciences 277(1699), 3401 –
715 3410. <https://doi.org/10.1098/rspb.2010.0612>
716
717 Legendre, P. and Legendre, L., 2012. Numerical Ecology- Chapter 8, Cluster Analysis.
718 Elsevier, Amsterdam.
719
720 Lindbladh, M, Fraver, S, Edvardsson, J. et al., 2013. Past forest composition, structures and
721 processes – How paleoecology can contribute to forest conservation. Biological
722 Conservation 168, 116 – 127.
723
724 Liu, A.G., Kenchington, C.G., Mitchell, E.G., 2015. Remarkable insights into the
725 paleoecology of the Avalonian Ediacaran macrobiota. Gondwana Research 27(4), 1355 –
726 1380. <https://doi.org/10.1016/j.gr.2014.11.002>
727
728 Longman, J., Veres, D. and Wennrich, V., 2019. Utilisation of XRF core scanning on peat
729 and other highly organic sediments. Quaternary International 514 (SI), 85 – 96.

730

731 Magyari, E.K., Jakab, G., Balint, M. et al., 2012. Rapid vegetation response to Lateglacial
732 and early Holocene climatic fluctuation in the South Carpathian Mountains (Romania).

733 Quaternary Science Reviews 35, 116 – 130. <https://doi.org/10.1016/j.quascirev.2012.01.006>

734

735 Majzlan, O., 2015. *Chrobáky (Coleoptera) Tatier*. Scientica, s.r.o, Bratislava. [In Slovakian].

736

737 McCain, C.M. and Colwell, R.K., 2011. Assessing the threat to montane biodiversity from
738 discordant shifts in temperature and precipitation in a changing climate. Ecology Letters 14,

739 1236 – 1245. <https://doi.org/10.1111/j.1461-0248.2011.01695.x>

740

741 Ministry of Environment of the Slovak Republic, 2005. The Fourth National Communication
742 of the Slovak Republic on Climate Change. <https://unfccc.int/resource/docs/natc/sknc4.pdf>

743

744 Mirkin, B., 2005. Clustering: a data recovery approach. Chapman and Hall, CRCPress.

745

746 Niedźwiedz, T., 2004. Rekonstrukcja warunków termicznych lata w Tatrach od roku 1550 [in
747 Polish], in: Kotarba, A. (Ed.), Rola Małej Epoki Lodowej w przekształcaniu środowiska

748 przyrodniczego Tatr. Prace Geogr 197, pp 57 – 88.

749

750 Nieto, A. and Alexander, K.N.A., 2010. European Red List of Saproxylic Beetles.

751 Luxembourg: Publications Office of the European Union.

752 [https://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_s](https://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_saproxylic_beetles.pdf)
753 [aproxylic_beetles.pdf](https://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_saproxylic_beetles.pdf)

754

755 Nikolov, C., Konôpka, B., Kajba, M. et al., 2014. Post-disaster Forest Management and Bark
756 Beetle Outbreak in Tatra National Park, Slovakia. Mountain Research and Development

757 34(4), 326 – 335. <https://doi.org/10.1659/MRD-JOURNAL-D-13-00017.1>

758

759 Oksanen, J., Blanchet, F.G., Friendly, M. et al., 2019. vegan: Community Ecology Package.
760 R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>

761

762 Olah, M., Boltižiar, M., Gallay, I., 2009. Transformation of the Slovak cultural landscape
763 since the 18th cent. and its recent trends. *Journal of Landscape Ecology* 2(2), 41 – 55.
764 <https://doi.org/10.2478/v10285-012-0018-z>

765

766 Overballe-Petersen, M.V. and Bradshaw, R.H.W., 2011. The selection of small forest
767 hollows for pollen analysis in boreal and temperate forest regions. *Palynology* 35, 146 – 153.
768 <https://doi.org/10.1080/01916122.2011.558173>

769

770 Overpeck, J.T., Webb, T., Prentice, I.C., 1985. Quantitative Interpretation of Fossil Pollen
771 Spectra—Dissimilarity Coefficients and the Method of Modern Analogs. *Quaternary*
772 *Research* 23(1), 87 – 108. [https://doi.org/10.1016/0033-5894\(85\)90074-2](https://doi.org/10.1016/0033-5894(85)90074-2)

773

774 Pavercsik, I., 2003. *Scepusia* in Hungarian historiography [in Hungarian], in: Gladkiewicz, R.,
775 Homza, M. (Eds.) *Terra Scepusiensis*, Lewoca-Wroclaw. ISBN 80-7114-457-6

776

777 Pielou, E.C., 1967. The use of information theory in the study of the diversity of biological
778 populations. *Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and*
779 *Probability, Volume 4: Biology and Problems of Health*, 163 – 177, University of California
780 Press, Berkeley, Calif. <https://projecteuclid.org/euclid.bsmsp/1200513792>

781

782 Poto, L., Gabrieli, J., Crowhurst, S. et al., 2015. Cross calibration between XRF and ICP-MS
783 for high spatial resolution analysis of ombrotrophic peat cores for palaeoclimatic studies.
784 *Anal Bioanal Chem* 407, 379 – 385.

785

786 Pfeffer, A., 1989. *Kůrovcovití Scolytidae a jádrohlodovití Platypodidae*. Academia, Praha [in
787 Czech]. ISBN 80-200-0089-5.
788

789 Punt, W. (Ed.) (1976-2003) *The Northwest European Pollen Flora I-VII*. Elsevier,
790 Amsterdam.
791

792 R Core Team (2018). R: A language and environment for statistical computing. R
793 Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
794

795 Rączkowska, Z., 2019. Human impact in the Tatra Mountains. *Cuadernos de Investigacion*
796 *Geografica* 45(1): 219 – 244. <https://doi.org/10.18172/cig.3661>
797

798 Renburg, I., Brännvall, M-L., Bindler, R. et al., 2009. Atmospheric Lead Pollution History
799 during Four Millennia (2000 BC to 2000 AD) in Sweden. *AMBIO A Journal of the Human*
800 *Environment* 29, 150 – 156. <https://doi.org/10.1579/0044-7447-29.3.150>
801

802 Reille, M., 1992–1998. *Pollen et spores d'Europe et d'Afrique du Nord*. Lab Bot Hist Palynol,
803 Marseille.
804

805 Reimer, P.J., Bard, E., Bayliss, A. et al., 2013. IntCal13 and Marine13 Radiocarbon Age
806 Calibration Curves 0–50,000 Years cal BP. *Radiocarbon* 55(4), 1869 – 1887.
807 https://doi.org/10.2458/azu_js_rc.55.16947
808

809 Robinson, M.A., 1991. The Neolithic and Late Bronze Age insect assemblages, in:
810 Needham, S., (Ed.), *Excavation and salvage at Runnymede Bridge, 1978: the Late Bronze*
811 *Age waterfront site*. British Museum Press, London, pp. 277 – 325.
812

813 Robinson, M.A., 2000. Coleopteran evidence for the elm decline, Neolithic activity in
814 woodland, clearance and the use of the landscape, in: Fairbairn, A.S. (Ed.), Plants in
815 Neolithic Britain and Beyond (Neolithic studies group seminar papers 5) Oxford: Oxbow
816 Books, pp. 27 – 36.

817

818 Schelhaas, M-J., Nabuurs, G-J, Schuck, A., 2003. Natural disturbances in the European
819 forests in the 19th and 20th centuries. *Global Change Biology* 9(11), 1620 – 1633.
820 <https://doi.org/10.1046/j.1365-2486.2003.00684.x>

821

822 Shannon, C.E. and Weaver, W., 1949. The mathematical theory of communication. The
823 University of Illinois Press, Urbana, 117pp.

824

825 Simpson, G.L., 2007. Analogue Methods in Palaeoecology: Using the analogue Package.
826 *Journal of Statistical Software* 22(2), 1 – 29. <https://doi.org/10.18637/jss.v022.i02>

827

828 Smith. D., Whitehouse, N., Bunting, J.M. et al., 2010. Can we characterise ‘openness’ in the
829 Holocene palaeoenvironmental record? Modern analogue studies of insect faunas and
830 pollen spectra from Dunham Massey deer park and Epping Forest, England. *The Holocene*
831 20(2), 215 – 229. <https://doi.org/10.1177/0959683610350392>

832

833 Turnock, D., 2002. Ecoregion-based conservation in the Carpathians and the land-use
834 implications. *Land Use Policy* 19(1), 47 – 63. [https://doi.org/10.1016/S0264-8377\(01\)00039-](https://doi.org/10.1016/S0264-8377(01)00039-4)
835 4

836

837 UNESCO: High Tatra Mountains biosphere reserve. [http://www.unesco.org/new/en/natural-](http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/europe-north-america/polandslovakia/tatra/)
838 [sciences/environment/ecological-sciences/biosphere-reserves/europe-north-](http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/europe-north-america/polandslovakia/tatra/)
839 [america/polandslovakia/tatra/](http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/europe-north-america/polandslovakia/tatra/)

840

841 Valsecchi, V., Carraro, G., Conedera, M. et al., 2010. Late-Holocene vegetation and land-
842 use dynamics in the Southern Alps (Switzerland) as a basis for nature protection and forest
843 management. *The Holocene* 20(4), 483 – 495. <https://doi.org/10.1177/0959683609355178>
844

845 van Dijk, A.I.J.M. and Keenan, R.J., 2007. Planted forests and water in perspective. *Forest*
846 *Ecology and Management* 251 (1–2), 1 – 9. <https://doi.org/10.1016/j.foreco.2007.06.010>
847

848 van Geel, B., Coope, G.R., van der Hammen, T., 1989. Paleoecology and stratigraphy of the
849 Late Glacial type section at Usselo (The Netherlands). *Review of Paleobotany and*
850 *Palynology* 60 (1–2), 25 – 129. [https://doi.org/10.1016/0034-6667\(89\)90072-9](https://doi.org/10.1016/0034-6667(89)90072-9)
851

852 Ward, J.H., 1963. Hierarchical Grouping to Optimize an Objective Function. *Journal of the*
853 *American Statistical Association* 58, 236 – 244
854 <https://doi.org/10.1080/01621459.1963.10500845>
855

856 Whitehouse, N.J., 2004. Mire ontogeny, environmental and climatic change inferred from
857 fossil beetle successions from Hatfield Moors, eastern England. *The Holocene* 14(1), 79 –
858 93. <https://doi.org/10.1191/0959683604hl691rp>
859

860 Whitehouse, N.J., 2006. The Holocene British and Irish ancient forest fossil beetle fauna:
861 implications for forest history, biodiversity and faunal colonization. *Quaternary Science*
862 *Reviews* 25, 1755 – 1789. <https://doi.org/10.1016/j.quascirev.2006.01.010>
863

864 Wickham, H., 2016. *Ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York,
865 2016.
866

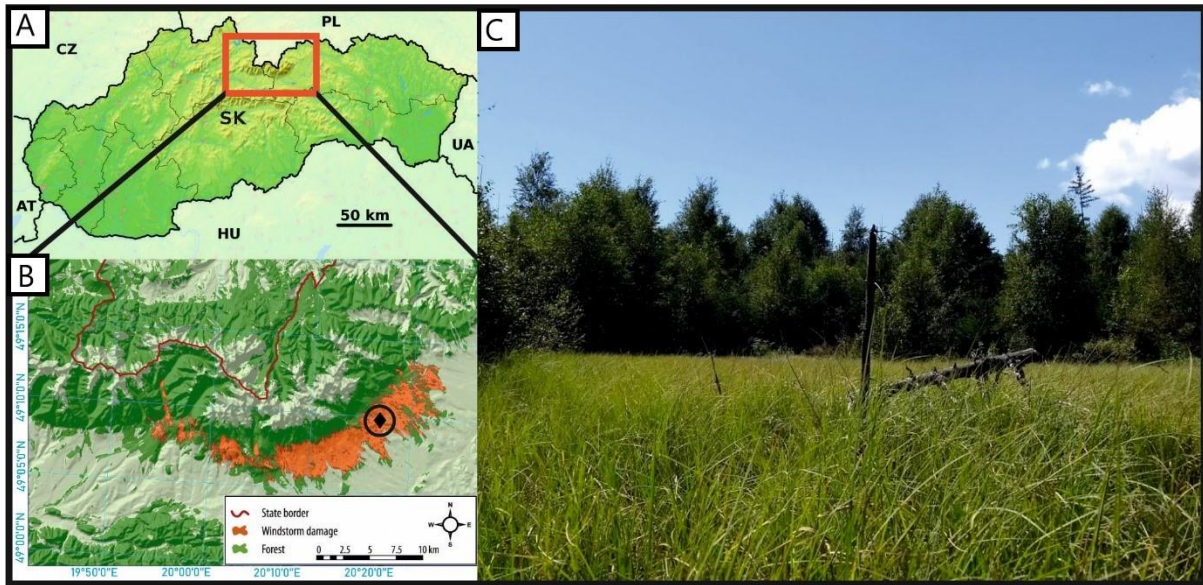
867 Wickham, H., 2017. tidyverse: Easily Install and Load the 'Tidyverse'. R package version
868 1.2.1. <https://CRAN.R-project.org/package=tidyverse>

869

870 Wickham, H., François, R., Henry, L., et al., 2019. dplyr: A Grammar of Data Manipulation. R

871 package version 0.8.3. <https://CRAN.R-project.org/package=dplyr>

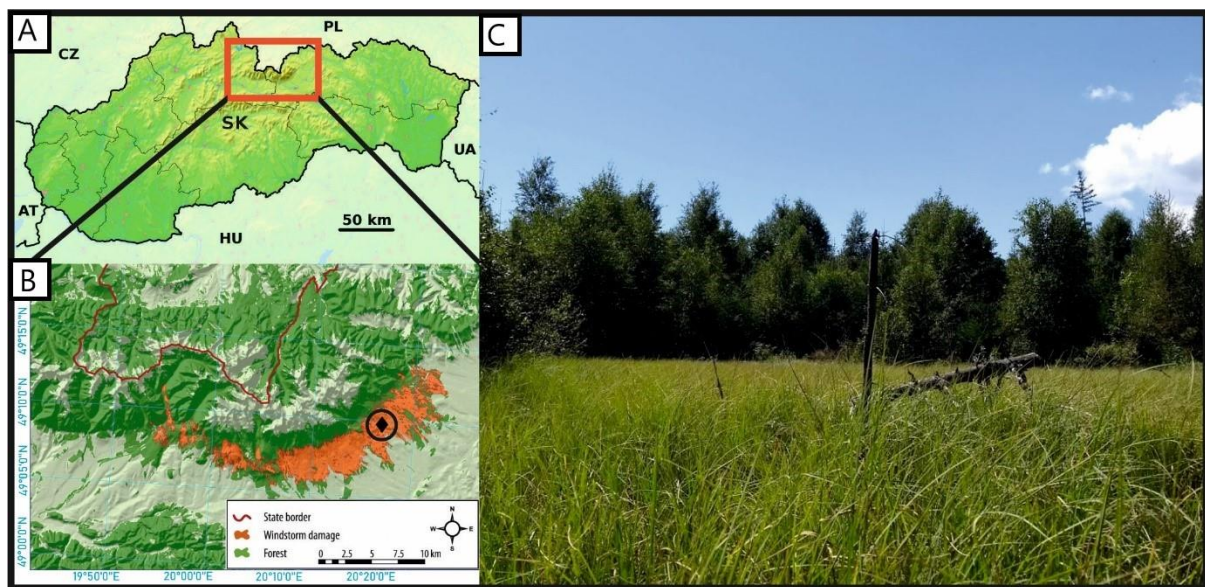
872



873

874 Zámečniková, H., 2008. Pastoralism. University of Zilina, ISBN 978-80-88923-16-9.

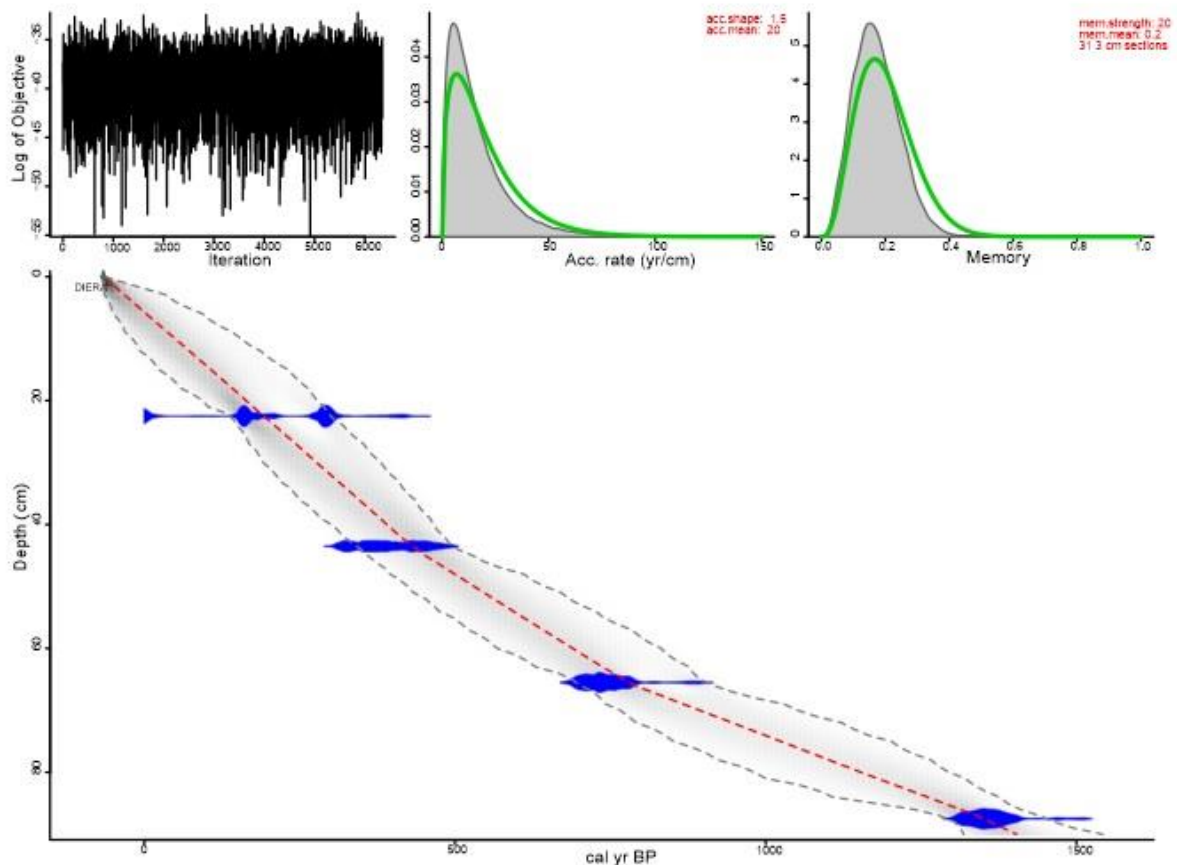
875 **Figure captions**



876

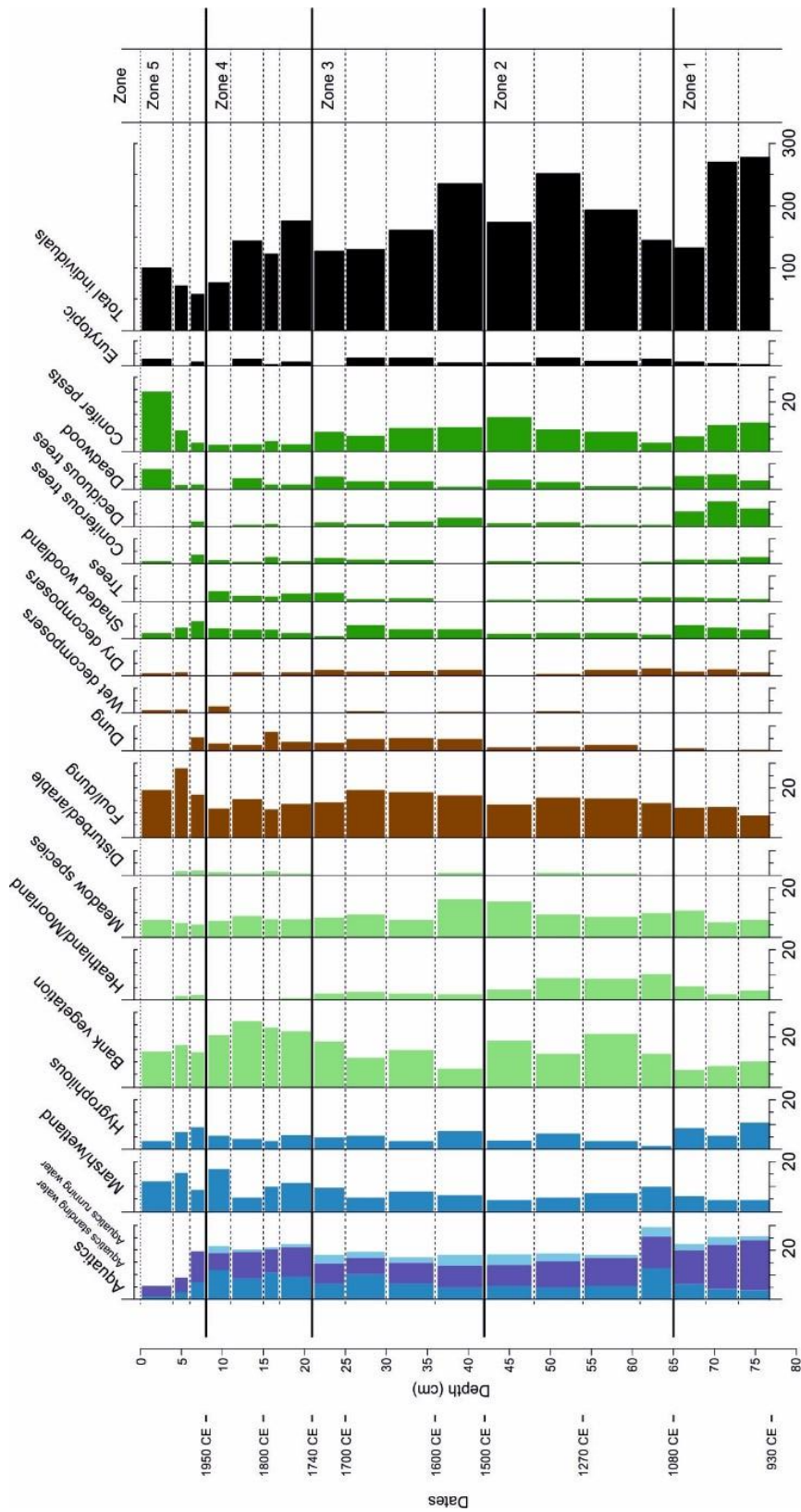
877

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



883

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



892

893

Figure 3 Coleoptera functional groups (in percentage of the total number of individuals) from Diera

894

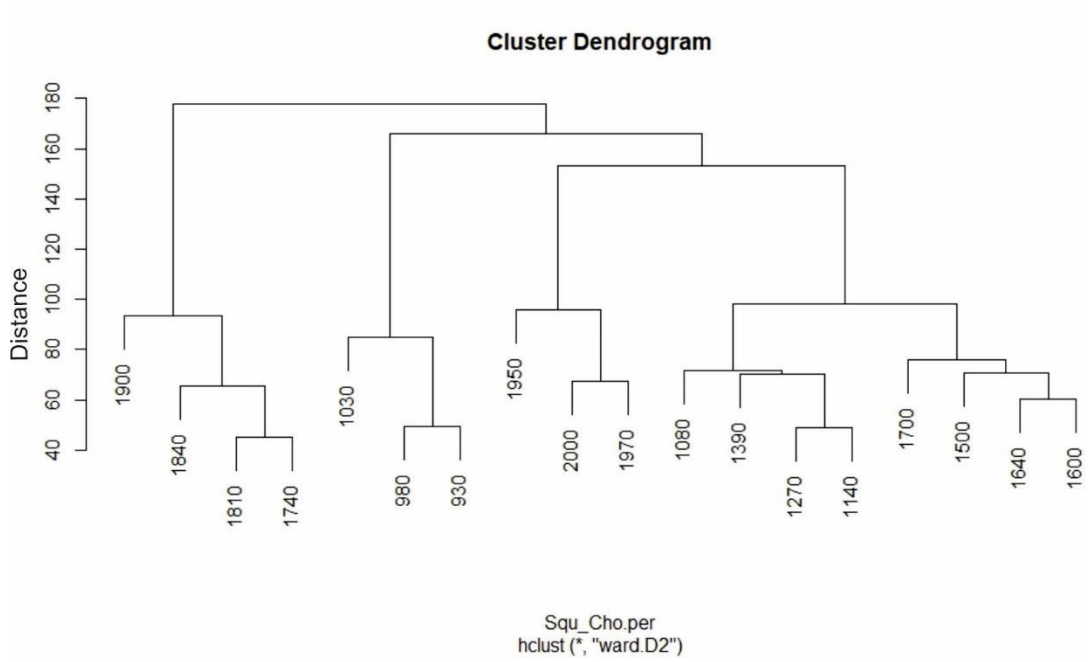
Hollow. According to a D-chord cluster analysis, the section was divided into five zones. Depth and age

895

are presented on the y-axis according to chronology based on a Bacon age-depth model (Figure S1).

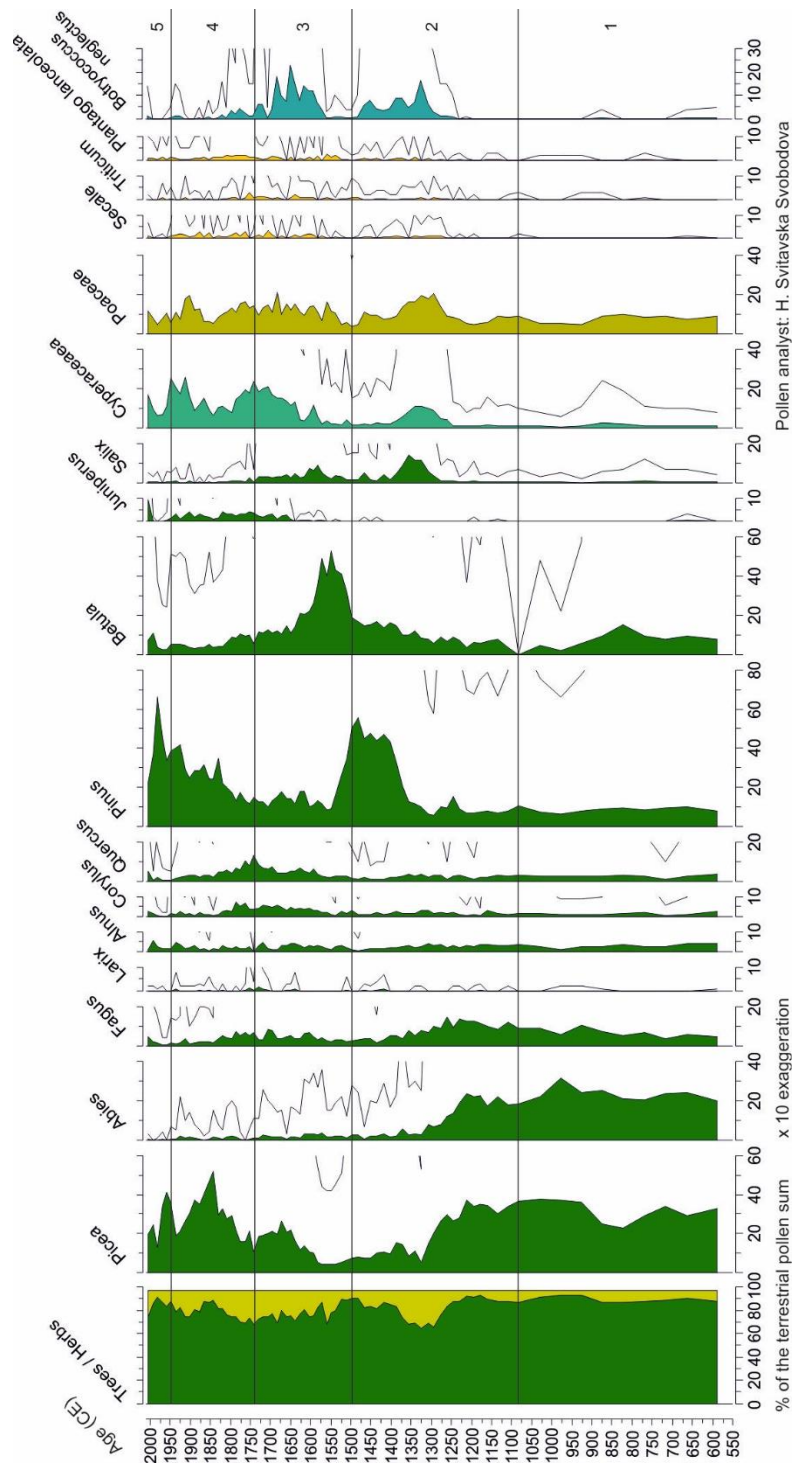
896

897
898
899



900
901
902
903

Figure 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.



904

905

Figure 5 Percentage pollen diagram from Diera Hollow. The pollen curves show the percentages of each

906

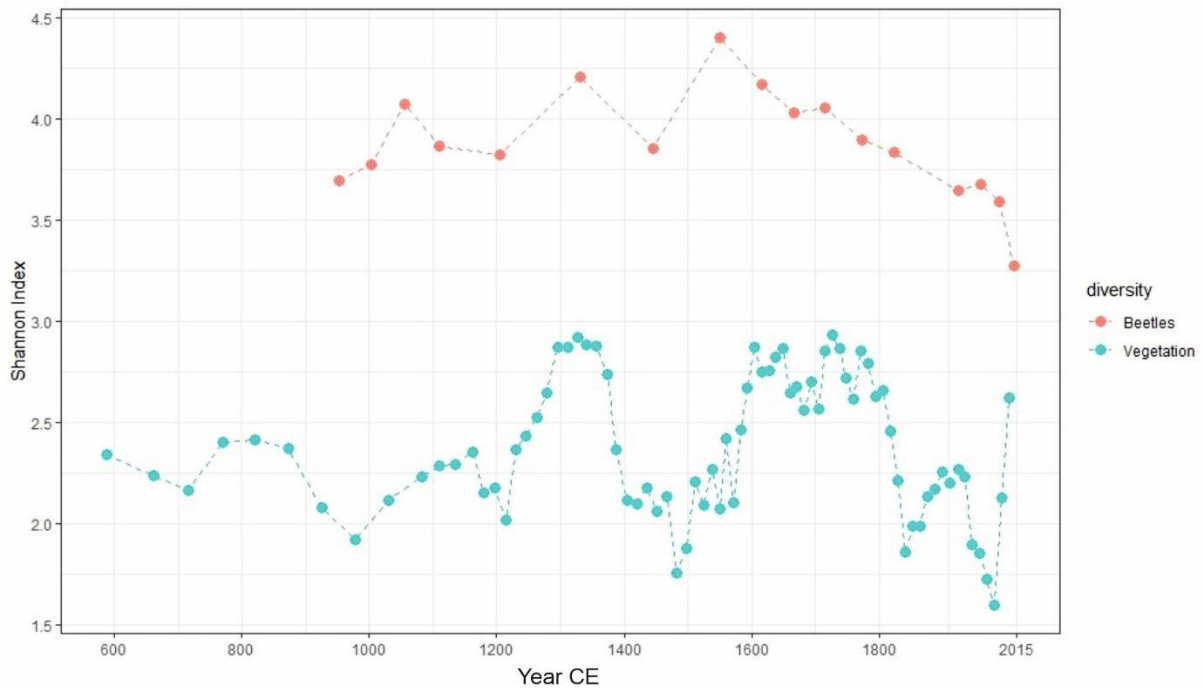
taxa calculated from the terrestrial pollen sum, with trees/shrubs and herb taxa pooled together in the

907

most-left column. Zonation is based on the cluster analysis of the fossil beetle assemblage from the

908

same site.

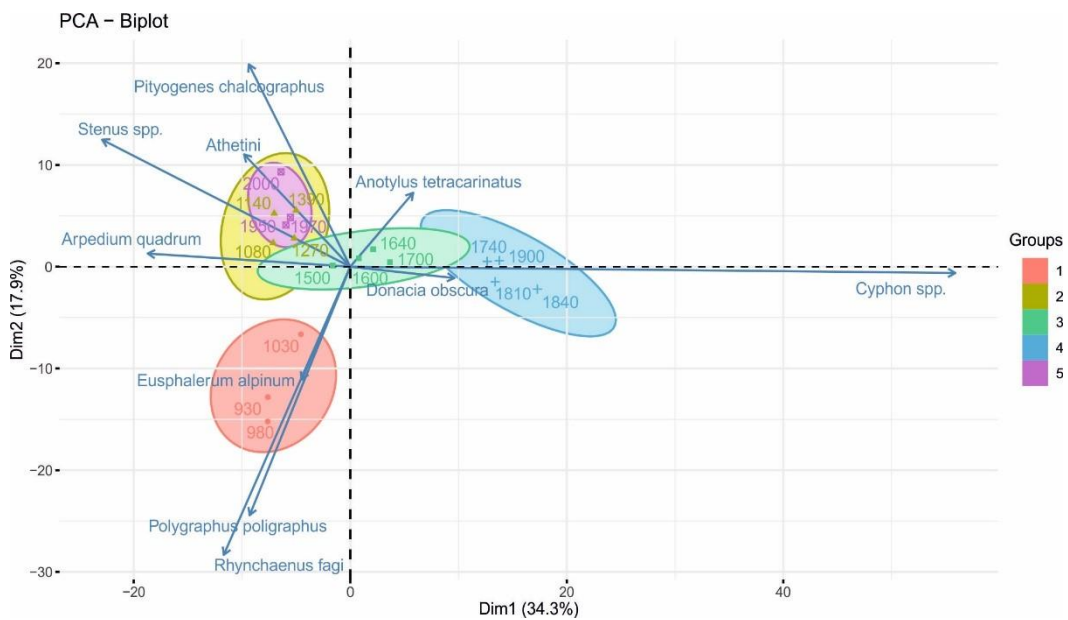


909

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

913

914



915

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

919

| Sample depth (cm) | Lab code | Dated material | Measured C¹⁴ age (BP) | Calibrated age (yr BP) | Mean (yr BP) |
|--------------------------|-----------------|------------------------|---|-------------------------------|---------------------|
| 22-23 | Poz-91232 | Botanical macrofossils | 230 ± 30 | 278-94 | 164 |
| 43-44 | Poz-91233 | Botanical macrofossils | 335 ± 30 | 491-336 | 426 |
| 65-66 | Poz-91235 | Botanical macrofossils | 830 ± 30 | 894-688 | 772 |
| 87-88 | Poz-91236 | Botanical macrofossils | 1470 ± 30 | 1440-1280 | 1340 |

920

921 **Table S1 Radiocarbon dates from core DIE-16, taken in 2016 from Diera Hollow, High Tatra Mountains,**
922 **Slovakia.**

923

924 **Table S2 Full species list of identified Coleoptera remains at Diera Hollow.**

925

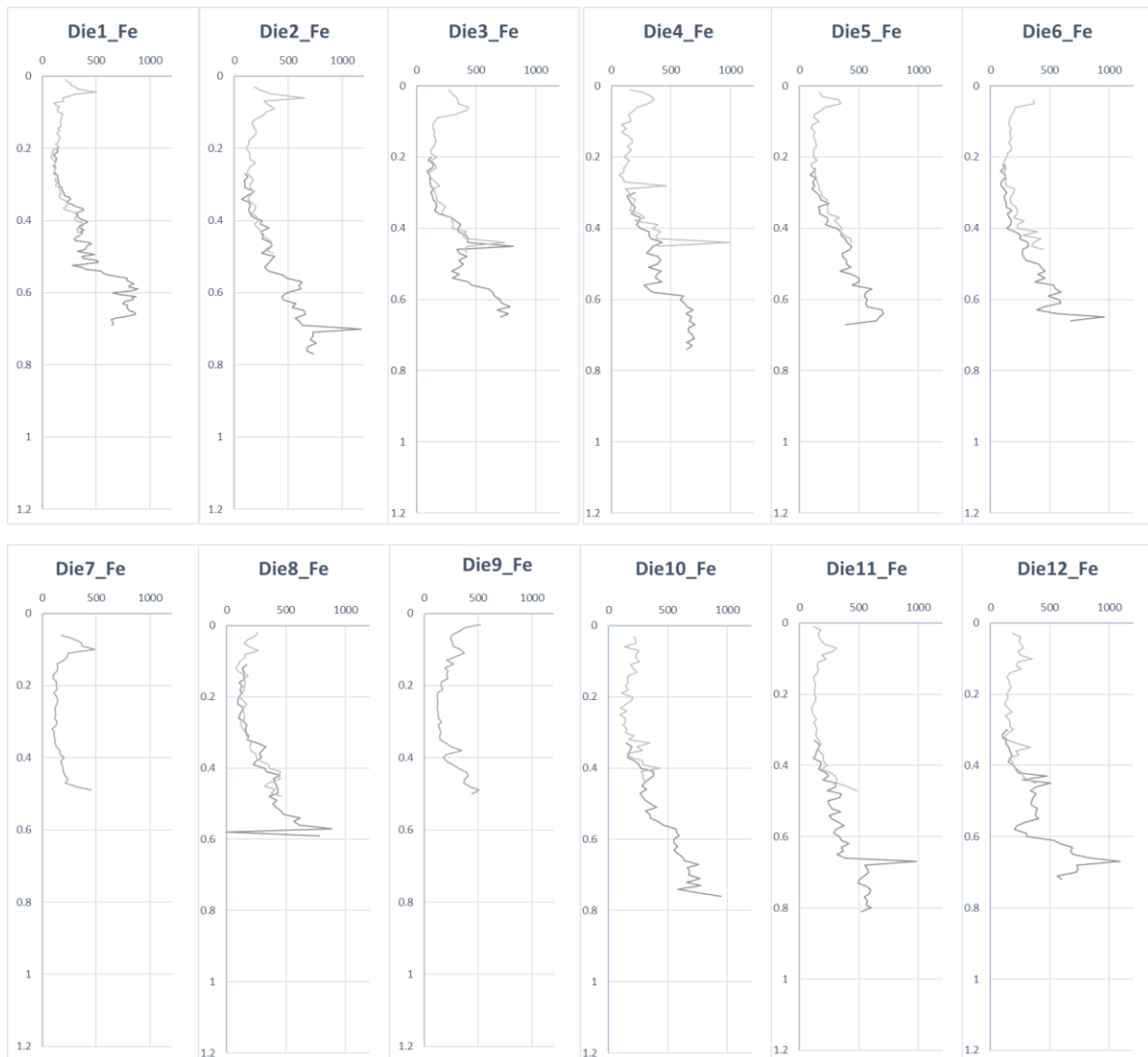


926

927 **Figure S1 XRF curves for atmospheric lead (Pb) for the 12 cores taken from Diera Hollow, together with**

928 **the XRF curve of master core DIE-16.**

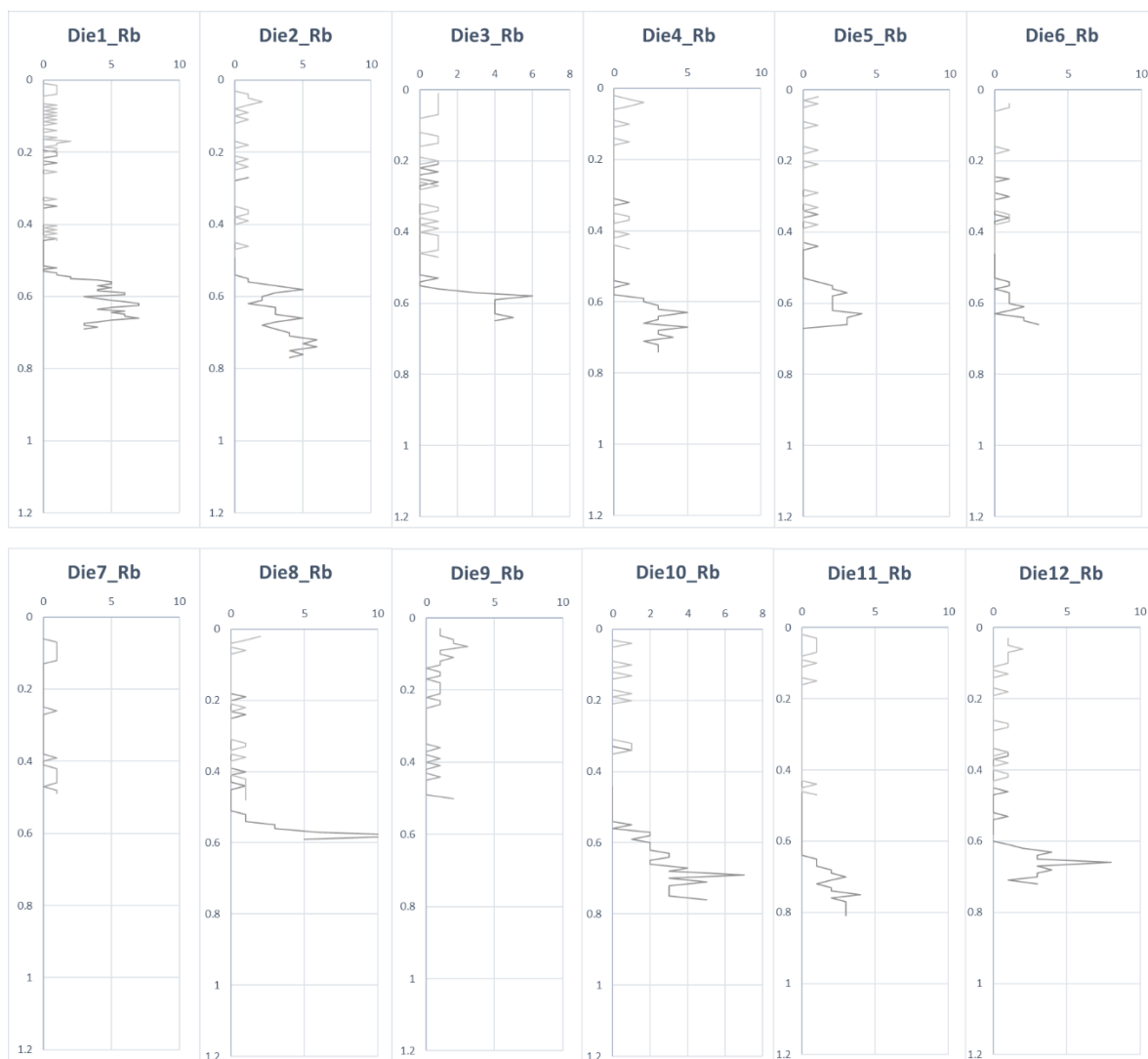
929



930

931 **Figure S2 XRF curves for rubidium (Rb) for the 12 cores taken from Diera Hollow, together with the XRF**
 932 **curve of master core DIE-16.**

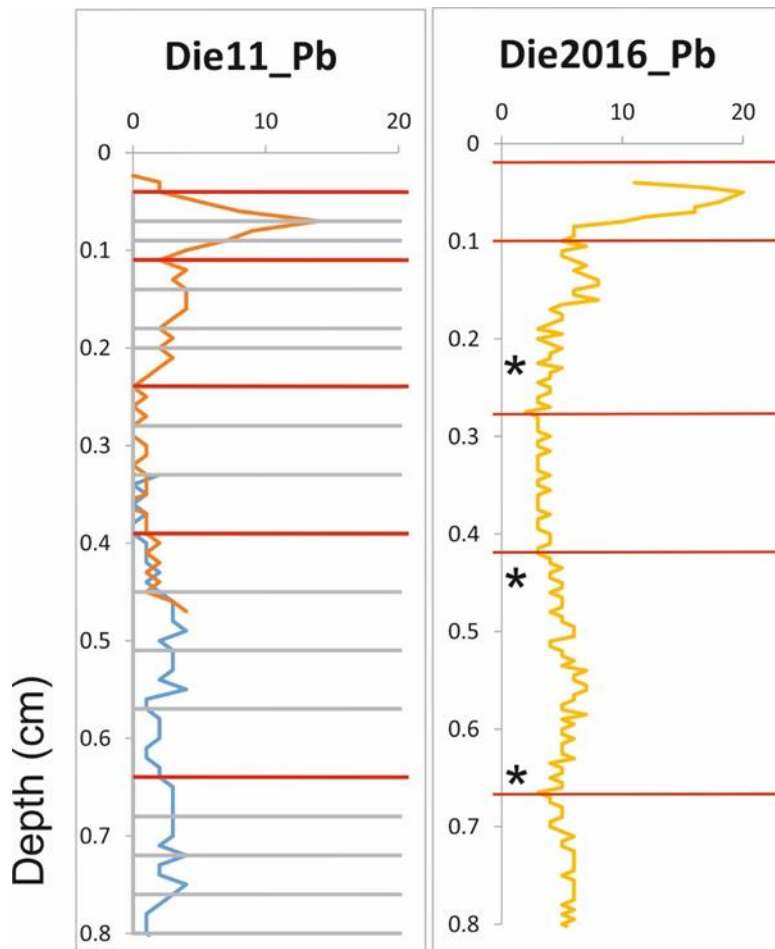
933



934

935 **Figure S3 XRF curves for iron (Fe) for the 12 cores taken from Diera Hollow, together with the XRF curve**
 936 **of master core DIE-16.**

937



Atmospheric lead (Pb) content

938

939

940

941

942

943

944

945

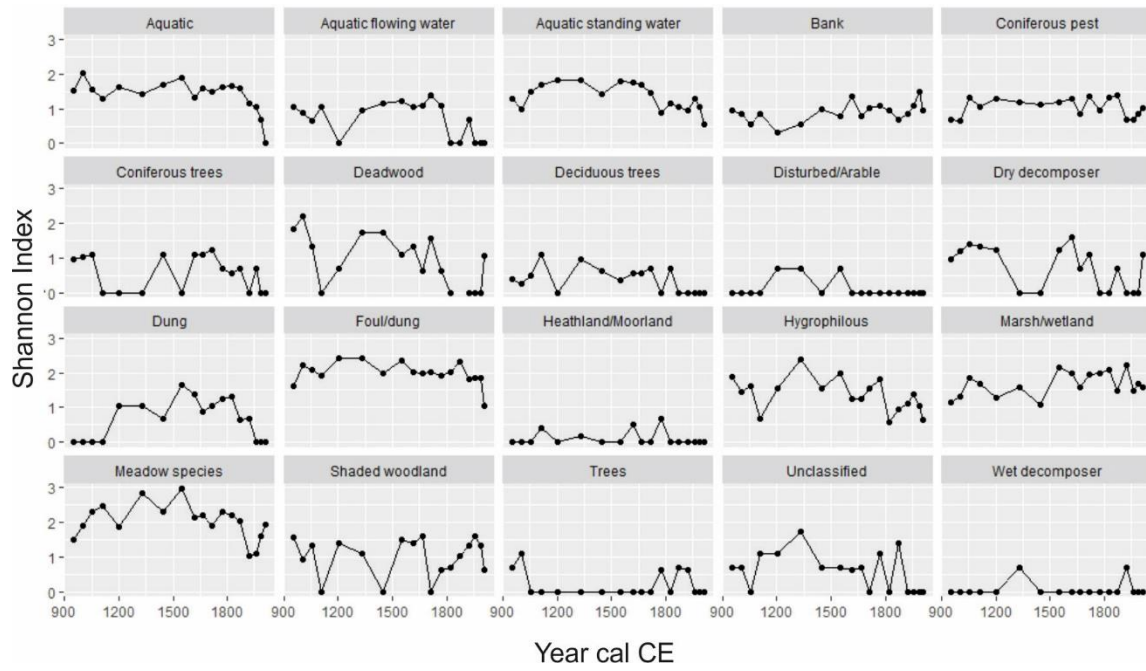
946

947

948

949

Figure S4 Comparison of the atmospheric lead (Pb) signals of core Die11 with the master core Die2016 which was radiocarbon dated at four different depths (Table S1, black asterix; three depicted). The cores were divided into five zones (red lines) according to the atmospheric lead signal and, primarily for the lower part of the cores, according to iron (Fe) and rubidium (Rb) concentrations. Cores Die1-Die10 and Die12 were correlated to Die11 in a similar way by wiggle-matching. Zones were divided in three or four samples, where possible in accordance with their geochemical signals. The lowest two zones were often less straightforward to distinguish and evenly divided in four samples. This resulted in 18 samples of unequal size. Depths of the upper and lower boundaries of each sample (red and grey bars in core Die11) were extrapolated to the depths of the master core and then compared to the age-depth model from the master core (See figure S1) in order to determine the upper and lower age boundary of each sample.



950

951 **Figure S5 Shannon Index partitioning for the different beetle ecological groups.**

952