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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**

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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

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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). 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

4

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 m^2) 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

5

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 (C_2H_5OH). 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 Roztoky 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

7

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 cm^3 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

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, Figure 3). In figure 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 Figure S1 – S4). The beetle record was divided into five distinctive zones according to the hierarchical cluster analysis (Figure 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 (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 abundant species (5.3 %) from the remaining 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

11

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

12

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

13

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

14

393   also *Silpha tristis*, known to feed on carrion (Koch, 1989a), *Limonius 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

15

421 increase in herding activities. Since both *S. lunatulum/ 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 Zámečniková, 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 restauration 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

561

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Figure captions

875

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

881

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

890

891 **Figure 3 Coleoptera functional groups (in percentage of the total number of individuals) from Diera**
892 **Hollow. According to a D-chord cluster analysis, the section was divided into five zones. Depth and age**
893 **are presented on the y-axis according to chronology based on a Bacon age-depth model (Figure S1).**

894

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

898

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

903

Figure 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.

Figure 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.

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

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

Figure S1 XRF curves for atmospheric lead (Pb) for the 12 cores taken from Diera Hollow, together with the XRF curve of master core DIE-16.

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

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

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 asterixis; 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.

936 from the master core (See figure S1) in order to determine the upper and lower age boundary of each

937 sample.

938

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

940