1   **Rising temperature modulates pH niches of fen species**

2   Running title: Climate modulates pH niches

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40

41   **Abstract**

42   Rising temperatures may endanger fragile ecosystems because their character and key species

43   show different habitat affinities under different climates. This assumption has only been

44   tested in limited geographical scales. In fens, one of the most endangered ecosystems in

45   Europe, broader pH niches have been reported from cold areas and are expected for colder

46   past periods. We used the largest European-scale vegetation database from fens to test the

47   hypothesis that pH interacts with macroclimate temperature in forming realised niches of fen

48   moss and vascular plant species. We calibrated the data set (29,885 plots after heterogeneity-

49   constrained resampling) with temperature, using two macroclimate variables, and with the

50   adjusted pH, a variable combining pH and calcium richness. We modelled temperature, pH,

51   and water level niches for one hundred species best characterising European fens using

52   Generalised Additive Models and tested the interaction between pH and temperature. Fifty-

53   five fen species showed a statistically significant interaction between pH and temperature

54   (adjP<0.01). Forty-six of them (84%) showed a positive interaction manifested by a shift or

55   restriction of their niche to higher pH in warmer locations. Nine vascular plants and no moss

56   showed the opposite interaction. Mosses showed significantly greater interaction. We

57   conclude that climate significantly modulates edaphic niches of fen plants, especially

58   bryophytes. This result explains previously reported regional changes in realised pH niches, a

59   current habitat-dependent decline of endangered taxa, and distribution changes in the past. A

60   warmer climate makes growing seasons longer and warmer, increases productivity, and may

61   lower the water level. These effects prolong the duration and intensity of interspecific

62   competition, support highly competitive *Sphagnum* mosses, and, as such, force niches of

63   specialised fen species towards narrower high-pH ranges. Recent anthropogenic landscape

64   changes pose a severe threat to many fen species and call for mitigation measures to lower

65   competition pressure in their refugia.

66

69

Introduction

Climate thermal regime alterations affected species composition and functioning of most habitats during the quaternary climate cycles, and the ongoing climate change has similar impacts (Essl, Dullinger, Moser, Rabitsch, & Kleinbauer, 2012; Gottfried et al., 2012). Nutrient-limited wetland ecosystems, such as small-sedge, tall-sedge and moss-sedge spring and quaking fens (according to the EUNIS habitat classification; Chytrý et al., 2020), are rapidly declining habitats worldwide because of direct destruction, groundwater drawdown, eutrophication, and changes in disturbance regimes (van Diggelen, Middleton, Bakker, Grootjans, & Wassen, 2006; Janssen et al., 2016; Spitale, 2021). As in other cold-adapted, low-productivity ecosystems, ongoing climate warming may accelerate the loss of diversity in fens (Jiménez-Alfaro, Garcia-Calvo, Garcia, & Acebes, 2016; Sperle & Bruelheide 2021). Many direct ecophysiological effects may act, such as phenological shifts to unfavourable parts of the year, respiration increasing more than photosynthesis, an imbalance between growth and water use efficiency, increased water stress by increasing transpiration, or stress from increased numbers of freeze-thaw cycles in winter (Crawford, 2008; Niu et al., 2011; He, He, & Hyvönen, 2016; Küttim, Laine, Küttim, Ilomets, & Robroek, 2019). However, indirect effects are of crucial importance. Increasing evapotranspiration decreases the water table if rainfall does not increase enough (Gong et al., 2012; Michel, Brauchli, Lehning, Schaefli, & Huwald, 2020). Increasing temperature and decreasing water table accelerate nutrient cycling by increased decomposition of soil organic matter (Friberg et al., 2009; Górecki et al., 2021). A warming climate is further associated with the growing season length and growing degree day sum in Europe (Ruosteenoja et al., 2016). All these processes may narrow the realised niches of specialist species by promoting competition by increasing productivity (Costa et al. 2018, Soliveres et al. 2018) and decreasing environmental stress

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(Spitale 2009, Olsen, Töpper, Skarpaas, Vandvik, & Klanderud, 2016). For fens, narrowing

the fundamental niche because of superior competitors is well documented (Rydin 1986,

Mulligan & Gignac 2002), and this also holds specifically for the pH gradient (Vicherová et

al. 2015, Udd et al. 2016).

Regional differences in the realised niches along environmental gradients of individual

mire species are well-known in Europe, often mentioned in textbooks and monographs

(Aletsee, 1967, Wheeler, 1999; Dierßen & Dierßen, 2001; Leuschner & Ellenberg 2017).

They hold especially for pH, the major determinant of mire and spring diversity (Joosten,

Tanneberger & Moen, 2017; Peterka, Hájek, et al., 2017; Cantonati et al., 2020), as evidenced

by inter-regional comparisons of Kooijman & Westhoff (1995), Hájková, Hájek, Apostolova,

Zelený, & Dítě (2008), Štechová, Hájek, Hájková, & Navrátilová (2008), Plesková et al.

(2016), Graham, Farr, Hedenäs, Devez, & Watts (2019), and Peterka, Hájková, et al. (2020).

Several studies report wide realised niches of mire species in Northern Europe, while the

same species are restricted to extreme pH values in Central, Western, and Southern Europe

(Odgaard, 1988; Kooijman & Westhoff, 1995; Dierßen, 1996; Hedenäs & Bisang, 2012). As

a result, there is a much higher threat to base-rich fens in Europe than acidic mires in terms of

their diversity and habitat conservation status (Janssen et al., 2016; Chytrý et al., 2020).

The causes of geographical differences in pH niches are not well known. Such

differences may be explained by either interaction with other ecological variables, such as

calcium content, nutrient availability or climate (Proctor, McHaffie, Legg, & Amphlett, 2009;

Plesková et al., 2016; Vicherová, Hájek, Šmilauer, & Hájek, 2017), or hypothetical ecotypes

resulting from refugial processes during the Holocene (Hájková et al., 2018). Plesková et al.

(2016) suggested combining pH and calcium into a single variable (named *adjusted pH*)

because these factors act synergistically in habitat filtering of specialised mire species. In their

study, the niches of more competitive bryophyte species to adjusted pH were widened by

119 nutrient enrichment, while the opposite held for competitively weak species. Similarly,

120 Kooijman & Westhoff (1995), Graham, et al., (2019), and Peterka, Hájková, et al. (2020)

121 found a niche shift of specialised fen brown mosses of the genus *Scorpidium* to higher pH

122 values in Western and Central Europe when compared to the colder and less polluted areas of

123 Scandinavia. These findings match the result of a resurvey study from the Bohemian Massif

124 in Central Europe (Hájek et al., 2015) that showed narrowing of the realised niches of

125 calcicole fen bryophyte species during the last decades, which were characterised by

126 increasing temperature and nutrient inputs. The results of Singh et al. (2019) even suggested

127 that the increasing competition in the moss layer may also restrict some specialised vascular

128 plants and outweigh the pH effects.

129   Although it is widely acknowledged that species may have different habitat affinities

130 under different climates (Walter & Walter 1953, Aletsee 1967, Proctor et al. 2009, Wagner et

131 al. 2017), no studies have tested the interactions between climate and critical local

132 environmental conditions in shaping niches of fen species at a continental scale. Gignac, Vitt,

133 Zoltai & Bayley (1991) and Gignac, Gauthier, Rochefort & Bubier (2004) demonstrated

134 distinct climate and pH niches of bryophyte and sedge species of mire habitats on the

135 continental scale of Canada. The response surfaces they presented suggest some interactions

136 between climate and pH, but the authors did not test them explicitly. Here, we hypothesise

137 that at the continental scale, pH niches vary with macroclimate temperature in fens, and this

138 interaction may explain regional differences in pH niches observed in previous regional

139 studies.

140

141 **Methods**

142 *Data set selection and its calibration with pH and water level*

143   For modelling realised niches of fen species, we used data from large phytosociological

144   databases aggregated in the European Vegetation Archive (Chytrý et al., 2016), most of them

145   being already utilised in Peterka et al. (2017). As in Peterka et al. (2017), we selected only

146   georeferenced plots of a size of 1–100 m^2, for which a complete list of moss and vascular

147   plant taxa was reported. Peterka, Syrovátka, et al. (2020) demonstrated that plot sizes of at

148   least 1 m^2 sufficiently describe the broad-scale pattern in the representation of fen specialists

149   and may be safely merged in broad-scale analyses with larger plots sizes, without introducing

150   substantial bias. Restriction to a narrower plot size range would have resulted in a

151   considerable loss of essential data from several regions. For details on the procedure of data

152   filtering see Hájek, Těšitel, et al. (2021); 10.5281/zenodo.4915753).

153   We selected 35.984 vegetation-plot records (Figure 1). To reduce the effect of

154   oversampling in specific regions on niche modelling, we resampled the data set by selecting a

155   maximum of five plots per grid cell of 1 km x 1 km. Because the random selection of five

156   plots could cause only the most frequently sampled vegetation type to be selected from the

157   grid, while less sampled or less represented ones to be lost, we used the Heterogeneity-

158   Constrained Random Resampling method (Lengyel, Chytrý, & Tichý, 2011). This method

159   generated a set of 50 random selections of five plots per grid, ranked them by both the

160   decreasing mean Sørensen dissimilarity between pairs of plots and the increasing variance of

161   these dissimilarities. The selection with the lowest summed rank was considered the most

162   evenly distributed in the multi-dimensional space and selected to the final stratified data set.

163   The resampling reduced the number of plots to 29,885 (83%).

164   In the next step, we imputed the estimated water pH and conductivity values for the

165   resulting data set. For this purpose, we used a calibration data set, i.e. the data subset with

166   measured pH and conductivities from springs and mires across Europe (for its geographical

167   coverage, see Hájek, Jiménez-Alfaro, et al. (2021). This calibration data set covers entire

168 Europe and the complete pH and conductivity gradients (the pH range 2.9-8.9; the

169 conductivity range 1-13,100 us.cm-1). The calibration data set contained 6299 records for pH,

170 while for conductivity, it contained 5073 records. This calibration data set, divided into the

171 training and the testing subset, was also used to compare the precision of the two imputation

172 methods, the imputation by weighted averaging and the compositional similarity (the MOSS

173 method of Tichý et al., 2010). For details and results of this testing and settings of the

174 methods, see Hájek, Těšitel, et al. (2021; 10.5281/zenodo.4915753). Because the MOSS

175 method performed better but did not apply to all plots (see Hájek, Těšitel, et al. 2021), the

176 missing values were imputed in the two steps. First, the imputation resulting from the MOSS

177 method was applied. After it, the missing values (16-21%, respectively) were imputed by the

178 weighted averaging method.

179   Based on direct measurements and imputations (see data repository for details on the

180 procedure and testing; Hájek, Těšitel, et al. (2021); we calculated, for the entire data set (i.e.

181 29,885 plots), the variable combining pH and calcium into a single value (the *adjusted pH*;

182 Plesková et al., 2016; Horsáková et al., 2018). The *adjusted pH* refers to the joined effects of

183 pH and calcium, e.g. in the uptake of toxic ions to mosses, ultimately affecting the bryophyte

184 layer (Plesková et al., 2016), which in turn affects the composition of vascular plants (Singh

185 et al., 2019). As the first step, conductivity was transformed to calcium concentration values

186 (in mg l^{-1}) using the equation y = 0.153x, where y is Ca^{2+} concentration in mg l^{-1}, and x is

187 conductivity in μS cm^{-1}. The equation is based on the regression relationship between Ca^{2+}

188 and conductivity (R^2 = 0.84; n = 2062) found on the European scale (Hájek, Jiménez-Alfaro,

189 et al., 2021). As the last step, we combine pH and calcium estimates into the *adjusted pH* by

190 adding the decadic logarithm of the millimolar Ca^{2+} concentration to the actual pH value

191 (formula 1 in Plesková et al., 2016). In Results and Discussion, we refer to this variable as

192 *pH*.

193   We further estimated a water level value for each vegetation-plot record in the data set

194   by averaging the tabled hydrological indicator values for all individual taxa occurring in the

195   record. We adopted the indicator values from the pan-European study of Hájek, Dítě,

196   Horsáková, et al. (2020) that assessed for each taxon, at the scale of 1–12, the values for

197   species optimum to water table depth, drought intolerance, flooding tolerance, and ecological

198   tolerance to water table (niche breadth). We averaged indicator values for drought intolerance,

199   with both the ecological tolerances and the percentage covers of individual taxa used as

200   weights. Hájek, Dítě, Horsáková et al. (2020) found that these settings resulted in the

201   strongest correlations with measured water level data in datasets containing different types of

202   mire habitats.

203

204   *Data analysis*

205   *Selection of climate predictors*

206   From the available set of macroclimate variables, we selected the two that best address the

207   effects of an ongoing climate warming on vegetation: the length and temperature of the

208   growing season (Fridley, Lynn, Grime & Askew, 2016) and the minimum winter temperature,

209   which is particularly significant to fen communities (Horsáková et al., 2018; Küttim et al.,

210   2019). To address the length of the growing season, we calculated the effective temperature

211   sum (growing degree days) at the baseline of 5°C (GDD5). GDD5 was calculated from

212   monthly temperature data available in the CHELSA database (Climatologies at High

213   resolution for the Earth's Land Surface Areas, Karger et al., 2017) for the 1979-2014 period.

214   We further extracted the Minimum Temperature of Coldest Month variable (coded as *bio6* in

215   the CHELSA database), which refers to the lowest temperature of any monthly daily mean

216   maximum temperature, to examine the effect of cold temperature anomalies in winter.

217   These two macroclimate variables were intercorrelated (Pearson $r = 0.716$). Therefore,

218   we applied a principal component analysis (PCA) on the climate variables and then used the

219   scores of the first PCA axis (accounting for 85.8% of variability) as a combined variable

220   named "*relative climate temperature*" (from now on referred to as *temperature*), scaled to

221   zero-mean and unit-variance, where high values relate to warm and long growing seasons and

222   warm winters. This variable did not correlate with adjusted pH in the resampled data set

223   (Pearson's product-moment correlation; t = 0.08, df = 29883, p-value = 0.93).

224

225   *Analysed taxa*

226   We limited the study to the prominent vascular plant and moss taxa (species or aggregates of

227   closely allied species) that frequently occur in European fens and simultaneously show their

228   ecological optimum either in fens or in wet, acidic mires in general (i.e., poor fens, bog

229   hollows and bog lawns) (see Supplementary Table 1 in data repository: Hájek et al. 2021a;

230   10.5281/zenodo.4915753). From now on, we refer to them as *fen species*. Their list is based

231   on the consensus list of European-scale diagnostic species of sedge-moss vegetation that

232   grows in fens and bog hollows (the *Scheuchzerio-Caricetea fuscae* class). The kernel of the

233   list is the species classification used in the current overview of European vegetation (Mucina

234   et al., 2016), updated by Peterka et al. (2017) and Horsáková et al. (2018). Hepatics were not

235   considered because they are not always reliably recorded in the database data. Notably, the

236   selected fen species are not always strict indicators of fens, and approximately one-quarter of

237   them characterises, according to Mucina et al. (2016), also other vegetation classes in some

238   parts of the study area, most often ombrotrophic raised bogs, and nutrient-enriched or

239   seasonally desiccating fen wetlands, such as alder carrs or wet grasslands. We limited the

240   analysis to taxa occurring in at least 200 vegetation plots. A simulation study by Coudun &

241 Gégout (2006) reports 50 occurrences as the minimum frequency needed for reliable niche

242 modelling, with even higher sample sizes required if optima lying either at one extreme of the

243 gradient or wide amplitudes are expected. We, therefore, set a stricter minimum frequency to

244 prevent the prevalence of taxa that may show less reliable results.

245   Some frequent taxa showed a temperature or pH niche too narrow to allow meaningful

246 interaction testing between these two variables. Their inclusion might cause a flawed

247 generalization of the results. In order to exclude taxa showing narrow niches, we calculated

248 the 10th-90th percentile range for each fen species. We included only fen species for which this

249 range was higher than one-quarter (an arbitrary threshold) of the entire range of the variable in

250 the data set (i.e., > 0.099 for temperature and > 1.625 for pH). These criteria led to selecting

251 100 fen species (37 bryophyte and 63 vascular plant species) that best characterise European

252 fens (at least in a part of the study area) and are frequent enough.

253   We calculated the 10th percentile (0.1), 90th percentile (0.9) and 10th-90th

254 interpercentile range of water level, temperature and adjusted pH for each taxon. In order to

255 demonstrate fundamental ecological differences among the selected prominent fen species, we

256 subjected the final matrix of taxa and these percentiles and ranges to the Principal Component

257 Analysis (PCA), in which individual fen species acted as samples. The PCA was centred and

258 standardised, i.e. correlation matrix was employed as a cross-products matrix. The results are

259 presented in Figure S1.1 in Supplementary Materials).

260

261 *Generalised Additive Models*

262 We used generalised additive models (GAMs) to model ecological niches of 100 prominent

263 fen species to the environmental gradients of pH, temperature, and water level. We primarily

264 focused on temperature and pH and their interaction to address the principal hypothesis of the

265　study. Models for water level are additional and are graphically presented only in a data

266　repository (Hájek, Těšitel, et al., 2021).

267　　　　Species abundance data were transformed to presence/absence. Thus GAMs with

268　binomial error distribution were used. Before niche modelling, we trimmed 0.5% extremes of

269　all the gradients (961 records) to prevent the excessive effects of extreme values on the

270　resulting models. This step reduced the data set size to 28,924 plots.

271　　　　For each fen species, we ran two GAM models. Model 1 included purely additive

272　effects of the three gradients (water level, temperature, pH). To avoid overfitting, we limited

273　degrees of freedom (d.f.) to maximum 4 for smoothers for each tested variable. Model 2 was

274　identical to model 1 but included the interaction between pH and temperature as a parametric

275　predictor. The inclusion of this term allowed the pH niche to change along the climate

276　gradient. We compared the two models by the likelihood-ratio test, with the resulting p-values

277　adjusted by Holm correction because of multiple testing. The model containing the interaction

278　was selected only in case of being significantly better than the purely additive model (adjusted

279　p-value < 0.01). Standardised interaction coefficients were obtained by refitting the GAM

280　model with predictors standardised by subtracting the mean and subsequent division of

281　standard deviation while the binomial responses were left intact (Agresti, 2006). Only models

282　with interaction $p < 0.01$ and bimodal models were embedded in figures located in the main

283　text, whereas all models are presented in the data repository (Hájek, Těšitel, et al., 2021).

284　We present the resulting niche models graphically with *pH* and *temperature* by a 2-d contour

285　plot to display the interaction between the two gradients. Dashed lines indicate species optima

286　along the environmental gradients, defined as the environmental values where the species

287　probability of occurrence is maximal. Whenever the interaction between temperature and pH

288　was significant, its slope is displayed by a regression line. The line intercept was set to force

289 the regression line to pass through the niche optimum to the pH and temperature gradient. The

290 probabilities displayed for pH and climate correspond to an optimum water level. In the data

291 repository (Hájek, Těšitel, et al., 2021), we further present models for water level as a 1-d line

292 plot.

293 All analyses were conducted in R, version 4.02 (R Core Team, 2020). Generalised

294 additive models were fitted in package mgcv (Wood, 2017), and the graphical outputs were

295 constructed in the ggplot2 package (Wickham, 2016). R scripts are stored in the data

296 repository (Hájek, Těšitel, et al., 2021).

297

298 *Taxonomic nomenclature*

299 The nomenclature follows the Euro+Med checklist for vascular plants and Hill et al. (2016)

300 for mosses. See Peterka et al. (2017) for the content of aggregates of closely allied species,

301 which are not always well separated in the source databases. Additionally, we considered

302 *Primula farinosa* an aggregate taxon because of the unclear taxonomic position of *Primula*

303 *farinosa* subsp. *exigua,* which is assigned to the allied species *P. frondosa* in the Euro+Med

304 checklist.

305

306 **Results**

307 *Niche modelling and testing*

308 Fifty-five taxa (55%) showed a significant interaction between pH and temperature in forming

309 their realised niche (adjusted $p < 0.01$). Of these fifty-five taxa, forty-six (84 %) taxa showed

310 positive interaction (Figure 2, Figure 3). The total deviances explained by interaction were

311 generally higher for positive than negative interactions (Figure 2). The taxa showing the

positive interaction manifested a restriction or shift of pH niche to higher pH in warmer

locations. They involve twenty-two moss taxa (100%) and twenty-five (73.5%) vascular plant

taxa. The opposite interaction was rare (no moss and nine vascular plant taxa; Figure 4).

Some of the species showing the positive interaction tend to show a bimodality for

either temperature (*Eriophorum scheuchzeri*, *Paludella squarrosa*, *Sphagnum obtusum*,

Sphagnum squarrosum) or pH (*Drosera longifolia*) (Figure 3). Four species showed apparent

bimodal response to either *temperature* (*Carex buxbaumii* agg., *Meesia triquetra*,

Trichophorum alpinum) or adjusted pH (*Trichophorum cespitosum*), without significant

interaction between pH and temperature (Figure 5). For graphical outputs for all taxa, see the

data repository (Hájek, Těšitel, et al., 2021).

There was a significant difference between bryophytes and vascular plants in the

standardised interaction coefficients (Mann-Whitney test; $W = 807$, p-value $= 0.011$; Figure

6). Bryophytes showed a narrower range of standardised interaction coefficients than vascular

plants, but only a few of them were negative. None of these negative interactions was

statistically significant (Figure 6). The moss species showing the highest interaction between

temperature and pH (Figure 2) are primarily non-sphagnaceous brown mosses (e.g.,

Campylium stellatum agg.*, Cinclidium stygium, Paludella squarrosa, Pseudocalliergon*

trifarium, Scorpidium scorpioides, S. revolvens agg.). Most of them prefer high-pH sites

(Appendix S1, Figure S1.1) but shift their occurrence to even higher pH if the climate is warm

(Figure 4). Some *Sphagnum* species, the most strongly *S. teres* (Figures 2, Figure 3), also

show the positive interaction and shift or extend from the central part of the pH gradient

towards somewhat higher pH, but not as high as in the case of most brown mosses (Figure 2).

The group of vascular plants that show the positive interaction includes (i) the low-

competitive tiny or short-lived taxa (*Eriophorum gracile, Hammarbya paludosa, Saxifraga*

hirculus, Drosera longifolia, Pedicularis palustris, Pinguicula vulgaris) and (ii) the taxa with

337   the optimum outside warm areas (Appendix S1, Figure S1.1), showing only isolated relict

338   occurrences here (*Comarum palustre, Eriophorum scheuchzeri, Ligularia sibirica,*

339   *Menyanthes trifoliata*).

340   Nine frequent vascular plant species showed significant yet slight (Figure 2) negative

341   interaction between temperature and pH. They include species highly associated with acidic

342   sites (Appendix S1, Figure S1.1), such as poor fens and bogs in warm areas and extending

343   their niche towards higher pH in cold areas. *Andromeda polifolia*, also showing a tendency

344   toward bimodality to pH, is a typical example. Four species of high-pH fens (*Carex hostiana,*

345   *C. panicea, Eleocharis quinqueflora and Juncus alpinoarticulatus*; Appendix S1, Figure S1.1)

346   showed the negative interaction while keeping their optimum in extremely high-pH fens also

347   in warm areas (Figure 4).

348

349   **Discussion**

350

351   *Niche shifts and extensions to high-pH sites in a warmer climate*

352

353   Our analysis demonstrates a case of interaction between local factors (pH, water level) and

354   climate in shaping species distributions at the broad geographic scales in fens, similar to other

355   habitats (Chauvier et al., 2021). Using an extensive data set with a wide geographic range of

356   European fens, we demonstrated that climate significantly modulates edaphic niches of plant

357   taxa. This novel result explains previously reported regional changes in realised niches of fen

358   plants, a current habitat-dependent decline of endangered taxa in some regions, and

359   distribution changes of fen species during Quaternary climate cycles.

360   More than half of the analysed one hundred specialised and frequent European fen

361   species showed a statistically significant interaction between pH niche and macroclimate

362 temperature at the European scale. In the cold range of the European climate gradient, niches

363 of many species of base-rich fens extend to moderately acidic conditions, and niches of some

364 species of acidic fens to neutral or moderately alkaline conditions contrary to the warmer

365 climate range. The interaction between climate and pH niches explains niche shifts reported

366 by previous comparisons between Scandinavia and Western or Central Europe (Kooijman &

367 Westhoff, 1995; Graham, Farr, Hedenäs, Devez & Watts, 2019, Peterka, Hájková, et al.,

368 2020), or between cold mountains of the Balkans and warmer Central-European fens

369 (Hájková et al., 2008). The same explanation may apply to observations that the occurrences

370 of some fen mosses had become more limited to the most base-rich fens during recent

371 decades across Europe (Hájek et al., 2015; Kolari, Korpelainen, Kumpula, & Tahvanainen

372 2021).

373

374 *Competitive release as the leading cause of observed niche shifts?*

375 Across different ecosystems, many reports explain regional niche shifts or extensions

376 by competitive release (Lawrey, 1981, Prinzing, Durka, Klotz, & Brandl, 2002, Coudun &

377 Gégout, 2005, Reinecke, et al., 2016). This explanation seems the most plausible for our

378 results, considering that niche restrictions in warmer areas are inclined towards a narrower

379 high-pH range. Longer and warmer growing seasons may increase inter-specific competitive

380 interactions and benefit species with high growth rates. The effect is intensified by increasing

381 nutrient availability, promoted by a high temperature that increases decomposition rates

382 directly (Djukic et al., 2018) and indirectly by lowering the water table if precipitation sum

383 does not increase enough (Ise, Dunn, Wofsy, & Moorcroft, 2008; Górecki et al., 2021).

384 A wide array of studies from mires demonstrate a clear competitive hierarchy, with

385 acidophytic poor-fen species being superior to calcium-tolerant species of rich fens (e.g.,

16

386 *Sphagnum warnstorfii*, *S. contortum, S. teres*) and the latter being superior to calcicole species

387 such as most of the non-sphagnaceous brown mosses (Kooijman & Baker, 1995; van

388 Breemen, 1995; Granath, Strengbom, & Rydin, 2010; Paulissen, er al., 2014; Udd, Sundberg,

389 & Rydin, 2016; Vicherová, M. Hájek, Šmilauer, & T. Hájek, 2017). These hierarchies

390 frequently occur on the water table gradient and show significant phylogenetic background

391 (Johnson et al. 2015). The same holds for the hierarchies on the pH and productivity gradients

392 that also might emerge at the evolutionary scale, as illustrated by the results of Vicherová,

393 Glinwood, Hájek, Šmilauer & Ninkovic (2020). They found that the rich-fen bryophyte

394 *Hamatocaulis vernicosus* can react to the presence of its competitor, acidophytic peat moss of

395 *S. recurvum* agg., and emit volatile organic compounds to adjust and synchronize the growth

396 of its individuals.

397   Increasing temperature and nutrient availability alter competitive hierarchies among

398 dominant peat mosses (Breeuwer, Heijmans, Robroek, Limpens, & Berendse, 2008; Breeuwer

399 et al., 2009; Bu, Zheng, Rydin, Moore, & Ma, 2013) or between bryophytes and vascular

400 plants (Pouliot, Rochefort, Karofeld, & Mercier, 2011), as demonstrated by studies from

401 ombrotrophic bogs. Altered competitive hierarchies may explain most of the interactions

402 between temperature and pH found in our study. Niche extension of acidophytic and calcium-

403 tolerant species towards high-pH habitats is facilitated when nutrient, especially potassium,

404 availability is improved or if the level of alkaline groundwater decreases in warmer climates.

405 Previous studies across Europe (Kooijman, & Bakker, 1995, Kooijman, 2012, Hájek et al.

406 2015, Plesková et al. 2016; Vicherová, Hájek, Šmilauer, & Hájek, 2017; Kolari et al.. 2021)

407 have indeed demonstrated expansion of *Sphagnum teres, S. squarrosum, S. magellanicum* or

408 *S. recurvum* agg. into base-rich fens. The same taxa extended the pH niche towards higher

409 macroclimate temperature in our study (Figure 2).

410   Acidophytic species growing in mires may hence, to some extent, benefit from the

411   extension of their pH niche in warmer climates. In a pristine boreal rich fen, Kolari et al.

412   (2021) found an increase of peat mosses (*Sphagnum recurvum* agg., *S. magellanicum*) at the

413   expense of brown mosses during the past 20 years when the mean annual temperature in the

414   region had risen by +1.0 °C, while pH had not changed. The growth of *Sphagnum* mosses is

415   generally accelerated by climate warming (Dorrepaal, Aerts, Cornelissen, Van Logtestijn, &

416   Callaghan, 2006; Küttim, Küttim, Ilomets, & Laine, 2020; Bengtsson et al., 2021). The spread

417   of acidicole peat moss species to high-pH fens increases competition pressure to non-

418   sphagnaceous brown mosses. The niches of brown moss taxa that are highly endangered in

419   warm areas of Europe, such as *Pseudocalliergon trifarium, Scorpidium scorpioides* or

420   *Paludella squarrosa*, indeed showed a shift to higher pH values in warmer areas in our study.

421   Rapidly growing *Sphagnum* mosses compete effectively also with seedlings or young ramets

422   of vascular plants specialised to base-rich fens. Singh et al. (2019) showed that most species

423   of alkaline fens tended to prefer brown-moss patches against *Sphagnum*-rich ones, regardless

424   of pH and water table. Again, some of them showed positive interaction between temperature

425   and pH in our study (*P. farinosa* agg.*, P. vulgaris, S. hirculus, E. latifolium*).

426   A tremendous competitive ability of acidophytic *Sphagnum* mosses may explain why

427   many bryophyte and vascular plant fen species have narrower high-pH niches in warmer

428   climates. The combination of high pH and high calcium concentrations, expressed by *adjusted*

429   *pH* in our study, is lethal to acidophytic *Sphagnum* mosses, with the lethality threshold being

430   shifted towards higher pH values if nutrient availability is enhanced (Plesková et al. 2016,

431   Vicherová et al. 2017). In our study, the positive interactions between temperature and pH

432   occurred significantly more often in bryophytes than in vascular plants, corroborating the

433   previously reported significant effects of competition shaping bryophyte communities in

434   mires (Bu, Zheng, Rydin, Moore, & Ma, 2013; Udd, Sundberg, & Rydin, 2016; Ma et al.,

435   2020).

436   Climate warming and increasing nutrient availability lower the environmental

437   extremity of fens (Hájek et al., 2020). Our conclusion that decreasing environmental

438   extremity strengthens competitive inter-specific interactions is supported by ecological

439   theory, specifically the Stress Gradient Hypothesis (Pouliot, Rochefort, Karofeld, & Mercier,

440   2011; Bu, Zheng, Rydin, Moore, & Ma, 2013; Olsen et al., 2016).

441

442   *Role of nutrient availability*

443   Macroclimate temperature tightly coincides with nutrient availability, and these two factors

444   act in concert in forming the species´ responses to climate change (Jeppesen et al., 2010;

445   Sperle & Bruelheide, 2021). Enhanced temperature causes a higher decomposition of organic

446   matter and, in turn, increases nutrient availability. Increased nutrient availability increases

447   productivity and hence competition pressure. Increased competition narrows the pH niches of

448   specialised plant species because of natural competitive hierarchies along the pH gradient.

449   The pH niche shifts were indeed observed between climatically different regions as well as

450   between the regions differing in nutrient status (Plesková et al. 2016). However, the

451   predictions of future changes in species distributions should also consider the changes in the

452   availability of individual nutrients and the nature of nutrient limitation. Nutrients derived

453   from organic matter decomposition are differently available to plants depending on soil pH.

454   The more acidic and calcium-poor conditions, the higher nitrogen and phosphorus

455   mineralisation, the higher ammonium: nitrate ratio in soil and the lower N:P ratios in biomass

456   occur (Waughman 1980, Paulissen et al. 2004, Rozbrojová & Hájek 2008, Kooijman &

457   Hedenäs 2009). The low N:P ratio and high ammonium: nitrate ratio support acidicole

458 *Sphagnum* species over species specialised to more calcium-rich fens (Paulissen et al. 2004,

459 Kooijman & Hedenäs 2009). Organic matter decomposition triggered by increasing

460 temperature will deepen the differences in nutrient limitation between alkaline and acidic fens

461 because phosphorus is released less in more minerotrophic and more alkaline conditions

462 (Aerts et al. 1999, Bragazza et al. 2007). This contrast may prevent the spread of

463 competitively superior acidophytic taxa into the most alkaline fens. Indeed, acidophytic

464 *Sphagnum* taxa enlarged their niches to fens with higher pH (adjusted pH 6-7) in our study

465 and the previous study of Plesková et al. (2016), but not to fens with adjusted pH above 7.

466 The increasing overall content of available nutrients due to decomposition facilitates their

467 survival in moderately calcium-rich fens with higher pH (Kooijman 2012, Vicherová et al.

468 2015), but further niche shifts towards even more alkaline environments are unlikely because

469 of calcium toxicity and substantial phosphorus limitation (Vicherová et al. 2015, Rozbrojová

470 & Hájek 2008, Kooijman & Hedenäs 2009).

471

472 *Negative interactions between pH and temperature niches and bimodal responses*

473

474 Broader niches in colder areas were also found for acidophytic taxa *Andromeda polifolia,*

475 *Eriophorum vaginatum* and *Vaccinium oxycoccos* agg., showing negative interactions

476 between pH and temperature. These taxa frequently occur also in ombrotrophic bogs (Proctor

477 et al., 2009; Mucina et al., 2016; Robroek et al., 2017), and in warm areas, they are strongly

478 associated with acidic mires and do not occur in high-pH sites. A similar pattern was found

479 for *Trichophorum cespitosum*, but the interaction between pH and temperature was not

480 significant, and the cold-loving nature of the species appeared to be a dominant cause of its

481 ecological behaviour. Together with *A. polifolia* and *Drosera longifolia*, the latter species

482   further showed the most apparent sights of bimodality to pH. Further research is needed to

483   determine whether this bimodality is caused by genetically ingrained ecotypes (Schwarzer &

484   Joshi, 2019).

485   Bimodal responses to *temperature* might be caused by the uneven occurrence of some

486   habitats (e.g., quaking fens) across Europe or even by uneven sampling. Nevertheless,

487   because all species showing bimodal responses but *Sphagnum squarrosum* are considered to

488   be glacial relicts in Central Europe (Dítě et al., 2018; Peterka, Hájková, et al., 2020), the

489   bimodality might arise from uneven distribution of long-term stable, refugial habitats that had

490   not experienced Middle-Holocene wood encroachments or shifts to acidic bogs (Hájková et

491   al., 2018).

492

493   *A need to protect and manage fen refugia in warm areas*

494

495   The pattern of positive pH-climate interaction has important implications for

496   explaining the past and current distribution patterns and habitat affinities of endangered

497   calcicole rich-fen species in Central and Southern Europe (Dítě et al., 2018; Hájková et al.,

498   2018; Peterka, Hájková, et al., 2020; Sperle & Bruelheide 2021). These species are expected

499   to have had much wider niches and distributions in cold and wet periods of the Quaternary

500   (Jiménez-Alfaro, Garcia-Calvo, Garcia, & Acebes, 2016; Dítě et al., 2018), as evidenced for

501   *Carex dioica, C. limosa, Cinclidium stygium, Eriophorum gracile, Ligularia sibirica,*

502   *Paludella squarrosa, Primula farinosa* agg., *Pseudocalliergon trifarium, Saxifraga hirculus,*

503   *Scorpidium scorpioides* and *Sphagnum obtusum* (Hájek et al., 2011; Dítě et al., 2018). Their

504   pH niches might be broader during the colder climate phases, and their current distributional

505   restriction results from a narrowed pH niche. Indeed, palaeoecological studies sometimes

506   report their co-occurrence, at the scale of square centimetres, with the acidophytic species

507   (Drzymulska & Jadwiszczak, 2020), while recently such combinations are rare, being

508   observed especially in cold high-mountain or arctic habitats (Dierssen, 1996; Pérez-Haase, &

509   Ninot, 2017) or in the Baltic region under specific conditions (Pakalne, 1994). Woodland or

510   *Sphagnum* expansions to fens during Middle-Holocene warming (Hájková et al., 2018) or

511   even fen-to-bog transitions (Hughes, 2000; Väliranta et al., 2017) had likely increased

512   competition pressure and restricted relict species to refugia, where their niches still may have

513   remained much broader than they are today (Hájek et al., 2015). Although deforestation and

514   anthropogenic disturbances since late prehistory and Middle Ages gave a second chance to

515   these light-demanding relict species (Hájková et al., 2018), current changes in the landscape

516   down them again. The recent retreat of low-competitive fen species is probably more

517   profound than the retreat during the Middle Holocene because of the unprecedented

518   anthropogenic transformation of landscapes. It has decreased connectivity of fen habitats and,

519   thus, disrupted metacommunity and metapopulation structures that are important for insular

520   habitats such as fens (Soomers, Karssenberg, Verhoeven, Verweij, & Wassen, 2013; Jamin,

521   Peintinger, Gimmi, Holderegger, & Bergamini, 2020) and made fens highly endangered

522   (Janssen et al., 2016).

523   During the ongoing century, precipitation is anticipated to increase in the north while

524   decreasing in the south, but near-surface soil moisture content is projected to decrease

525   virtually everywhere in Europe because of increasing evapotranspiration (Ruosteenoja et al.

526   2018). Together with warming, a decreased water table due to increasing evapotranspiration

527   will accelerate organic matter decomposition and associated nutrient releases and acidification

528   by organic acids not buffered by alkaline groundwater. In high-pH fens in Southern Europe,

529   where precipitation decreases, increasing temperatures and summer droughts stress the moss

530   layer, reducing the number of specialised taxa (Horsáková et al. 2018), and contributing to fen

531   transformations into wet grasslands.

532   With low population density and less severe land-use history, the northern boreal areas

533   have harboured many high-pH fen habitats until recently. Approximately 64 % of rich fen

534   habitats among all E.U. countries are in Finland and Sweden (Janssen et al., 2016), mainly in

535   the northernmost and alpine areas. However, groundwaters in the glaciated northern areas

536   have comparably low calcium concentrations (M. Hájek, Jiménez-Alfaro, et al., 2021), and

537   northern fens may, therefore, be particularly sensitive to changes triggered by the niche shifts

538   reported in our study. Warming may narrow the ecological niche of rich-fen species by

539   increasing competitive pressure. Even if enhanced precipitation in northern Europe would

540   increase groundwater recharge despite increasing evapotranspiration and keep the water table

541   in groundwater-fed fens high in some specific geological or geomorphological settings, the

542   pH and calcium content would decrease because of the shorter residence time of groundwater

543   (Hájek et al. 2021). In addition, the spread of competitively superior acidophytic *Sphagnum*

544   mosses would accelerate because of lower pH and abundant rainfall (Vicherová et al., 2017).

545   The high-pH fens will not change into wet grasslands like in southern Europe. Instead, they

546   will be colonised by competitive acidophytic species. Despite their wide distribution in

547   northern boreal regions in Europe, high-pH fen habitats are not safe from global change

548   factors, and attention should be paid to monitoring and conservation management.

549   Ongoing warming may trigger the negative development of rich fens in cold areas,

550   such as the Alps, Southern-European high mountains or Fennoscandia, and endanger fen

551   species in their last low-elevation refugia even if they are legally protected (Sperle &

552   Bruelheide 2021). The increasing competition seems to play an essential role in this process,

553   suppressing habitat specialists more than generalist species (Denelle, Violle, DivGrass

554   Consortium, & Munoz, 2020; Spitale, 2021). Therefore, conservation-oriented disturbances,

such as mowing with hay removal or moderate grazing in less damaged fen grasslands (Ross et al., 2019; Hájek, Horsáková, et al., 2020; Spitale, 2021), or removal of expansive late-successional peat mosses, sod, shrubs, and trees in successionally changed fens (Singh et al., 2021) should be applied to mitigate the effects of current anthropogenic environmental changes.

579

Data availability statement

The working data sheets (presence-absence data for individual fen species and corresponding data on adjusted pH, water level estimated by indicator values and climate data), details on data selection from the databases, the list of utilised vegetation databases, R scripts and complete results for individual species are accessible at https://www.zenodo.org/ (last access: 10 August 2021); 10.5281/zenodo.4915753; Hájek, Těšitel, et al., 2021).

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References

Aerts, R., Verhoeven, J. T. A., & Whigham, D. F. (1999). Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology, 80, 2170-2181.

Agresti, A. (2006). An Introduction to Categorical Data Analysis (2nd Ed.). Hoboken: Wiley, Wiley Series in Probability and Statistics.

Aletsee, L. (1967). Begriffliche und floristische Grundlagen zu einer pflanzengeographischen Analyse der europäischen Regenwassermoorstandorte. Beitr. Biol. Pflanzen, 43, 117–283.

Bengtsson, F., Rydin, H., Baltzer, J. L., Bragazza, L., Bu, Z. J., Caporn, S. J., ... Granath, G. (2021). Environmental drivers of *Sphagnum* growth in peatlands across the Holarctic region. Journal of Ecology, 109(1), 417-431. doi:10.1111/1365-2745.13499

Bragazza, L., Siffi, C., Iacumin, P., & Gerdol, R. (2007). Mass loss and nutrient release during litter decay in peatland: The role of microbial adaptability to litter chemistry. Soil Biology and Biochemistry, 39, 257-267.

Breeuwer, A., Heijmans, M., Robroek, B. J., Limpens, J., & Berendse, F. (2008). The effect
    of increased temperature and nitrogen deposition on decomposition in bogs. Oikos,
    117(8), 1258-1268. doi:10.1111/j.0030-1299.2008.16518.x

Breeuwer, A., Robroek, B. J., Limpens, J., Heijmans, M. M., Schouten, M. G., & Berendse, F.
    (2009). Decreased summer water table depth affects peatland vegetation. Basic and
    Applied Ecology, 10(4), 330-339. doi:10.1016/j.baae.2008.05.005

Bu, Z. J., Zheng, X. X., Rydin, H., Moore, T., & Ma, J. (2013). Facilitation vs. competition:
    Does interspecific interaction affect drought responses in Sphagnum? Basic and applied
    ecology, 14(7), 574-584. doi:10.1016/j.baae.2013.08.002

Cantonati, M., Poikane, S., Pringle, C. M., Stevens, L. E., Turak, E., Heino, J., ... Znachor, P.
    (2020): Characteristics, main impacts, and stewardship of natural and artificial
    freshwater environments: Consequences for biodiversity conservation. W, 12(1),
    ater260. doi:10.3390/w12010260

Chauvier, Y., Thuiller, W., Brun, P., Lavergne, S., Descombes, P., Karger, … Zimmermann,
    N. E (2021). Influence of climate, soil, and land cover on plant species distribution in
    the European Alps. Ecological Monographs, 91(2), doi:10.1002/ecm.1433

Chytrý, M., Hennekens, S. M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F., ...
    Yamalov, S. (2016). European Vegetation Archive (E.V.A.): an integrated database of
    European vegetation plots. Applied vegetation science, 19(1), 173-180.
    doi:10.1111/avsc.12191

Chytrý, M., Tichý, L., Hennekens, S. M., Knollová, I., Janssen, J. A. M., Rodwell, J.S., …
    Schaminée J.H.J. (2020). EUNIS Habitat Classification: expert system, characteristic
    species combinations and distribution maps of European habitats. Applied Vegetation
    Science, 23(4), 648-675. doi:10.1111/avsc.12519

626   Costa, D.S., Gerschlauer, F., Kiese, R., Fischer, M., Kleyer, M., & Hemp, A. (2018). Plant

627   niche breadths along environmental gradients and their relationship to plant functional

628   traits. Diversity and Distributions, 24, 1869-1882.

629   Coudun, C., & Gégout, J. C. (2005). Ecological behaviour of herbaceous forest species along

630   a pH gradient: a comparison between oceanic and semicontinental regions in northern

631   France. Global Ecology and Biogeography, 14, 263-270. doi: 10.1111/j.1466-

632   822X.2005.00144.x

633   Coudun, C., & Gégout, J. C. (2006). The derivation of species response curves with Gaussian

634   logistic regression is sensitive to sampling intensity and curve characteristics.

635   Ecological Modelling, 199, 164-175.

636   Crawford, R. M. (2008). Cold climate plants in a warmer world. Plant Ecology & Diversity,

637   1(2), 285-297. doi:10.1080/17550870802407332

638   Denelle, P., Violle, C., DivGrass Consortium, & Munoz, F. (2020). Generalist plants are more

639   competitive and more functionally similar to each other than specialist plants: insights

640   from network analyses. Journal of Biogeography, 47(9), 1922-1933.

641   doi:10.1111/jbi.13848

642   Dierßen, K. & Dierßen, B. (2001). Moore. Ökosysteme Mitteleuropas aus geobotanischer

643   Sicht. Ulmer, Stuttgart.

644   Dierßen, K. (1996). Vegetation Nordeuropas. Stuttgart: Verlag Eugen Ulmer.

645   Dítě, D., Hájek, M., Svitková, I., Košuthová, A., Šoltés, R., & Kliment, J. (2018). Glacial-

646   relict symptoms in the Western Carpathian flora. Folia Geobotanica, 53(3), 277-300.

647   doi:10.1007/s12224-018-9321-8

648   Djukic, I., Kepfer-Rojas, S., Schmidt, I. K., Larsen, K. S., Beier, C., Berg, B., & Verheyen, K.

649   (2018). Early stage litter decomposition across biomes. Science of the Total

650   Environment, 628, 1369-1394. doi:10.1016/j.scitotenv.2018.01.012

651   Dorrepaal, E., Aerts, R., Cornelissen, J. H. C., Van Logtestijn, R. S. P., & Callaghan, T. V.

652   (2006). Sphagnum modifies climate-change impacts on subarctic vascular bog

653   plants.   Functional Ecology, 20(1), 31-41. doi:10.1111/j.1365-

654   2435.2006.01076.x

655   Drzymulska, D., & Jadwiszczak, P. (2020). Towards the reconstruction of subfossil

656   vegetation: an unexpected plant record in Early Holocene sediments of a mire in NE

657   Poland. Boreal Environment Research, 25, 171-183.

658   Essl, F., Dullinger, S., Moser, D., Rabitsch, W., & Kleinbauer, I. (2012). Vulnerability of

659   mires under climate change: implications for nature conservation and climate change

660   adaptation. Biodiversity and Conservation, 21(3), 655-669. doi:10.1007/s10531-011-

661   0206-x

662   Friberg, N., Dybkjaer, J. B., Olafsson, J. S., Gislason, G. M., Larsen, S. E., & Lauridsen, T. L.

663   (2009). Relationships between structure and function in streams contrasting in

664   temperature. Freshwater Biology, 54(10), 2051-2068. doi:10.1111/j.1365-

665   2427.2009.02234.x

666   Fridley, J. D., Lynn, J. S., Grime, J. P., & Askew, A. P. (2016). Longer growing seasons shift

667   grassland vegetation towards more-productive species. Nature Climate Change, 6(9),

668   865-868. doi:10.1038/nclimate3032

669   Gignac, L. D., Gauthier, R., Rochefort, L., & Bubier, J. (2004). Distribution and habitat

670   niches of 37 peatland Cyperaceae species across a broad geographic range in Canada.

671   Canadian Journal of Botany, 82(9), 1292-1313. doi:10.1139/b04-081

672   Gignac, L. D., Vitt, D. H., Zoltai, S. C., & Bayley, S. E. (1991). Bryophyte response surfaces

673   along climatic, chemical, and physical gradients in peatlands of western Canada. Nova

674   Hedwigia, 53(1-2), 27-71.

Gong, J., Wang, K., Kellomäki, S., Zhang, C., Martikainen, P. J., & Shurpali, N. (2012). Modelling water table changes in boreal peatlands of Finland under changing climate conditions. Ecological Modelling, 244, 65-78. doi:10.1016/j.ecolmodel.2012.06.031

Górecki, K., Rastogi, A., Stróżecki, M., Gąbka, M., Lamentowicz, M., Łucóv, D., … Juszczak, R. (2021). Water table depth, experimental warming, and reduced precipitation impact on litter decomposition in a temperate Sphagnum-peatland. Science of The Total Environment, 771, 145452. doi:10.1016/j.scitotenv.2021.145452

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J. L. B., ... Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. Nature Climate Change, 2(2), 111-115. doi:10.1038/nclimate1329

Graham, J., Farr, G., Hedenäs, L., Devez, A., & Watts, M. J. (2019). Using water chemistry to define ecological preferences within the moss genus Scorpidium, from Wales, UK. Journal of Bryology, 41(3), 197-204. doi:10.1080/03736687.2019.1603416

Granath, G., Strengbom, J., & Rydin, H. (2010). Rapid ecosystem shifts in peatlands: linking plant physiology and succession. Ecology, 91(10), 3047-3056. doi:10.1890/09-2267.1

Hájek, M., Dítě, D., Horsáková, V., Mikulášková, E., Peterka, T., Navrátilová, J., … Horsák, M. (2020). Towards the pan-European bioindication system: Assessing and testing updated hydrological indicator values for vascular plants and bryophytes in mires. Ecological Indicators, 116, 106527. doi:10.1016/j.ecolind.2020.106527

Hájek, M., Horsák, M., Tichý, L., Hájková, P., Dítě, D., & Jamrichová, E. (2011). Testing a relict distributional pattern of fen plant and terrestrial snail species at the Holocene scale: a null model approach. Journal of Biogeography, 38(4), 742-755. doi:10.1111/j.1365-2699.2010.02424.x

Hájek, M., Horsáková, V., Hájková, P., Coufal, R., Dítě, D., Němec, T., & Horsák, M. (2020). Habitat extremity and conservation management stabilise endangered calcareous fens in

a changing world. Science of The Total Environment, 719, 134693.

doi:10.1016/j.scitotenv.2019.134693

Hájek, M., Jiménez-Alfaro, B., Hájek, O., Brancaleoni, L., Cantonati, M., Carbognani, M., ...

Horsák, M. (2021). A European map of groundwater pH and calcium. Earth System

Science Data, 13(3), 1089-1105. doi:10.5194/essd-13-1089-2021

Hájek, M., Jiroušek, M., Navrátilová, J., Horodyská, E., Peterka, T., Plesková, Z., … Hájek,

T. (2015). Changes in the moss layer in Czech fens indicate early succession triggered

by nutrient enrichment. Preslia, 87(3), 279-301.

Hájek, M., Těšitel, J., Tahvanainen, T., Peterka, T., Jansen, F., Pérez-Haase, A. …

Mikulášková, E. (2021). Data, script, full methods and full results for: Rising

temperature modulates pH niches of fen species (2.0). 10.5281/zenodo.4915753

Hájková, P., Hájek, M., Apostolova, I., Zelený, D., & Dítě, D. (2008). Shifts in the ecological

behaviour of plant species between two distant regions: evidence from the base richness

gradient in mires. Journal of Biogeography, 35(2), 282-294. doi:10.1111/j.1365-

2699.2007.01793.x

Hájková, P., Štechová, T., Šoltés, R., Šmerdová, E., Plesková, Z., Dítě, D., … Hájek, M.

(2018). Using a new database of plant macrofossils of the Czech and Slovak Republics

to compare past and present distribution of hypothetically relict fen mosses. Preslia,

90(4), 367-386. doi:10.23855/preslia.2018.367

He, X., He, K. S., & Hyvönen, J. (2016). Will bryophytes survive in a warming world?

Perspectives in Plant Ecology, Evolution and Systematics, 19, 49-60.

doi:10.1016/j.ppees.2016.02.005

Hedenäs, L., & Bisang, I. (2012). Drepanocladus trifarius – an example of unsuspected niche

widths among mosses. Nordic Journal of Botany, 30(6), 747-753. doi:10.1111/j.1756-

1051.2012.01526.x

725 Hill, M. O., Bell, N., Bruggeman-Nannenga, M. A., Brugués, M., Cano, M. J., Enroth, J., ...

726   Söderström, L. (2006). An annotated checklist of the mosses of Europe and

727   Macaronesia. Journal of Bryology, 28(3), 198-267. doi:10.1179/174328206X119998

728 Horsáková, V., Hájek, M., Hájková, P., Dítě, D., & Horsák, M. (2018). Principal factors

729   controlling the species richness of European fens differ between habitat specialists and

730   matrix-derived species. Diversity and Distributions, 24(6), 742-754.

731   doi:10.1111/ddi.12718

732 Hughes, P. D. M. (2000). A reappraisal of the mechanisms leading to ombrotrophy in British

733   raised mires. Ecology Letters, 3(1), 7-9. doi:10.1046/j.1461-0248.2000.00118.x

734 Ise, T., Dunn, A. L., Wofsy, S. C., & Moorcroft, P. R. (2008). High sensitivity of peat

735   decomposition to climate change through water-table feedback. Nature Geoscience,

736   1(11), 763–766. doi:10.1038/ngeo331

737 Jamin, A., Peintinger, M., Gimmi, U., Holderegger, R., & Bergamini, A. (2020). Evidence for

738   a possible extinction debt in Swiss wetland specialist plants. Ecology and Evolution,

739   10(3), 1264-1277. doi:10.1002/ece3.5980

740 Janssen, J. A. M., Rodwell, J. S., García-Criado, M., Gubbay, S., Haynes, T., Nieto, A., …

741   Valachovič, M. (2016). European red list of habitats, Part 2, Terrestrial and freshwater

742   habitats. European Commission, Luxembourg. doi:10.2779/091372

743 Jeppesen, E., Moss, B., Bennion, H., Carvalho, L., DeMeester, L., Feuchtmayr, H., ...

744   Verhoeven, J. T. (2010). Interaction of climate change and eutrophication. In M.

745   Kernan, R. W. Battarbee & B. Moss (Eds.), Climate change impacts on freshwater

746   ecosystems (pp. 119-151). Oxford: Blackwell Publishing Ltd.

747 Jiménez-Alfaro, B., Garcia-Calvo, L., Garcia, P., & Acebes, J. L. (2016). Anticipating

748   extinctions of glacial relict populations in mountain refugia. Biological Conservation,

749   201, 243-251. doi:10.1016/j.biocon.2016.07.015

750   Johnson, M. G., Granath, G., Tahvanainen, T., Pouliot, R., Stenøien, H. K., Rochefort, L., ...

751   & Shaw, A. J. (2015). Evolution of niche preference in *Sphagnum* peat mosses.

752   Evolution, 69, 90-103.

753   Joosten, H., Tanneberger, F., & Moen, A. (Eds.) (2017). Mires and peatlands of Europe:

754   Status, distribution and conservation. Stuttgart: Schweizerbart Science Publishers.

755   Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., … Kessler,

756   M. (2017). Climatologies at high resolution for the Earth land surface areas. Scientific

757   Data, 4(1), 1-20. doi:10.1038/sdata.2017.122

758   Kolari, T. H. M., Korpelainen, P., Kumpula, T., & Tahvanainen, T. (2021). Acceleration of

759   vegetation succession but no hydrological change in a boreal fen during 20 years of

760   recent climate change. Ecology and Evolution, 11(12), 7602-7621. doi:

761   10.1002/ece3.7592.

762   Kooijman, A. M. (2012). Poor rich fen mosses': atmospheric N-deposition and P-

763   eutrophication in base-rich fens. Lindbergia, 35, 42-52.

764   Kooijman, A. M., & Bakker, C. (1995). Species replacement in the bryophyte layer in mires:

765   the role of water type, nutrient supply and interspecific interactions. Journal of Ecology,

766   83, 1-8. doi:10.2307/2261145

767   Kooijman, A., & Hedenäs, L. (2009). Changes in nutrient availability from calcareous to acid

768   wetland habitats with closely related brown moss species: increase instead of decrease

769   in N and P. Plant and Soil, 324, 267-278.

770   Kooijman, A. M., & Westhoff, V. (1995). Variation in habitat factors and species composition

771   of Scorpidium scorpioides communities in NW-Europe. Vegetatio, 117(2), 133-150.

772   doi:10.1007/BF00045505

773 Küttim, M., Küttim, L., Ilomets, M., & Laine, A. M. (2020). Controls of Sphagnum growth

774   and the role of winter. Ecological Research, 35(1), 219-234. doi: /10.1111/1440-

775   1703.12074

776 Küttim, M., Laine, A. M., Küttim, L., Ilomets, M., & Robroek, B. J. (2019). Winter climate

777   change increases physiological stress in calcareous fen bryophytes. Science of the

778   Total Environment, 695, 133867. doi:10.1016/j.scitotenv.2019.133867

779 Lawrey, J. D. (1981). Evidence for competitive release in simplified saxicolous lichen

780   communities. American Journal of Botany, 68, 1066-1073.

781 Lengyel, A., Chytrý, M., & Tichý, L. (2011). Heterogeneity-constrained random resampling

782   of phytosociological databases. Journal of Vegetation Science, 22, 175-183. doi:

783   10.1111/j.1654-1103.2010.01225.x

784 Leuschner, C., & Ellenberg, H. (2017). Mires. In C. Leuschner & H. Ellenberg (Eds.) Ecology

785   of Central European Non-Forest Vegetation: Coastal to Alpine, Natural to Man-Made

786   Habitats (pp. 117-187). Cham: Springer. doi:10.1007/978-3-319-43048-5.

787 Ma, J. Z., Chen, X., Mallik, A. U., Bu, Z. J., Zhang, M. M., Wang, S. Z., & Sundberg, S.

788   (2020). Environmental together with interspecific interactions determine bryophyte

789   distribution in a protected mire of Northeast China. Frontiers in Earth Science, 8, 32.

790   doi:10.3389/feart.2020.00032

791 Michel, A., Brauchli, T., Lehning, M., Schaefli, B., & Huwald, H. (2020). Stream temperature

792   and discharge evolution in Switzerland over the last 50 years: annual and seasonal

793   behaviour. Hydrology and earth system sciences, 24(1), 115-142. doi:10.5194/hess-24-

794   115-2020

795 Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J. P., Raus, T., Čarni, A., ... Tichý, L.

796   (2016). Vegetation of Europe: hierarchical floristic classification system of vascular

797 plant, bryophyte, lichen, and algal communities. Applied Vegetation Science, 19, 3-264.

798 doi:10.1111/avsc.12257

799 Mulligan, R. C., & Gignac, L. D. (2002). Bryophyte community structure in a boreal poor fen

800 II: interspecific competition among five mosses. Canadian Journal of Botany, 80, 330-

801 339.

802 Niu, S., Xing, X., Zhang, Z. H. E., Xia, J., Zhou, X., Song, B., … Wan, S. (2011). Water-use

803 efficiency in response to climate change: from leaf to ecosystem in a temperate steppe.

804 Global Change Biology, 17(2), 1073-1082. doi:10.1111/j.1365-2486.2010.02280.x

805 Odgaard, B. V. (1988). Glacial Relicts - and the Moss Meesia Triquetra in Central and

806 Western Europe. Lindbergia, 14, 73-78.

807 Olsen, S. L., Töpper, J. P., Skarpaas, O., Vandvik, V., & Klanderud, K. (2016). From

808 facilitation to competition: Temperature-driven shift in dominant plant interactions

809 affects population dynamics in seminatural grasslands. Global Change Biology, 22(5),

810 1915-1926. doi:10.1111/gcb.13241

811 Pakalne, M. (1994). Mire vegetation in the coastal lowland of Latvia. Colloques

812 Phytosociologiques, 23, 487-509.

813 Paulissen, M. P., Van Der Ven, P. J., Dees, A. J., & Bobbink, R. (2004). Differential effects

814 of nitrate and ammonium on three fen bryophyte species in relation to pollutant nitrogen

815 input. New Phytologist, 164, 451-458.

816 Paulissen, M. P., Schaminée, J. H., During, H. J., Wieger Wamelink, G. W., & Verhoeven, J.

817 T. (2014). Expansion of acidophytic late-successional bryophytes in Dutch fens

818 between 1940 and 2000. Journal of Vegetation Science, 25, 525-533.

819 doi:10.1111/jvs.12089

820   Pérez-Haase, A., & Ninot, J. M. (2017). Hydrological heterogeneity rather than water

821   chemistry explains the high plant diversity and uniqueness of a Pyrenean mixed mire.

822   Folia Geobotanica, 52(2), 143-160. doi:10.1007/s12224-017-9291-2

823   Peterka, T., Hájková, P., Mikulášková, E., Aunina, L., Dítě, D., Pawlikowski, P., ... Hájek, M.

824   (2020). Vegetation affinity of the moss species Meesia triquetra, Paludella squarrosa,

825   Pseudocalliergon trifarium and Scorpidium scorpioides across European regions. Nova

826   Hedwigia, Beihefte, 150, 133-158. doi:10.1127/nova-suppl/2020/133

827   Peterka, T., Hájek, M., Jiroušek, M., Jiménez-Alfaro, B., Aunina, L., Bergamini, A., ...

828   Chytrý, M. (2017). Formalised classification of European fen vegetation at the alliance

829   level. Applied Vegetation Science, 20(1), 124-142. doi:10.1111/avsc.12271

830   Peterka, T., Syrovátka, V., Dítě, D., Hájková, P., Hrubanová, M., Jiroušek, M., … Hájek, M.

831   (2020). Is variable plot size a serious constraint in broad-scale vegetation studies? A

832   case study on fens. Journal of Vegetation Science, 31, 594– 605. doi:10.1111/jvs.12885

833   Plesková, Z., Jiroušek, M., Peterka, T., Hájek, T., Dítě, D., Hájková, P., … Hájek, M. (2016).

834   Testing inter-regional variation in pH niches of fen mosses. Journal of Vegetation

835   Science, 27(2), 352-364. doi:10.1111/jvs.12348

836   Pouliot, R., Rochefort, L., Karofeld, E., & Mercier, C. (2011). Initiation of Sphagnum moss

837   hummocks in bogs and the presence of vascular plants: Is there a link? Acta Oecologica,

838   37(4), 346-354. doi:10.1016/j.actao.2011.04.001

839   Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2002). Geographic variability of ecological

840   niches of plant species: are competition and stress relevant? Ecography, 25, 721–729.

841   doi: 10.1034/j.1600-0587.2002.250608.x

842   Proctor, M. C., McHaffie, H. S., Legg, C. J., & Amphlett, A. (2009). Evidence from water

843   chemistry as a criterion of ombrotrophy in the mire complexes of Abernethy Forest,

844   Scotland. Journal of Vegetation Science, 20(1), 160-169. doi:10.1111/j.1654-

845   1103.2009.05643.x

846 R Core Team (2020). R: A language and environment for statistical computing. R Foundation

847   for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

848 Reinecke, J., Wulf, M., Baeten, L., Brunet, J., Decocq, G., De Frenne, P., ... & Naaf, T.

849   (2016). Acido-and neutrophilic temperate forest plants display distinct shifts in

850   ecological pH niche across north-western Europe. Ecography, 39, 1164-1175.

851   doi:10.1111/ecog.02051

852 Robroek, B. J., Jassey, V. E., Payne, R. J., Martí, M., Bragazza, L., Bleeker, A., Buttler, A.,

853   Caporn, S. J. M., Dise, N. B., Kattge, J., Zając, K., Svensson, B. H., Van Ruijven, J., &

854   Verhoeven, J. T. (2017). Taxonomic and functional turnover are decoupled in European

855   peat bogs. Nature Communications, 8, 1-9. doi:10.1038/s41467-017-01350-5

856 Ross, L. C., Speed, J. D., Øien, D. I., Grygoruk, M., Hassel, K., Lyngstad, A., & Moen, A.

857   (2019). Can mowing restore boreal rich-fen vegetation in the face of climate change?

858   PloS one, 14(2), e0211272. doi:10.1371/journal.pone.0211272

859 Rozbrojová, Z., & Hájek, M. (2008). Changes in nutrient limitation of spring fen vegetation

860   along environmental gradients in the West Carpathians. Journal of Vegetation Science,

861   19, 613-620.

862 Ruosteenoja, K., Räisänen, J., Venäläinen, A., & Kämäräinen, M. (2016). Projections for the

863   duration and degree days of the thermal growing season in Europe derived from CMIP5

864   model output. International Journal of Climatology, 36, 3039-3055.

865 Ruosteenoja, K., Markkanen, T., Venäläinen, A., Räisänen, P., & Peltola, H. (2018). Seasonal

866   soil moisture and drought occurrence in Europe in CMIP5 projections for the 21st

867   century. Climate Dynamics, 50(3), 1177-1192.

Rydin, H. (1986). Competition and niche separation in *Sphagnum*. Canadian Journal of
    Botany, 64, 1817-1824.

Schwarzer, C., & Joshi, J. (2019). Ecotypic differentiation, hybridisation and clonality
    facilitate the persistence of a cold-adapted sedge in European bogs. Biological Journal
    of the Linnean Society, 128(4), 909-925. doi:10.1093/biolinnean/blz141

Singh, P., Ekrtová, E., Holá, E., Štechová, T., Grill, S., & Hájek, M. (2021). Restoration of
    rare bryophytes in degraded rich fens: The effect of sod-and-moss removal. Journal for
    Nature Conservation, 59, 125928. doi:10.1016/j.jnc.2020.125928

Singh, P., Těšitel, J., Plesková, Z., Peterka, T., Hájková, P., Dítě, D., … Hájek, M. (2019).
    The ratio between bryophyte functional groups impacts vascular plants in rich fens.
    Applied Vegetation Science, 22(4), 494-507. doi:10.1111/avsc.12454

Soliveres, S., Lehmann, A., Boch, S., Altermatt, F., Carrara, F., Crowther, T. W., ... & Allan,
    E. (2018). Intransitive competition is common across five major taxonomic groups and
    is driven by productivity, competitive rank and functional traits. Journal of Ecology,
    106, 852-864.

Soomers, H., Karssenberg, D., Verhoeven, J. T., Verweij, P. A., & Wassen, M. J. (2013). The
    effect of habitat fragmentation and abiotic factors on fen plant occurrence. Biodiversity
    and Conservation, 22(2), 405-424. doi:10.1007/s10531-012-0420-1

Sperle, T. & Bruelheide, H. (2021). Climate change aggravates bog species extinctions in the
    Black Forest (Germany). Diversity and Distributions, 27, 282– 295.
    doi:10.1111/ddi.13184

Spitale, D. (2009). Switch between competition and facilitation within a seasonal scale
    at colony level in bryophytes. Oecologia, 160, 471-482.

891   Spitale, D. (2021). A warning call from mires of the Southern Alps (Italy): impacts which are

892   changing the bryophyte composition. Journal for Nature Conservation, 125994.

893   doi:10.1016/j.jnc.2021.125994

894   Štechová, T., Hájek, M., Hájková, P., & Navrátilová, J. (2008). Comparison of habitat

895   requirements of the mosses *Hamatocaulis vernicosus, Scorpidium cossonii* and

896   *Warnstorfia exannulata* in different parts of temperate Europe. Preslia, 80, 399-410.

897   Tichý, L., Hájek, M., & Zelený, D. (2010). Imputation of environmental variables for

898   vegetation plots based on compositional similarity. Journal of Vegetation Science, 21,

899   88-95.

900   Udd, D., Sundberg, S., & Rydin, H. (2016). Multi-species competition experiments with

901   peatland bryophytes. Journal of Vegetation Science, 27(1), 165-175.

902   doi:10.1111/jvs.12322

903   Väliranta, M., Salojärvi, N., Vuorsalo, A., Juutinen, S., Korhola, A., Luoto, M., & Tuittila, E.

904   S. (2017). Holocene fen–bog transitions, current status in Finland and future

905   perspectives. The Holocene, 27(5), 752-764. doi:10.1177/0959683616670471

906   van Breemen, N. (1995). How Sphagnum bogs down other plants. Trends in Ecology &

907   Evolution, 10(7), 270-275. doi:10.1016/0169-5347(95)90007-1

908   van Diggelen, R., Middleton, B., Bakker, J., Grootjans, A., & Wassen, M. (2006). Fens and

909   floodplains of the temperate zone: present status, threats, conservation and restoration.

910   Applied Vegetation Science, 9(2), 157-162. doi:10.1111/j.1654-109X.2006.tb00664.x

911   Vicherová, E., Glinwood, R., Hájek, T., Šmilauer P., & Ninkovic V. (2020) Bryophytes can

912   recognise their neighbours through volatile organic compounds. Scientific Reports, 10,

913   7405. doi:10.1038/s41598-020-64108-y

914   Vicherová, E., Hájek, M., & Hájek, T. (2015). Calcium intolerance of fen mosses:

915   physiological evidence, effects of nutrient availability and successional drivers.

916   Perspectives in Plant Ecology, Evolution and Systematics, 17, 347-359.

917 Vicherová, E., Hájek, M., Šmilauer, P., & Hájek, T. (2017). Sphagnum establishment in

918   alkaline fens: Importance of weather and water chemistry. Science of the Total

919   Environment, 580, 1429-1438. doi:10.1016/j.scitotenv.2016.12.109

920 Wagner, V., Chytrý, M., Zelený, D., von Wehrden, H., Brinkert, A., Danihelka, J., ... Wesche,

921   K. (2017). Regional differences in soil pH niche among dry grassland plants in Eurasia.

922   Oikos, 126, 660-670. doi:10.6084/m9.figshare.3860124

923 Walter, H. & Walter, E. (1953). Einige allgemeine Ergebnisse unserer Forschungsreise nach

924   Südwestafrika 1952/1953: das Gesetz der relativen Standortskonstanz; das Wesen der

925   Pflanzengemeinschaften. Berichte der Deutshen Botanischen Gessellschaft, 66, 227–

926   235.

927 Waughman, G. J. (1980). Chemical aspects of the ecology of some south German peatlands.

928   Journal of Ecology, 68, 1025-1046.

929 Wheeler, D.B. (1999). Water and plants in freshwater wetlands. In A. J. Baird & R L. Wilby

930   (Eds.), Eco-Hydrology: Plants and water in terrestrial and aquatic environments (pp.

931   127–180). London: Routledge.

932 Wickham. H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New

933   York.

934 Wood, S.N. (2017). Generalised Additive Models: An Introduction with R (2nd edition).

935   Chapman and Hall/C.R.C.

936

937

938 **Figure 1.** Distribution of fen vegetation-plot records in Europe selected for this study.
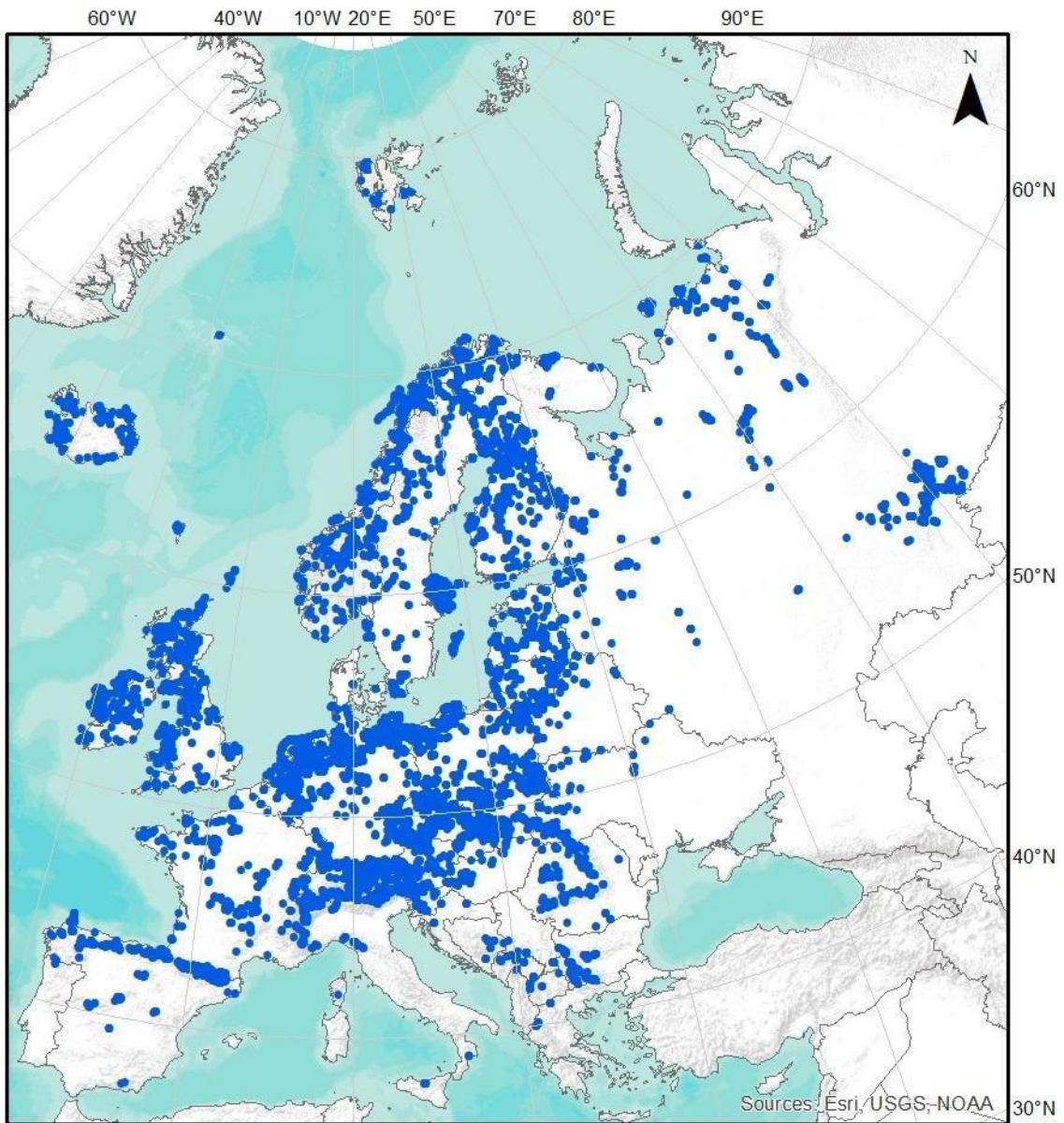
939

940

941 **Figure 2.** Total deviances explained by the interaction between macroclimate temperature and

942 pH in generalised additive modelling of realised niches of one hundred European fen species

943 plotted against standardised interaction coefficients. Each circle represents one taxon. For the

944 full names of taxa, see Supplementary Table 1 in Hájek, Těšitel, et al. (2021);

945 10.5281/zenodo.4915753.

946
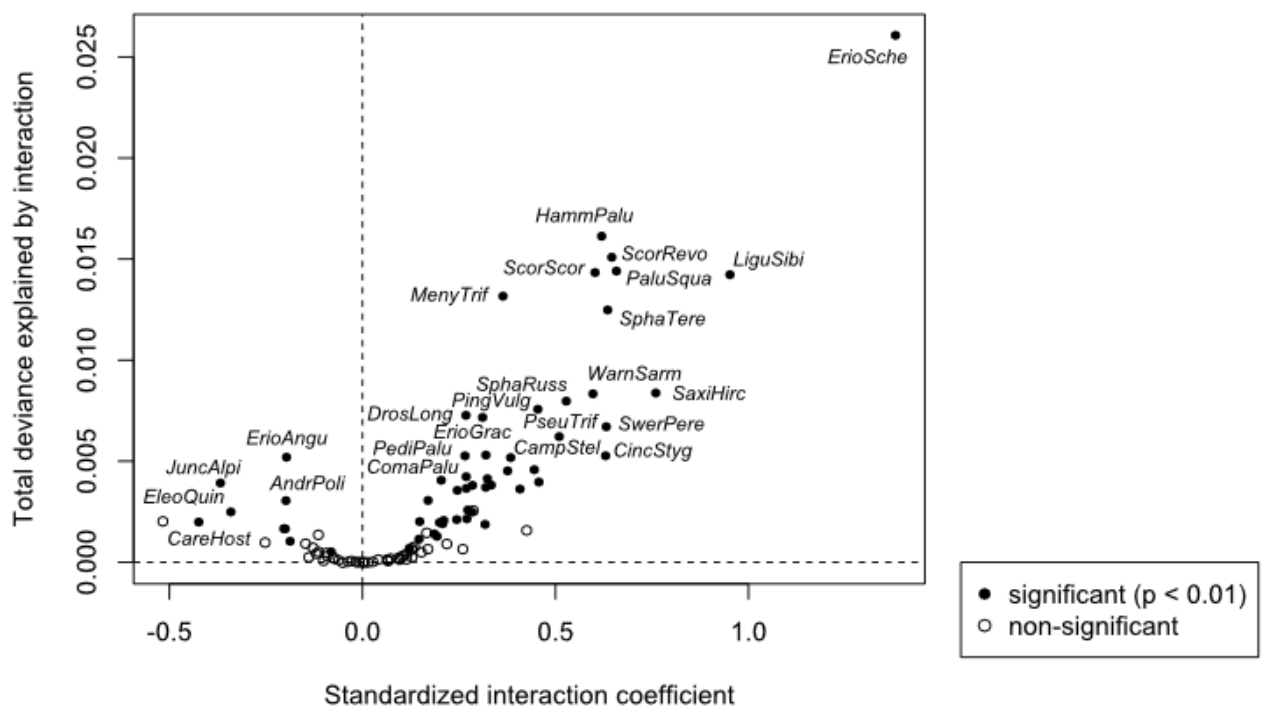
947

Figure 3. Contour plots representing GAM models of fen species to pH and macroclimate temperature. Species with a positive parametric effect of the interaction between the two gradients are displayed (significant at p < 0.01 after Holm correction).
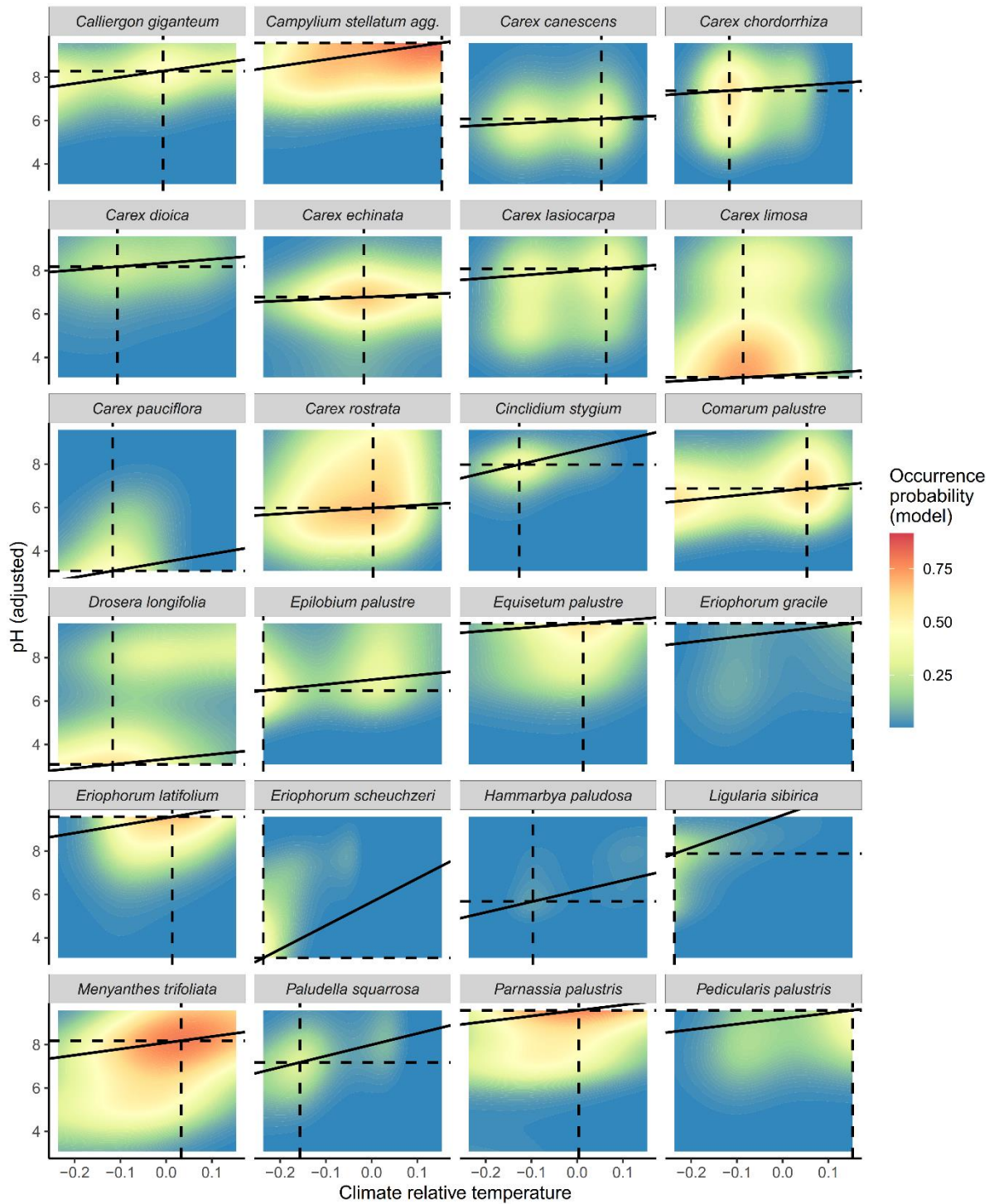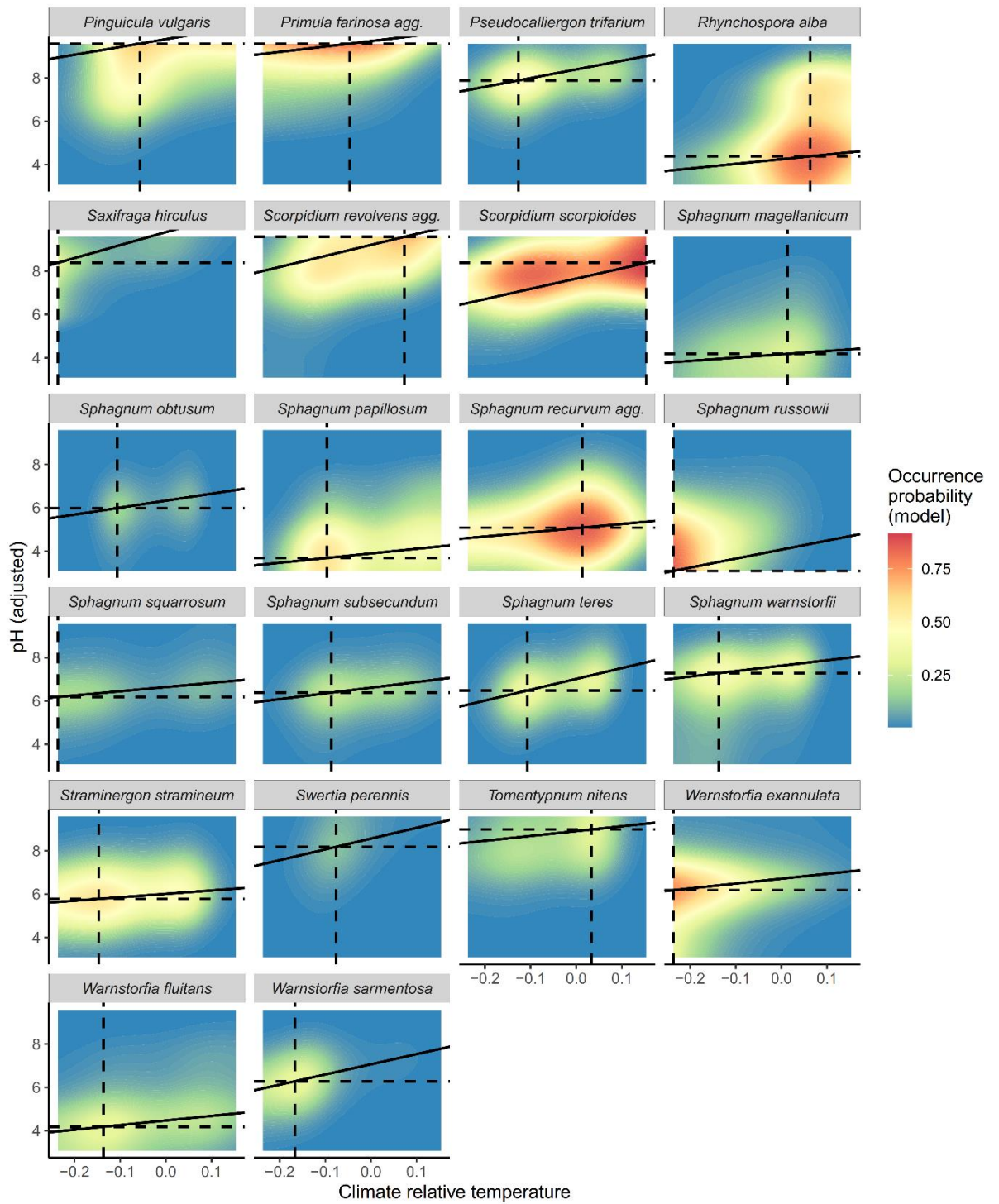
Figure 4. Contour plots representing GAM models of fen species to pH and climate temperature. Species with the negative parametric effect of the interaction between the two gradients are displayed (significant at p < 0.01 after Holm correction).
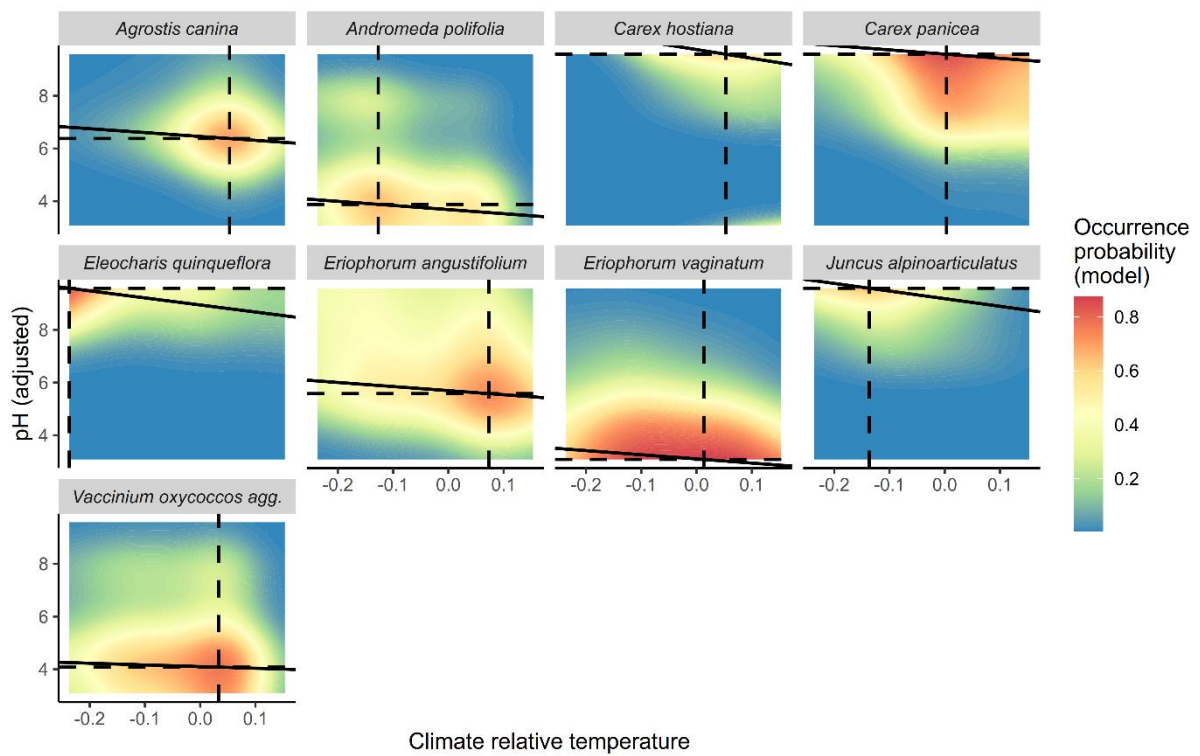
Figure 5. Contour plots representing GAM models of fen species to pH and climate temperature. Ecological niches of species displayed here show an apparent bimodal pattern to either temperature or pH, without significant interaction between the two gradients (p > 0.05 after Holm correction).
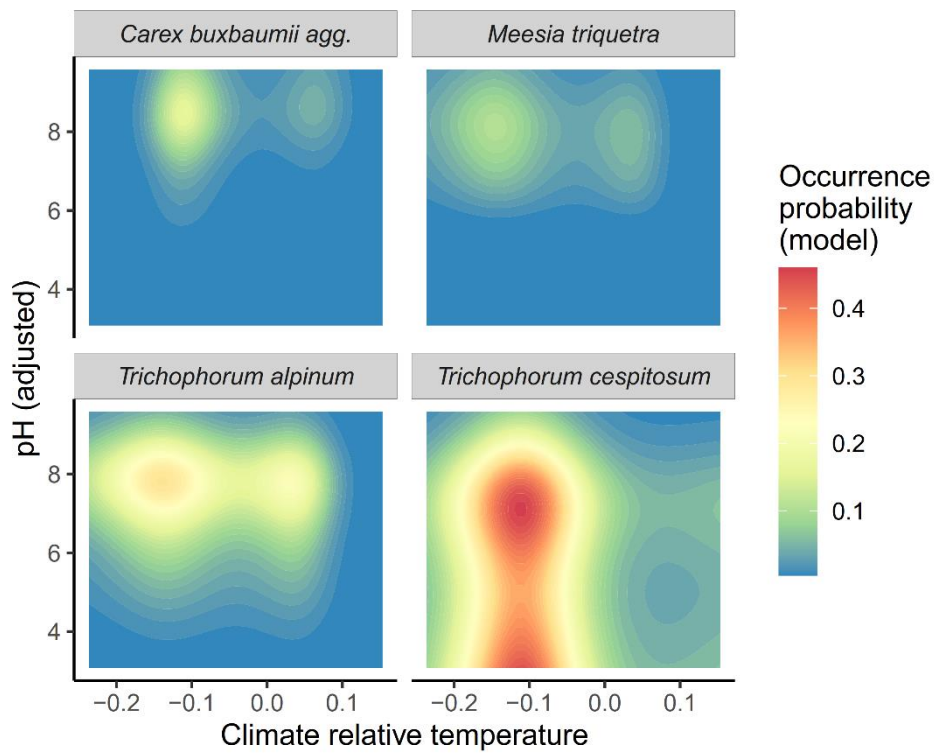
Figure 6. The bean plot showing the difference in standardised interaction coefficient (interaction between temperature and pH in Generalised Additive Models) between mosses and vascular plants. Each taxon is represented by the line, with statistically significant interaction indicated by the red colour.

Author contributions