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1 **Recent changes in chironomid communities and hypolimnetic oxygen conditions**
2 **relate to organic carbon in subarctic ecotonal lakes**

3

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26 **Abstract**

27

28 A key question in aquatic elemental cycling is related to the influence of bottom water oxygen
29 conditions in regulating the burial and release of carbon under climate warming. In this study, we
30 used head capsules of Chironomidae larvae to assess community and diversity change between the
31 past (estimated as Pre-Industrial Period) and present and to reconstruct changes in hypolimnetic
32 oxygen conditions from 30 subarctic ecotonal lakes (northeastern Lapland) using the top-bottom
33 paleolimnological approach applying surface sediment (topmost 0-2 cm) and reference (4-5 cm)
34 samples. Subsequently, we tested the findings against dissolved organic carbon (DOC)
35 concentration of the sites. We found that the benthic communities were statistically dissimilar
36 between the past and the present with largest changes occurring in the more transparent oligo-
37 mesohumic lakes. However, murky polyhumic lakes displayed uniformly a decrease in diversity.
38 The chironomid-inferred oxygen values showed a general decrease towards the present with largest
39 shifts in low-DOC lakes, whereas no significant changes were found in the hypolimnetic oxygen
40 conditions of high-DOC lakes, which were often located in wetland areas. These finding suggest
41 that lakes associated with constant organic carbon inputs are more resilient toward climate-induced
42 reductions in hypolimnetic oxygen.

43

44 *Keywords:* Chironomidae; dissolved oxygen; Lapland; DOC; paleolimnology; top-bottom approach

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51 **1 Introduction**

52

53 Carbon storage in high-latitude peatlands represents a major share of the global soil carbon pool
54 (Tranvik et al., 2009; Schuur et al., 2015). With permafrost thawing and subsequent formation of
55 thaw lakes, larger emissions of carbon dioxide (CO₂) and methane (CH₄) are expected (Walter et
56 al., 2006; Wauthy et al., 2018). Since lakes are important sources of greenhouse gases (Aben et al.,
57 2017), in the context of climate change, it is essential to understand how carbon release is regulated
58 by different levels of oxygen availability at the surface-sediment interface of lakes (Liikanen et al.,
59 2002). Although there is CH₄ formation also in oxic water layers (Tang et al., 2016), CH₄ is mostly
60 produced by anoxic decomposition of organic carbon and, importantly for the ongoing climate
61 change, it has a multifold atmospheric warming potential compared to CO₂ (Deemer et al., 2016).

62 While in lakes with well-oxygenated bottom waters a significant part of the produced
63 CH₄ is oxidized into CO₂ and not emitted to the atmosphere, a contrasting situation occurs in
64 oxygen depleted lakes. In addition to hypolimnetic oxygen, there appears to be a consistent
65 temperature dependency of CH₄ fluxes across microbial to ecosystem scales (Yvon-Durocher et al.,
66 2014) that well-represents the cascading climate change impacts and feedback systems. In
67 particular, methanogenesis, carried out by strictly anaerobic Archaea, is the terminal step in the
68 remineralization of organic matter and, like most other forms of metabolism, methanogenesis is
69 temperature-dependent (Yvon-Durocher et al., 2014). Therefore, since climate warming is
70 emphasized in subarctic and arctic regions (Linderholm et al., 2018), northern lakes play a
71 significant role in the ongoing climate change through their functions in carbon release and
72 sequestration.

73 Chironomid (Insecta: Diptera: Chironomidae) larvae take part in benthic processes
74 that are essential for lake ecosystem functions (Benke and Huryn, 2010; Hölker et al., 2015). Most
75 importantly, chironomids living in the water-sediment interface have a major role in the

76 biogeochemical cycling of carbon, nitrogen and phosphorus (Nogaro et al., 2008; Belle et al., 2017).
77 The functional roles of chironomids are mostly reflected by their feeding preferences (Heino, 2008;
78 Luoto and Nevalainen, 2015), but their taxonomical compositions typically respond to climate
79 conditions at the regional scale (Brooks, 2006) and hypolimnetic oxygen and nutrient conditions at
80 the local/site-specific scale (Brodersen and Quinlan, 2006). In Finnish Lapland, the most important
81 environmental factors controlling chironomid distribution and abundance are temperature, organic
82 content of the sediment, nutrients/oxygen and water depth (Olander et al., 1997; Nyman et al., 2005;
83 Luoto et al., 2016). Hence, chironomids contribute as sensitive indicators of climate changes,
84 limnology and elemental cycling. The influence of temperature on chironomids can be direct
85 (metabolism) or indirect (e.g. habitat) and mediated through air (flying adults) or water (aquatic
86 larval stage) temperature (Eggermont and Heiri, 2012), whereas the influence of hypolimnetic
87 oxygen is related to the species-specific respiration rates and oxygen demands (Brodersen et al.,
88 2008). Using the transfer function approach (calibration-in-space), it is possible to provide long-
89 term quantitative reconstructions of these variables (Quinlan and Smol, 2002; Luoto et al., 2017;
90 Wohlfarth et al., 2018).

91 In this study, we investigate chironomid assemblages and changes in chironomid-
92 inferred hypolimnetic oxygen conditions in 30 subarctic lakes in northern Finnish Lapland using the
93 top-bottom (or before-after) paleolimnological approach (Quinlan and Smol, 2002), where the
94 surface sediment samples (top) represent the present and the reference samples (bottom) the past.
95 We examine the findings against the modern dissolved organic carbon (DOC) gradient of the lakes
96 to find out potential differences caused by catchment characteristics, with special interest on the
97 influence of peatlands.

98

99 **2 Material and Methods**

100

101 2.1 Study sites and sampling strategy

102

103 The study sites include 30 lakes from northeastern Finnish Lapland (68°47'–69°55'N) with a
104 catchment gradient from mixed pine and birch forest to mountain birch woodland and barren tundra
105 (Fig. 1). The study area is located in a sporadic permafrost region. All the lakes are small and
106 shallow (<7.5 m) and distributed along a truncated mean July air temperature transect from 12.3 to
107 13.3 °C. While minimizing the temperature gradient, the lakes were sampled to characterize
108 different catchment types from forest and bog environments to tundra vegetation to encompass a
109 broad dissolved organic carbon (DOC) gradient from 1.7 to 16.6 mg l⁻¹. The sampling strategy was
110 originally designed to study spatio-temporal zooplankton responses to UV radiation (the DOC
111 screening effect) (Nevalainen et al., 2018) and to investigate the sources and controls of organic
112 carbon in these lakes (Rantala et al., 2016a). The dataset consists of 15 oligohumic (DOC <4 mg l⁻¹
113 ¹), 10 mesohumic (DOC = 4-6 mg l⁻¹) and 5 polyhumic (DOC >6 mg l⁻¹) lakes. Total phosphorus in
114 the lakes varies from 5 to 24 µg l⁻¹, total nitrogen from 138 to 806 µg l⁻¹ and pH from 5.1 to 8.4.
115 Environmental characteristics and limnology of the study sites are described in detail in Rantala et
116 al. (2016a). The lakes and their codes (numbers) are the same as in Rantala et al. (2016a), with the
117 exception that one tundra site (#34) was removed from this study due to low number of chironomid
118 head capsules.

119 Surface (top, 0–2 cm in core depth) and reference (bottom, 4-5 cm) sediment samples
120 were collected from the centres of the lakes using a Limnos gravity corer (Kansanen et al., 1991) in
121 July 2014. According to several sediment cores dated from the study area (Luoto & Sarmaja-
122 Korjonen, 2011; Luoto et al., 2017b; Rantala et al., 2016b), the average sediment accumulation in
123 the lakes refer to past 20 years in the “top” surface sediment samples and to 150 years in the
124 “bottom” reference samples. The top and bottom samples are discussed herein as modern and Pre-
125 Industrial age samples, respectively, but since the samples were not independently dated, we

126 emphasize that these general timeframes are only tentative and the bottom sample may not always
127 represent Pre-Industrial times. Although the widely employed top-bottom (or before-and-after)
128 approach allows for efficient spatio-temporal regional assessment of environmental change, the
129 disadvantage of this approach is that there are no continuous data on the timing or rate of changes
130 occurring between the two points in time represented by those samples (Smol, 2017). In addition, it
131 cannot be assumed that there is only one Pre-Industrial/reference environmental state from which
132 lakes have deviated (Perren et al., 2009). These limitations of the applied approach should be kept
133 in mind when interpreting the data.

134

135 *2.2 Chironomid analysis*

136

137 Standard methods were applied in fossil chironomid analysis (Brooks et al., 2007). The wet
138 sediment was sieved through a mesh (100- μ m) and the residue was examined under a
139 stereomicroscope. Larval head capsules were extracted and mounted permanently with Euparal on
140 microscope slides. Taxonomic identification following Brooks et al. (2007) was performed under a
141 light microscope. The minimum chironomid head capsule number per sample was set to 50 (Heiri
142 and Lotter, 2001; Larocque, 2001; Quinlan and Smol, 2001). Two split head capsules were
143 considered as one individual. The surface sediment chironomid assemblages have been previously
144 published in Luoto et al. (2016), whereas the reference samples were analyzed in this study by the
145 same chironomid analyst using identical methodology and taxonomy.

146

147 *2.3 Numerical methods*

148

149 Bray-Curtis similarity was used as a measure to assess the difference between present and past
150 chironomid communities. In this measure, 0 refers to a completely different community and 1 to an

151 analogous community. N2 (Hill, 1973) was used as a diversity measure, corresponding to effective
152 number of occurrences, i.e. the effective diversity of a sample's community.

153 Minimum hypolimnetic dissolved oxygen (DO) was reconstructed using a 30-lake
154 chironomid-based calibration model for Finland, where the calibration sites range from anoxic
155 ($O_2 < 0.5 \text{ mg l}^{-1}$) to hypersaturated sites ($O_2 = 18.1 \text{ mg l}^{-1}$) (Luoto and Nevalainen, 2011; Luoto and
156 Salonen, 2010). The weighted averaging partial least squares model has a cross-validated (leave-
157 one-out) coefficient of determination of 0.74 and a root mean squared error of prediction of 2.3 mg
158 l^{-1} . The suitability of the calibration model for the chironomid assemblages in the surface and
159 bottom samples were assessed using representation of fossil taxa in the calibration set (cutoff for
160 good representativeness 95%) and the modern analogue technique (MAT) using squared chi-square
161 distances of the 10 closest modern analogues (cutoff for a good modern analogue 5% squared chi-
162 square distance) (Birks et al., 2014). Furthermore, Generalized Linear Modeling (GLM) was used to
163 assess taxa that significantly ($P \leq 0.05$) respond to oxygen conditions. The GLMs were run using
164 Poisson distribution. Samples where majority of the taxa have significant relationship with the
165 environmental variable of interest can be considered to produce reliable reconstructions (Rees et al.,
166 2008; Luoto et al., 2010).

167

168 **3 Results**

169

170 The counting sum of chironomid individuals varied between 50 and 60 in the sediment samples.

171 The most common and abundant chironomids in the bottom samples were the same as in the surface
172 sediment samples (Fig. 2), including *Psectrocladius septentrionalis*-type (bottom = 27 occurrences,
173 mean abundance 12.6%, maximum abundance 48.9%; top = 23, 12.0%, 45.2%), *P. sordidellus*-type
174 (bottom = 28, 12.4%, 39.3%; top = 27, 10.2%, 23.6%) and *Tanytarsus lugens*-type (bottom = 28,
175 8.0%, 28.3%; top = 25, 5.9%, 19.0%). The most common taxa with largest decreases in their mean

176 abundance from bottom to top samples included *Polypedilum nubeculosum*-type (-2.5%), *P.*
177 *sordidellus*-type (-2.2%) and *T. lugens*-type (-2.1%), whereas the largest increases were observed
178 with *Paratanytarsus penicillatus*-type (3.2%), *Microtendipes pedellus*-type (2.1%) and *Tanytarsus*
179 *glabrescens*-type (2.0%). *Protanypus*, which was present in 11 bottom samples, was encountered
180 only in a single surface sample. On the contrary, *Tantarsus mendax*-type that was absent in the
181 bottom samples appeared in 10 surface samples.

182 According to the similarity analysis, oligotrophic tundra lakes had the largest shifts in
183 taxa assemblages between the past and present (average Bray-Curtis similarity 0.44), whereas
184 polyhumic lakes, located in pine and birch forest (0.50) and mountain birch woodland (0.55),
185 exhibited less changes (Table 1; Fig. 3). However, unlike oligohumic and mesohumic sites, the
186 polyhumic sites showed consistently decreased diversity (Table 1; Fig. 3).

187 The chironomid-inferred hypolimnetic oxygen varied between 3.0 and 13.5 mg l⁻¹ in
188 the surface samples and between 6.6 and 17.1 mg l⁻¹ in the bottom samples (Fig. 3). In all, the
189 average chironomid-inferred oxygen for the surface sediments was 9.4 mg l⁻¹ and for the bottom
190 samples 12.6 mg l⁻¹. According to the MAT, all the surface and bottom samples had good modern
191 analogues (<5% squared chi-square distance) in the calibration set. However, the surface sample
192 from lake #27 had taxa representativeness slightly less than the cutoff value of 95% due to absence
193 of *Paratendipes nudisquama*-type from the calibration set. Nonetheless, since 94.7% of the fossil
194 taxa were present in the calibration set, this did not produce a significant error source for the
195 reconstruction. In the surface sediment samples, 71.7-100% (average 91.0%) of the taxa present
196 (relative community abundance) had significant relationship with oxygen conditions, whereas in the
197 reference samples 73.1-100% (average 89.3%) were significantly associated with oxygen. Hence all
198 samples had the needed coverage of statistically significant oxygen indicators. The most abundant
199 taxon without significant relationship with hypolimnetic oxygen was *Procladius*, which occurred in
200 the samples with a relatively low mean abundance of 2.4% (maximum abundance 7.4%). When

201 comparing the shifts in inferred oxygen values and their relative change (Fig. 4), the polyhumic
202 sites showed no significant changes, mesohumic sites showed decrease with only one exception (an
203 outlier lake with a pH of 5.1) and the oligohumic sites illustrated a coherent decrease in oxygen.

204

205 **4 Discussion**

206

207 *4.1 Ecological change*

208

209 The chironomid assemblages in the 30 study sites in northern Lapland showed clear shifts when
210 comparing the reference (tentative age estimate 150 years in average) and modern surface sediment
211 samples. *Paratanytarsus penicillatus*-type, which was rare in the bottom samples, showed increase
212 especially in the low-DOC lakes (Fig. 2). Also several other collector-filterers consistently
213 increased, such as *Tanytarsus mendax*-type and *T. glabrescens*-type, though remaining relatively
214 low in their abundances. When interpreting the community changes, it should be noted, according
215 to the species-area relationship (Lomolino, 2000), that the time-intervals between the top and
216 bottom samples may differ and cause uncertainties in comparisons of rare taxa occurrences.

217 Nonetheless, the recent increase of *T. mendax*-type is very typical in the northern lakes in the area
218 (Shala et al., 2014). *T. mendax*-type has a high modern temperature optimum in Lapland (Luoto et
219 al., 2014) and elsewhere in Europe (Heiri et al., 2011). Therefore, this taxon appears to represent an
220 example of a chironomid that clearly benefits from climate warming. In contrast, the cold-indicating
221 *Protanypus* has disappeared from the surface sediments of the study sites suggesting that the
222 temperature range of the lakes is no longer suitable for it to survive. In addition to temperature, *T.*
223 *mendax*-type and *Protanypus* have strict preferences for meso-eutrophic and oligotrophic lakes,
224 respectively (Luoto, 2011; Medeiros and Quinlan, 2011). For chironomids, the influence of nutrient
225 conditions is in most part mediated through the direct physiological effects of hypolimnetic oxygen

226 conditions (Brodersen and Quinlan, 2006), as oligotrophic lakes tend to be well-oxygenized and
227 eutrophic lakes often oxygen depleted.

228 According to the Bray-Curtis similarity, the polyhumic study sites with DOC >9 $\mu\text{g l}^{-1}$
229 had smallest and the oligo-mesohumic lakes largest community changes (Fig. 3). While displaying
230 relatively little change in community assemblages, the polyhumic sites appeared to have uniformly
231 suffered a loss in their diversity. Hence, the chironomid communities of the polyhumic sites have
232 not significantly changed in their dominating taxa, instead there have been general decreases in the
233 less abundant taxa (Fig. 2). As all the current lakes are situated in an ecotonal area, the ecological
234 impacts of climate change are typically magnified (Pienitz and Vincent, 2000). Therefore, the larger
235 community shifts occurring in the low-DOC lakes (Fig. 3) are not surprising owing to oligohumic
236 and oligotrophic lakes being generally poorly buffered against environmental perturbations (Gunn
237 et al., 2001). Overall, the findings from the chironomid assemblages suggest that ecological changes
238 in taxonomic composition and/or diversity occur between the reference samples and the present,
239 with direction and magnitude depending on the lake type. As the status of aquatic ecosystems as
240 carbon sinks or sources is very likely to change owing to the ongoing climate change, the
241 biodiversity of freshwater ecosystems across most of the Arctic will also likely be altered (Wrona et
242 al., 2006). Accordingly, our results provide further evidence that these changes are proceeding in
243 subarctic lakes of Lapland, where chironomids play a significant functional role through regulation
244 of organic matter decomposition, and subsequently, take a major part in the biogeochemical cycling
245 of nutrients (including carbon).

246

247 *4.2 Oxygen change*

248

249 As the chironomid assemblages had good modern analogues in the calibration set according to the
250 MAT and based on the GLMs the taxonomic compositions included sensitive oxygen indicators

251 (Luoto and Salonen, 2010), such as the low-oxygen *Sergentia coracina*-type and high-oxygen
252 *Tanytarsus lugens*-type and *Psectrocladius* taxa, we were able to reliably reconstruct the
253 hypolimnetic oxygen conditions from the top and bottom samples of the study sites. The results
254 showed differences in chironomid-inferred oxygen levels between different lake types in past and
255 modern samples (Fig. 3). Whereas the oxygen decrease from the estimated Pre-Industrial Age was
256 3.2 mg l^{-1} on average, which clearly exceed the model's prediction error, largest reductions were
257 observed in the oligohumic lakes (Figs 3-4). With the outlier (lake #5 with anomalous pH)
258 excluded, also mesohumic lakes distinctly suffered from decreased oxygen levels. On contrast, the
259 polyhumic lakes with present-day DOC $>6 \text{ mg l}^{-1}$ had no or little change in their oxygen levels
260 between the past and the present. Therefore, the larger oxygen change in the oligo-mesohumic lakes
261 compared to polyhumic lakes is probably due to their generally poorer buffering ability against
262 environmental changes (Gunn et al., 2001). The lower buffering ability, or resilience, of low-DOC
263 lakes most probably relates to their light environment (more transparent water column), trophic
264 status (less nutrients), variable limnological conditions (such as in pH) and diverse catchment
265 characteristics compared to the murky, low-pH polyhumic lakes with boggy catchments (Korhola et
266 al., 2002; Rautio et al., 2011; Rantala et al., 2016a).

267 When observing the oxygen change since the estimated Pre-Industrial Age to the
268 present (Fig. 4) in the light of climate warming, it becomes apparent that polyhumic lakes are less
269 influenced. This is probably due to the fact that polyhumic sites have generally been subjected to
270 low oxygen conditions through their polyhumic lake state, especially during the winter season when
271 oxygen is consumed under ice following the excessive decay of plant material derived from the
272 catchment wetlands (Mathias and Barica, 1980). It has been shown that while colored lakes are
273 typically naturally oxygen depleted, the profundal oxygen values have a weak relationship with lake
274 trophic state (Crisman et al., 1998). Instead, the oxygen conditions in lakes are closely connected
275 with temperature. For example, oxygen conditions were generally improved during the cold Little

276 Ice Age (~1300-1900 CE) but deteriorated during the warm Medieval Climate Anomaly (800-1300
277 CE) and also under the present climate warming in oligohumic and polyhumic boreal lakes of
278 Finland (Luoto and Salonen, 2010). The current results show that even though the hypolimnetic
279 oxygen levels have decreased in the oligo-mesohumic lakes, none of the lakes have become anoxic
280 thus far (Fig. 3). However, despite the fact that the bottom reference samples represent a time
281 period that may correspond to the Little Ice Age and may consequently represent naturally higher
282 values, the decreasing oxygen trend in these lakes is evident, and the future therefore holds a
283 potential risk that the lakes may become oxygen depleted as climate warming proceeds.

284

285 **5 Conclusions**

286

287 The chironomid assemblages in the past and modern sediment samples of the 30 lakes showed
288 dissimilar communities between the past and the present with largest shifts in the more transparent
289 oligo-mesohumic lakes. Although there was no significant change in the taxonomic communities of
290 the murky polyhumic lakes, they displayed a decrease in diversity driven by disappearance of rare
291 specialized taxa. The chironomid-inferred hypolimnetic oxygen values generally decreased from the
292 Pre-Industrial Age to the present, with largest change in low-DOC lakes but no significant changes
293 were found in the oxygen conditions of high-DOC lakes. Since the polyhumic study lakes were
294 often located in wetland areas, our findings suggest mechanisms that prohibit oxygen decline in
295 sites associated with continual organic carbon inputs making them more resilient against climate-
296 induced reductions in hypolimnetic oxygen. Consequently, although contributing less to the total
297 carbon release from northern lakes when compared to polyhumic lakes, the low-DOC oligohumic
298 lakes of the northern treeline are generally more prone to climate change impacts with increased
299 potential of higher CH₄ emissions under reduced bottom water oxygen levels.

300

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302

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307

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517 **8 Tables**

518 **Table 1** Mean values and range (in brackets) in present-day wetland coverage and dissolved organic
 519 carbon (DOC) in the 30 subarctic lakes in northeastern Finnish Lapland in comparison with Bray-
 520 Curtis similarity and changes in N2 diversity and hypolimnetic oxygen between the surface (top)
 521 and reference (bottom) samples.

	Pine and birch forest	Mountain birch woodland	Tundra
Wetland area of catchment (%)	5.8 (0...16.6)	15.6 (0.1...49.3)	2.9 (0...8.9)
DOC (mg l ⁻¹)	4.8 (2.2...9.6)	7.6 (2.5...16.6)	3.4 (1.7...7.4)
Similarity (Bray-Curtis)	0.50 (0.37...0.68)	0.55 (0.40...0.71)	0.44 (0.27...0.58)
Effective diversity change (N2)	0.12 (-5.03...2.35)	-1.69 (-7.64...6.54)	-0.74 (-8.61...7.59)
Oxygen change (mg l ⁻¹)	-3.0 (-7.0...4.0)	-1.9 (-7.0...0.5)	-4.5 (-9.6...-0.2)

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537 **9 Figure captions**

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539 **Fig.1** Map. Study sites along the northern forest zones in northeastern Finnish Lapland. The
540 numbers present lake codes, which are the same as in Rantala et al. (2016a).

541

542 **Fig. 2** Community compositions. Chironomid assemblages in the surface (top = gray) and reference
543 (bottom = black) sediment samples in the 30 lakes in northeastern Finnish Lapland. The lakes are
544 arranged according to their modern dissolved organic carbon (DOC) concentration and the
545 threshold of 4 mg l^{-1} (between oligo- and mesohumic) is marked with a dashed line.

546

547 **Fig. 3** Ecological changes. Bray-Curtis similarity (0 = dissimilar, 1 = similar) between the surface
548 and reference chironomid assemblages in lakes in northeastern Finnish Lapland compared with
549 Hill's (1973) N_2 effective number of occurrences (diversity) and chironomid-inferred hypolimnetic
550 oxygen along the dissolved organic carbon (DOC) gradient in the surface (top = gray) and reference
551 (bottom = black) sediment samples.

552

553 **Fig. 4** Oxygen changes. Difference between chironomid-inferred hypolimnetic oxygen in the
554 surface and reference sediment samples (negative values refer to decreased oxygen towards the
555 present) compared with modern measured dissolved organic carbon (DOC) in the 30 lakes in
556 northeastern Finnish Lapland. The samples are colored according to DOC thresholds of 4 and 6 mg
557 l^{-1} (separating oligo-, meso- and polyhumic sites) and the site with anomalously high pH (an outlier)
558 is marked with an x.