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

2 Running title: Climate modulates pH niches

3

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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 the 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 the
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 ($\text{adj}P < 0.01$). Forty-six of them (84%) showed the positive interaction manifested by a shift or
55 restriction of a 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
61 lowers 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

67 **Key words:** biodiversity loss, bryophytes and vascular plants, competition, climate change,
68 continental-scale vegetation data, distribution, mire, shifts in realised niche

70 **Introduction**

71 Climate thermal regime alterations affected species composition and functioning of most
72 habitats during the quaternary climate cycles, and the ongoing climate change has similar
73 impacts (Essl, Dullinger, Moser, Rabitsch, & Kleinbauer, 2012; Gottfried, et al., 2012).
74 Nutrient-limited wetland ecosystems, such as small-sedge, tall-sedge and moss-sedge spring
75 and quaking fens (according to the EUNIS habitat classification; Chytrý, et al., 2020), are
76 rapidly declining habitats worldwide because of direct destruction, groundwater drawdown,
77 eutrophication, and changes in disturbance regimes (van Diggelen, Middleton, Bakker,
78 Grootjans, & Wassen, 2006; Janssen et al., 2016; Spitale, 2021). As in other cold-adapted,
79 low-productive ecosystems, ongoing climate warming may accelerate the loss of diversity in
80 fens (Jiménez-Alfaro, Garcia-Calvo, Garcia, & Acebes, 2016; Sperle & Bruelheide 2021).
81 Many direct ecophysiological effects may act, such as phenological shifts to unfavourable
82 part of the year, respiration increasing more than photosynthesis, an imbalance between
83 growth and water use efficiency, increased water stress by increasing transpiration, or stress
84 from increased numbers of freeze-thaw cycles in winter (Crawford, 2008; Niu et al., 2011;
85 He, He, & Hyvönen, 2016; Küttim, Laine, Küttim, Ilomets, & Robroek, 2019). However,
86 indirect effects are of crucial importance. Increasing temperature leads to decreases in the
87 water table (Gong et al., 2012; Michel, Brauchli, Lehning, Schafli, & Huwald, 2020) and
88 accelerates nutrient cycling by the increasing decomposition of soil organic matter (Friberg et
89 al., 2009; Górecki, et al., 2021). Warming climate may narrow realised niches of specialised
90 low-competitive fen species, along with increasing nutrient availability, because the
91 significance of adaptations to environmental stress is reduced while productivity and
92 competition increase.

93 Regional differences in the realised niches of individual mire species are a well-known
94 phenomenon in Europe, often mentioned in textbooks and monographs (Aletsee, 1967,
95 Wheeler, 1999; Dierßen & Dierßen, 2001; Leuschner & Ellenberg 2017). They hold
96 especially for pH, the major determinant of mire and spring diversity (Joosten, Tanneberger &
97 Moen, 2017; Peterka, Hájek, et al., 2017; Cantonati et al., 2020), as evidenced by inter-
98 regional comparisons of Kooijman & Westhoff (1995), Hájková, Hájek, Apostolova, Zelený,
99 & Dítě (2008), Štechová, Hájek, Hájková, & Navrátilová (2008), Plesková et al. (2016),
100 Graham, Farr, Hedenäs, Devez, & Watts (2019), and Peterka, Hájková, et al. (2020). Several
101 studies report wide realised niches of mire species in northern Europe, while the same species
102 are restricted to extreme pH values in Central, Western, and Southern Europe (Odgaard, 1988;
103 Kooijman & Westhoff, 1995; Dierßen, 1996; Hedenäs & Bisang, 2012). As a result, there is a
104 much higher threat to base-rich fens in Europe than acidic mires in terms of their diversity and
105 habitat conservation status (Janssen et al., 2016; Chytrý et al., 2020).

106 The causes of geographical differences in pH niches are not well known. Such
107 differences may be explained by either interaction with other ecological variables, such as
108 calcium content, nutrient availability or climate (Proctor, McHaffie, Legg, & Amphlett, 2009;
109 Plesková et al., 2016; Vicherová, Hájek, Šmilauer, & Hájek, 2017), or hypothetical ecotypes
110 resulting from refugial processes during the Holocene (Hájková et al., 2018). Plesková et al.
111 (2016) suggested combining pH and calcium into a single variable (named *adjusted pH*)
112 because these two factors act synergistically in habitat filtering of specialised mire species. In
113 their study, the niches of more competitive bryophyte species to adjusted pH were widened by
114 nutrient enrichment, while the opposite held for competitively weak species. Similarly,
115 Kooijman & Westhoff (1995), Graham, et al., (2019), and Peterka, Hájková, et al. (2020)
116 found a niche shift of specialised fen brown mosses of the genus *Scorpidium* to higher pH
117 values in Western and Central Europe when compared to the colder and less polluted areas of

118 Scandinavia. These findings match the result of a resurvey study from the Bohemian Massif
119 in Central Europe (Hájek et al., 2015) that showed narrowing of the realised niches of
120 calcicole fen bryophyte species during the last decades, which were characterised by
121 increasing temperature and nutrient inputs. The results of Singh et al. (2019) even suggested
122 that the increasing competition in the moss layer may also restrict some specialised vascular
123 plants and outweigh the pH effects.

124 Although it is widely acknowledged that species may have different habitat affinities
125 under different climates (Walter & Walter 1953, Aletsee 1967, Proctor, et al. 2009, Wagner et
126 al. 2017), no studies have tested the interactions between climate and critical local
127 environmental conditions in shaping niches of fen species at a continental scale. Gignac, Vitt,
128 Zoltai & Bayley (1991) and Gignac, Gauthier, Rochefort & Bubier (2004) demonstrated
129 distinct climate and pH niches of bryophyte and sedge species of mire habitats on the
130 continental scale of Canada. The response surfaces they presented suggest some interactions
131 between climate and pH, but the authors did not test them explicitly. Here, we hypothesise
132 that at the continental scale, pH niches vary with macroclimate temperature in fens, and this
133 interaction may explain regional differences in pH niches observed in previous regional
134 studies.

135

136 **Methods**

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

138 For the modelling of realised niches of fen species, we used data from large phytosociological
139 databases aggregated in the European Vegetation Archive (Chytrý et al., 2016), most of them
140 being already utilised in Peterka et al. (2017). As in Peterka et al. (2017), we selected only
141 georeferenced plots of a size of 1–100 m², for which a complete list of moss and vascular
142 plant taxa was reported. Peterka, Syrovátka, et al. (2020) demonstrated that plot sizes of at

143 least 1 m² sufficiently describe the broad-scale pattern in the representation of fen specialists
144 and may be safely merged in broad-scale analyses with larger plot sizes, without introducing
145 substantial bias. Restriction to a narrower plot size range would have resulted in a
146 considerable loss of essential data from several regions. For details on the procedure of data
147 filtering see Hájek, Těšitel, et al. (2021); [10.5281/zenodo.4915753](https://zenodo.org/record/4915753)).

148 We selected 35,984 vegetation-plot records (Figure 1). To reduce the effect of
149 oversampling in specific regions on niche modelling, we resampled the data set by selecting a
150 maximum of five plots per grid cell of 1 km x 1 km. When the number of plots exceeded this
151 number, we used heterogeneity constrained resampling (Lengyel, Chytrý, & Tichý, 2011) to
152 maximise internal beta-diversity based on the Sørensen distance metric over a random
153 selection of 50 plots per grid cell. The resampling reduced the number of plots to 29,885.

154 For imputation of missing values of water pH and conductivity, we used a calibration
155 data set, i.e., the data subset with measured pH and conductivities from springs and mires; for
156 details, see Hájek, Jiménez-Alfaro, et al. (2021). The calibration data set contained 6299
157 records for pH, while for conductivity, it contained 5073 records.

158 Based on direct measurements and imputations (see data repository for details on the
159 procedure and testing; Hájek, Těšitel, et al. (2021); we calculated, for the entire data set (i.e.
160 29,885 plots), the variable combining pH and calcium into a single value (the *adjusted pH*;
161 Plesková, et al., 2016; Horsáková, et al., 2018). The *adjusted pH* refers to the joined effects of
162 pH and calcium, e.g. in the uptake of toxic ions to mosses, ultimately affecting the bryophyte
163 layer (Plesková, et al., 2016), which in turn affects the composition of vascular plants (Singh
164 et al., 2019). As the first step, conductivity was transformed to calcium concentration values
165 (in mg l⁻¹) using the equation $y = 0.153x$, where y is Ca²⁺ concentration in mg l⁻¹, and x is
166 conductivity in $\mu\text{S cm}^{-1}$. The equation is based on the regression relationship between Ca²⁺

167 and conductivity ($R^2 = 0.84$; $n = 2062$) found on the European scale (Hájek, Jiménez-Alfaro,
168 et al., 2021). As the last step, we combine pH and calcium estimates into the *adjusted pH* by
169 adding the decadic logarithm of the millimolar Ca^{2+} concentration to the actual pH value
170 (formula 1 in Plesková, et al., 2016). In Results and Discussion, we refer to this variable as
171 *pH*.

172 Each vegetation-plot record in the data set was further calibrated by an indicator value
173 for water level, using a minimum value of an ecological tolerance expressed at the scale 1-12
174 (Hájek, Dítě, Horsáková, et al., 2020). The average value per each vegetation-plot record was
175 weighted by both the niche amplitude (using labelled values presented in Hájek, Dítě, et al.,
176 2020) and the percentage cover of an individual taxon. Hájek, Dítě, et al. (2020) found that
177 weighting with niche amplitude and cover causes highest correlation with measured water
178 level data in the datasets containing different habitats.

179

180 *Data analysis*

181 *Selection of climate predictors*

182 From the available set of macroclimate variables, we selected the two that best address the
183 effects of an ongoing climate warming on vegetation: the length and temperature of the
184 growing season (Fridley, Lynn, Grime & Askew, 2016) and the minimum winter temperature,
185 which is particularly significant to fen communities (Horsáková et al., 2018; Küttim, et al.,
186 2019). To address the length of the growing season, we calculated the effective temperature
187 sum (growing degree days) at the baseline of 5°C (GDD5). GDD5 was calculated from
188 monthly temperature data available in the CHELSA database (Climatologies at high
189 resolution for the earth's land surface areas, Karger, et al., 2017) for the 1979-2014 period.
190 We further extracted the minimum temperature of the coldest month from the same database

191 to capture the winter thermal regime. These two macroclimate variables were intercorrelated
192 (Pearson $r = 0.716$). Therefore, we applied a principal component analysis (PCA) on the
193 climate variables and then used the scores of the first PCA axis (accounting for 85.8% of
194 variability) as a combined variable named “*relative climate temperature*” (from now on
195 referred to as *temperature*), scaled to zero-mean and unit-variance, where high values relate to
196 warm and long growing seasons and warm winters. This variable did not correlate with
197 adjusted pH in the resampled data set (Pearson's product-moment correlation; $t = 0.08$, $df =$
198 29883, p -value = 0.93).

199

200 *Analysed taxa*

201 We limited the study to the prominent vascular plant and moss taxa (species or aggregates of
202 closely allied species) that frequently occur in European fens, except for taxa with a narrow
203 climate or pH range, and simultaneously show their ecological optimum either in fens or in
204 wet, acidic mires in general (i.e., poor fens, bog hollows and bog lawns) (see Appendix S1 in
205 Supporting Information). From now on, we refer to them as *fen species*. Their list is based on
206 the consensus list of European-scale diagnostic species of sedge-moss vegetation that grows
207 in fens and bog hollows (the *Scheuchzerio-Caricetea fuscae* class). The kernel of the list is the
208 species classification used in the current overview of European vegetation (Mucina, et al.,
209 2016), updated by Peterka et al. (2017) and Horsáková et al. (2018). Hepatics were not
210 considered because they are not always reliably recorded in the database data. Notably, the
211 selected fen species are not always strict indicators of fens, and approximately one-quarter of
212 them characterises, according to Mucina et al. (2016), also other vegetation classes in some
213 parts of the study area, most often ombrotrophic raised bogs, and nutrient-enriched or
214 seasonally desiccating fen wetlands, such as alder carrs or wet grasslands. We limited the

215 analysis to common taxa, i.e. those occurring in at least 200 vegetation plots. In order to
216 exclude taxa showing narrow niches to temperature or pH, preventing meaningful testing of
217 the interaction between temperature and pH, we calculated the 10th-90th percentile range for
218 each fen species. We included only fen species for which this range was higher than one-
219 quarter of the entire range of the variable in the data set (i.e., > 0.099 for temperature and >
220 1.625 for pH). These criteria have led to selecting 100 fen species (37 bryophyte and 63
221 vascular plant species) that best characterise European fens (at least in a part of the study
222 area) and are frequent enough.

223 For each taxon we calculated 10th percentile (0.1), 90th percentile (0.9) and 10th-90th
224 interpercentile range of water level, temperature and adjusted pH. In order to demonstrate
225 basic ecological differences among the selected prominent fen species, we subjected the final
226 matrix of taxa and these percentiles and ranges to the Principal Component Analysis, in which
227 individual fen species acted as samples. The analysis was centered and standardised by
228 environmental variables. The results are presented in Appendix S1 (Figure S1.1).

229

230 *Generalised Additive Models*

231 We used generalised additive models (GAMs) to model ecological niches of 100 prominent
232 fen species to the environmental gradients of pH, temperature, and water level. We primarily
233 focused on temperature and pH and their interaction to address the principal hypothesis of the
234 study. Models for water level are additional and are graphically presented only in a data
235 repository (Hájek, Těšitel, et al., 2021).

236 Species abundance data were transformed to presence/absence. Thus GAMs with
237 binomial error distribution were used. Before niche modelling, we trimmed 0.5% extremes of

238 all the gradients (961 records) to prevent the excessive effects of extreme values on the
239 resulting models. This step reduced the data set size to 28,924 plots.

240 For each fen species, we ran two GAM models. The model 1 included purely additive
241 effects of the three gradients (water level, temperature, pH). We limited degrees of freedom
242 (d.f.) to maximum 4 for smoothers for each tested variable to avoid overfitting. The model 2
243 was identical to the model 1 but included the interaction between pH and temperature as a
244 parametric predictor. The inclusion of this term allowed the pH niche to change along the
245 climate gradient. We compared the two models by the likelihood-ratio test, with the resulting
246 p-values adjusted by Holm correction because of multiple testing. The model containing the
247 interaction was selected only in case of being significantly better than the purely additive
248 model (adjusted p-value < 0.01). Standardised interaction coefficients were obtained by
249 refitting the GAM model with predictors standardised by subtracting the mean and subsequent
250 division of standard deviation while the binomial responses were left intact (Agresti, 2006).
251 Only models with interaction $p < 0.01$ and bimodal models were embedded in figures located
252 in the main text, whereas all models are presented in the data repository (Hájek, Těšitel, et al.,
253 2021).

254 We present the resulting niche models graphically with *pH* and *temperature* by a 2-d contour
255 plot to display the interaction between the two gradients. Dashed lines indicate species optima
256 along the environmental gradients which are defined as the environmental values where the
257 species probability of occurrence is maximal. Whenever the interaction between temperature
258 and pH was significant, its slope is displayed by a regression line. The intercept of the line
259 was set to force the regression line to pass through the niche optimum in relation to the pH
260 and temperature gradient. In data repository (Hájek, Těšitel, et al., 2021), we further present
261 models for water level as a 1-d line plot. The probabilities displayed for pH and climate
262 correspond to an optimum to water level.

263 All analyses were conducted in R, version 4.02 (R Core Team, 2020). Generalised
264 additive models were fitted in package mgcv (Wood, 2017), and the graphical outputs were
265 constructed in the ggplot2 package (Wickham, 2016). R scripts are stored in the data
266 repository (Hájek, Těšitel, et al., 2021).

267

268 *Taxonomic nomenclature*

269 The nomenclature follows the Euro+Med checklist for vascular plants and Hill et al. (2016)
270 for mosses. See Peterka et al. (2017) for the content of aggregates of closely allied species,
271 which are not always well separated in the source databases. Additionally, we considered
272 *Primula farinosa* an aggregate taxon because of the unclear taxonomic position of *Primula*
273 *farinosa* subsp. *exigua*, which is assigned to the allied species *P. frondosa* in the Euro+Med
274 checklist.

275

276 **Results**

277 *Niche modelling and testing*

278 Fifty-five taxa (55%) showed a significant interaction between pH and temperature in forming
279 their realised niche (adjusted $p < 0.01$). Out of these fifty-five taxa, forty-six (84 %) taxa
280 showed positive interaction (Figure 2, Figure 3). The total deviances explained by interaction
281 were generally higher for positive than for negative interactions (Figure 2). The taxa showing
282 the positive interaction manifested a restriction or shift of pH niche to higher pH in warmer
283 locations. They involve twenty-two moss taxa (100%) and twenty-five (73.5%) vascular plant
284 taxa. The opposite interaction was rare (no moss and nine vascular plant taxa; Figure 4).

285 Some of the species showing the positive interaction tend to show a bimodality for
286 either temperature (*E. scheuchzeri*, *P. squarrosa*, *S. obtusum*, *S. squarrosus*) or pH (*Drosera*
287 *longifolia*) (Figure 3). Four species showed apparent bimodal response to either *temperature*
288 (*Carex buxbaumii* agg., *Meesia triquetra*, *Trichophorum alpinum*) or adjusted pH
289 (*Trichophorum cespitosum*), without significant interaction between pH and temperature
290 (Figure 5). For graphical outputs for all taxa, see data repository (Hájek, Těšitel, et al., 2021).

291 There was a significant difference between bryophytes and vascular plants in the
292 standardised interaction coefficients (Mann-Whitney test; $W = 807$, $p\text{-value} = 0.011$; Figure
293 6). Bryophytes showed a narrower range of standardised interaction coefficients than vascular
294 plants, but only a few of them were negative. None of these negative interactions was
295 statistically significant (Figure 6). The moss species showing the highest interaction between
296 temperature and pH (Figure 2) are primarily non-sphagnaceous brown mosses (e.g.,
297 *Campylium stellatum* agg., *Cinclidium stygium*, *Paludella squarrosa*, *Pseudocalliergon*
298 *trifarium*, *Scorpidium scorpioides*, *S. revolvens* agg.). Most of them prefer high-pH sites
299 (Appendix S1, Figure S1.1) but shift their occurrence to even higher pH if the climate is warm
300 (Figure 4). Some *Sphagnum* species, the most strongly *S. teres* (Figures 2, Figure 3), also
301 show the positive interaction and shift or extend from the central part of the pH gradient
302 towards somewhat higher pH, but not as high as in the case of most brown mosses (Figure 2).
303 The group of vascular plants that show the positive interaction includes (i) the low-
304 competitive tiny or short-lived taxa (*Eriophorum gracile*, *Hammarbya paludosa*, *Saxifraga*
305 *hirculus*, *Drosera longifolia*, *Pedicularis palustris*, *Pinguicula vulgaris*) and (ii) the taxa with
306 the optimum outside warm areas (Appendix S1, Figure S1.1), showing only isolated relict
307 occurrences here (*Comarum palustre*, *Eriophorum scheuchzeri*, *Ligularia sibirica*,
308 *Menyanthes trifoliata*).

309 Nine frequent vascular plant species showed significant yet slight (Figure 2) negative
310 interaction between temperature and pH. They include species highly associated with acidic
311 sites (Appendix S1, Figure S1.1) such as poor fens and bogs in warm areas and extending
312 their niche towards higher pH in cold areas. *Andromeda polifolia*, also showing a tendency
313 toward bimodality to pH, is a typical example. Four species of high-pH fens (*Carex hostiana*,
314 *C. panicea*, *Eleocharis quinqueflora* and *Juncus alpinoarticulatus*; Appendix S1, Figure S1.1)
315 showed the negative interaction but kept their optimum in extremely high-pH fens also in
316 warm areas (Figure 4).

317

318 **Discussion**

319

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

321

322 Our analysis demonstrates that both the local factors such as pH and water level and the
323 climate factors shape the distribution of fen plant taxa at the broad geographic scales, as in
324 other habitats (Chauvier, et al., 2021). Using an ultimate data set from European fens, we
325 demonstrated that climate significantly modulates edaphic niches of plant taxa. This novel
326 result explains previously reported regional changes in realised niches of fen plants, a current
327 habitat-dependent decline of endangered taxa in some regions, and distribution changes of fen
328 species during Quaternary climate cycles.

329 More than half of one hundred specialised and frequent European fen species showed
330 a statistically significant interaction between pH niche and macroclimate temperature at the
331 European scale. Many species of base-rich fens can occur in more acidic conditions, and some
332 species of acidic fens can occur in more alkaline conditions when the climate is colder. The
333 interaction between climate and pH niches explains niche shifts reported by previous

334 comparisons between Scandinavia and Western or Central Europe (Kooijman & Westhoff,
335 1995; Graham, Farr, Hedenäs, Devez & Watts, 2019, Peterka, Hájková, et al., 2020), or
336 between the two Central-European regions differing in nutrient status (Plesková et al. 2016),
337 or between cold mountains of the Balkans and warmer Central-European fens (Hájková et al.,
338 2008). The same explanation may apply to observations that the occurrences of some fen
339 mosses had become more limited to the most base-rich fens during recent decades across
340 Europe (Hájek et al., 2015; Kolari, Korpelainen, Kumpula, & Tahvanainen 2021).
341 Nevertheless, the effects of temperature *per se* and nutrient availability may not be easily
342 disentangled; they likely act in concert (Jeppesen et al., 2010; Sperle & Bruelheide, 2021).

343

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

345 Across different ecosystems, many reports explain regional niche shifts or extensions
346 by competitive release (Lawrey, 1981, Prinzing, Durka, Klotz, & Brandl, 2002, Coudun, &
347 Gégout, 2005, Reinecke, et al., 2016). This explanation seems the most plausible for our
348 results, considering that niche restrictions in warmer areas are inclined towards a narrower
349 high-pH range. Longer and warmer growing seasons may increase inter-specific competitive
350 interactions and benefit species with high growth rates. The effect is intensified by increasing
351 nutrient availability, promoted by a high temperature that increases decomposition rates
352 directly (Djukic, et al., 2018) and indirectly by lowering the water table (Ise, Dunn, Wofsy, &
353 Moorcroft, 2008; Górecki, et al., 2021). A wide array of studies from mires demonstrate a
354 clear competitive hierarchy, with acidophytic poor-fen species being superior to calcium-
355 tolerant species of rich fens (e.g., *Sphagnum warnstorffii*, *S. contortum*, *S. teres*) and the latter
356 being superior to calcicole species such as most of the non-sphagnaceous brown mosses
357 (Kooijman & Baker, 1995; van Breemen, 1995; Granath, Strengbom, & Rydin, 2010;

358 Paulissen, et al., 2014; Udd, Sundberg, & Rydin, 2016; Vicherová, M. Hájek, Šmilauer, & T.
359 Hájek, 2017). These hierarchies seem to be deeply entrenched evolutionally. Vicherová,
360 Glinwood, Hájek, Šmilauer & Ninkovic (2020) found that the rich-fen bryophyte
361 *Hamatocaulis vernicosus* can react to the presence of its competitor, acidophytic peat moss of
362 *S. recurvum* agg., and emit volatile organic compounds to adjust and synchronise the growth
363 of its individuals.

364 Increasing temperature alters competitive hierarchies among dominant peat mosses
365 (Breeuwer, Heijmans, Robroek, Limpens, & Berendse, 2008; Breeuwer et al., 2009; Bu,
366 Zheng, Rydin, Moore, & Ma, 2013) or between bryophytes and vascular plants (Pouliot,
367 Rochefort, Karofeld, & Mercier, 2011), as demonstrated by studies from ombrotrophic bogs.
368 Altered competitive hierarchies may explain most of the interactions between temperature and
369 pH found in our study. Niche extension of acidophytic and calcium-tolerant species towards
370 high-pH habitats is facilitated when nutrient, especially potassium, availability is improved or
371 if the level of alkaline groundwater at least slightly decreases in warm areas. Previous studies
372 across Europe (Kooijman, & Bakker, 1995, Kooijman, 2012, Hájek et al. 2015, Plesková et al.
373 2016; Vicherová, Hájek, Šmilauer, & Hájek, 2017; Kolari, et al.. 2021) have indeed
374 demonstrated expansion of *Sphagnum teres*, *S. squarrosum*, *S. magellanicum* or *S. recurvum*
375 agg. into base-rich fens. The same taxa showed an extension of the pH niche towards higher
376 macroclimate temperature in our study (Figure 2). Acidophytic species growing in mires may
377 hence, to some extent, benefit from the extension of their pH niche in warmer climates. In a
378 pristine boreal rich fen, Kolari et al. (2021) found an increase of peat mosses (*Sphagnum*
379 *recurvum* agg., *Sphagnum magellanicum*) at the expense of brown mosses during the past 20
380 years when the mean annual temperature in the region had risen by +1.0 °C, while pH had not
381 changed. The growth of *Sphagnum* mosses is generally accelerated by climate warming
382 (Dorrepaal, Aerts, Cornelissen, Van Logtestijn, & Callaghan, 2006; Küttim, Küttim, Ilomets,

383 & Laine, 2020; Bengtsson et al., 2021). The spread of acidicole peat moss species to high-pH
384 fens increases competition pressure to non-sphagnaceous brown mosses. The niches of brown
385 moss taxa that are highly endangered in warm areas of Europe, such as *Pseudocalliergon*
386 *trifarium*, *Scorpidium scorpioides* or *Paludella squarrosa*, indeed showed a shift to higher pH
387 values in warmer areas in our study. Rapidly growing *Sphagnum* mosses compete effectively
388 also with seedlings or young ramets of vascular plants specialised to base-rich fens. Singh et
389 al. (2019) showed that most species of alkaline fens tended to prefer brown-moss patches
390 against *Sphagnum*-rich ones, regardless of pH and water table. Again, some of them showed
391 positive interaction between temperature and pH in our study (*P. farinosa* agg., *P. vulgaris*, *S.*
392 *hirculus*, *E. latifolium*).

393 A great competitive ability of acidophytic *Sphagnum* mosses may explain why many
394 bryophyte and vascular plant fen species have narrower high-pH niches in warmer climates.
395 The combination of high pH and high calcium concentrations, expressed by *adjusted pH* in
396 our study, is lethal to acidophytic *Sphagnum* mosses, with the lethality threshold being shifted
397 towards higher pH values if nutrient availability is enhanced (Plesková et al. 2016, Vicherová
398 et al. 2017). In our study, the positive interactions between temperature and pH occurred
399 significantly more often in bryophytes than in vascular plants, corroborating the previously
400 reported significant effects of competition shaping bryophyte communities in mires (Bu,
401 Zheng, Rydin, Moore, & Ma, 2013; Udd, Sundberg, & Rydin, 2016; Ma et al., 2020).

402 Climate warming and increasing nutrient availability lower the environmental
403 extremity of fens (Hájek, et al., 2020). Our conclusion that decreasing environmental
404 extremity strengthens competitive inter-specific interactions is supported by ecological
405 theory, specifically by the Stress Gradient Hypothesis that predicts such pattern (Pouliot,
406 Rochefort, Karofeld, & Mercier, 2011; Bu, Zheng, Rydin, Moore, & Ma, 2013; Olsen,
407 Töpper, Skarpaas, Vandvik, & Klanderud, 2016).

408

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

410

411 Broader niches in colder areas were also found for acidophytic taxa *Andromeda polifolia*,
412 *Eriophorum vaginatum* and *Vaccinium oxycoccos* agg., showing negative interactions
413 between pH and temperature. These taxa frequently occur also in ombrotrophic bogs (Proctor,
414 et al., 2009; Mucina et al., 2016; Robroek et al., 2017), and in warm areas, they are strongly
415 associated with acidic mires and do not occur in high-pH sites. A similar pattern was found
416 for *Trichophorum cespitosum*, but the interaction between pH and temperature was not
417 significant, and the cold-loving nature of the species appeared to be a dominant cause of its
418 ecological behaviour. Together with *A. polifolia* and *Drosera longifolia*, the latter species
419 further showed the most apparent signs of bimodality to pH. Further research is needed to
420 determine whether this bimodality is caused by genetically ingrained ecotypes (Schwarzer &
421 Joshi, 2019).

422 Bimodal responses to *temperature* might be caused by the uneven occurrence of some
423 habitats (e.g., quaking fens) across Europe or even only by their uneven sampling.

424 Nevertheless, because all species showing bimodal responses but *S. squarrosum* are
425 considered to be glacial relicts in Central Europe (Dítě et al., 2018; Peterka, Hájková, et al.,
426 2020), the bimodality might arise from uneven distribution of long-term stable, refugial
427 habitats that had not experienced Middle-Holocene wood encroachments or shifts to acidic
428 bogs (Hájková et al., 2018).

429

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

431

432 The pattern of positive pH-climate interaction has important implications for
433 explaining the past and current distribution patterns and habitat affinities of endangered
434 calcicole rich-fen species in Central and Southern Europe (Dítě et al., 2018; Hájková et al.,
435 2018; Peterka, Hájková, et al., 2020; Sperle & Bruelheide 2021). These species are expected
436 to have had much wider niches and distributions in cold and wet periods of the Quaternary
437 (Jiménez-Alfaro, Garcia-Calvo, Garcia, & Acebes, 2016; Dítě et al., 2018), as evidenced for
438 *Carex dioica*, *C. limosa*, *Cinclidium stygium*, *Eriophorum gracile*, *Ligularia sibirica*,
439 *Paludella squarrosa*, *Primula farinosa* agg., *Pseudocalliergon trifarium*, *Saxifraga hirculus*,
440 *Scorpidium scorpioides* and *Sphagnum obtusum* (Hájek et al., 2011; Dítě et al., 2018). Their
441 pH niches might be broader during the colder climate phases, and their current distributional
442 restriction results from a narrowed pH niche. Indeed, palaeoecological studies sometimes
443 report their co-occurrence, at the scale of square centimetres, with the acidophytic species
444 (Drzymulska & Jadwiszczak, 2020), while recently such combinations are rare, being
445 observed especially in cold high-mountain or arctic habitats (Dierssen, 1996; Pérez-Haase, &
446 Ninot, 2017) or in the Baltic region under specific conditions (Pakalne, 1994). Woodland or
447 *Sphagnum* expansions to fens during Middle-Holocene warming (Hájková, et al., 2018) or
448 even fen-to-bog transitions (Hughes, 2000; Väiliranta, et al., 2017) had likely increased
449 competition pressure and restricted relict species to refugia, where their niches still may have
450 remained much broader than they are today (Hájek, et al., 2015). Although deforestation and
451 anthropogenic disturbances since late prehistory and Middle Ages gave a second chance to
452 these light-demanding relict species (Hájková, et al., 2018), current changes in the landscape
453 down them again. The recent retreat of low-competitive fen species is probably more
454 profound than the retreat during the Middle Holocene because of the unprecedented
455 anthropogenic transformation of landscapes. It has decreased connectivity of fen habitats and,

456 thus, disrupted metacommunity and metapopulation structures that are important for insular
457 habitats such as fens (Soomers, Karssenbergh, Verhoeven, Verweij, & Wassen, 2013; Jamin,
458 Peintinger, Gimmi, Holderegger, & Bergamini, 2020) and made fens highly endangered
459 (Janssen et al., 2016).

460 With low population density and less severe land-use history, the northern boreal areas
461 have harboured many high-pH fen habitats until recently. Approximately 64 % of rich fen
462 habitats among all E.U. countries are located in Finland and Sweden (Janssen et al., 2016),
463 mainly in the northernmost and alpine areas. However, groundwaters in the glaciated northern
464 areas have comparably low calcium concentrations (M. Hájek, Jiménez-Alfaro, et al., 2021),
465 and northern fens may therefore be particularly sensitive to changes. Our results indicate that
466 warming may narrow the ecological niche of rich-fen species by increasing competitive
467 pressure. Despite their wide distribution in northern boreal regions in Europe, high-pH fen
468 habitats are not safe from global change factors, and attention should be paid to monitoring
469 and conservation management.

470 Ongoing warming may trigger the negative development of rich fens in cold areas,
471 such as the Alps, Southern-European high mountains or Fennoscandia, and endanger fen
472 species in their last low-elevation refugia even if they are legally protected (Sperle &
473 Bruelheide 2021). The increasing competition seems to play an essential role in this process,
474 suppressing habitat specialists more than generalist species (Denelle, Violle, DivGrass
475 Consortium, & Munoz, 2020; Spitale, 2021). Therefore, conservation-oriented disturbances,
476 such as mowing with hay removal or moderate grazing in less damaged fen grasslands (Ross,
477 et al., 2019; Hájek, Horsáková, et al., 2020; Spitale, 2021), or removal of expansive late-
478 successional peat mosses, sod, shrubs, and trees in successionaly changed fens (Singh, et al.,
479 2021) should be applied to mitigate the effects of current anthropogenic environmental
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481

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500

501 **Data availability statement**

502 The working data sheets (presence-absence data for individual fen species and corresponding
503 data on adjusted pH, water level estimated by indicator values and climate data), details on
504 data selection from the databases, the list of utilised vegetation databases, R scripts and

505 complete results for individual species are accessible at <https://www.zenodo.org/> (last access:
506 10 August 2021); [10.5281/zenodo.4915753](https://doi.org/10.5281/zenodo.4915753); Hájek, Těšitel, et al., 2021).

507

508

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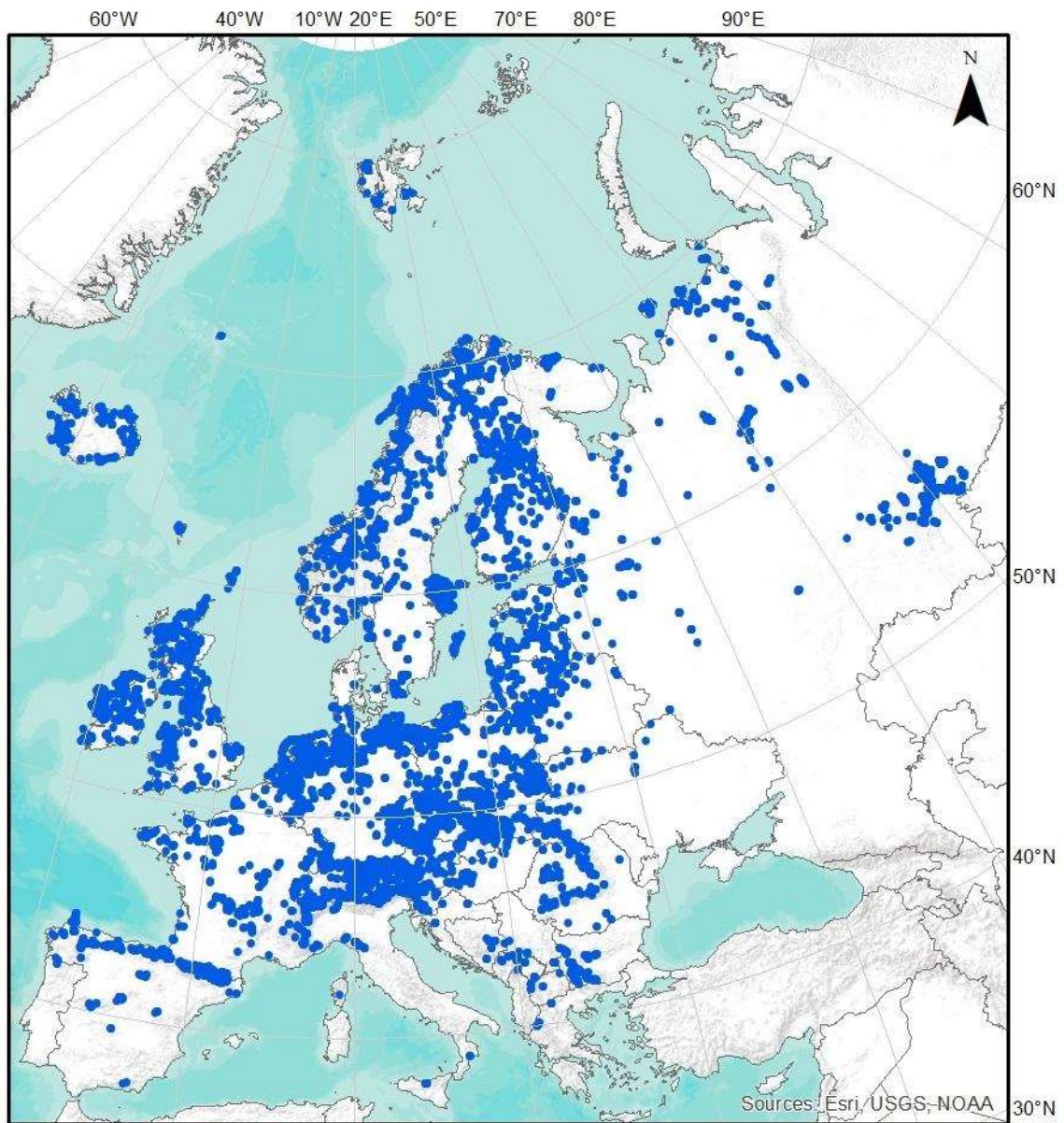
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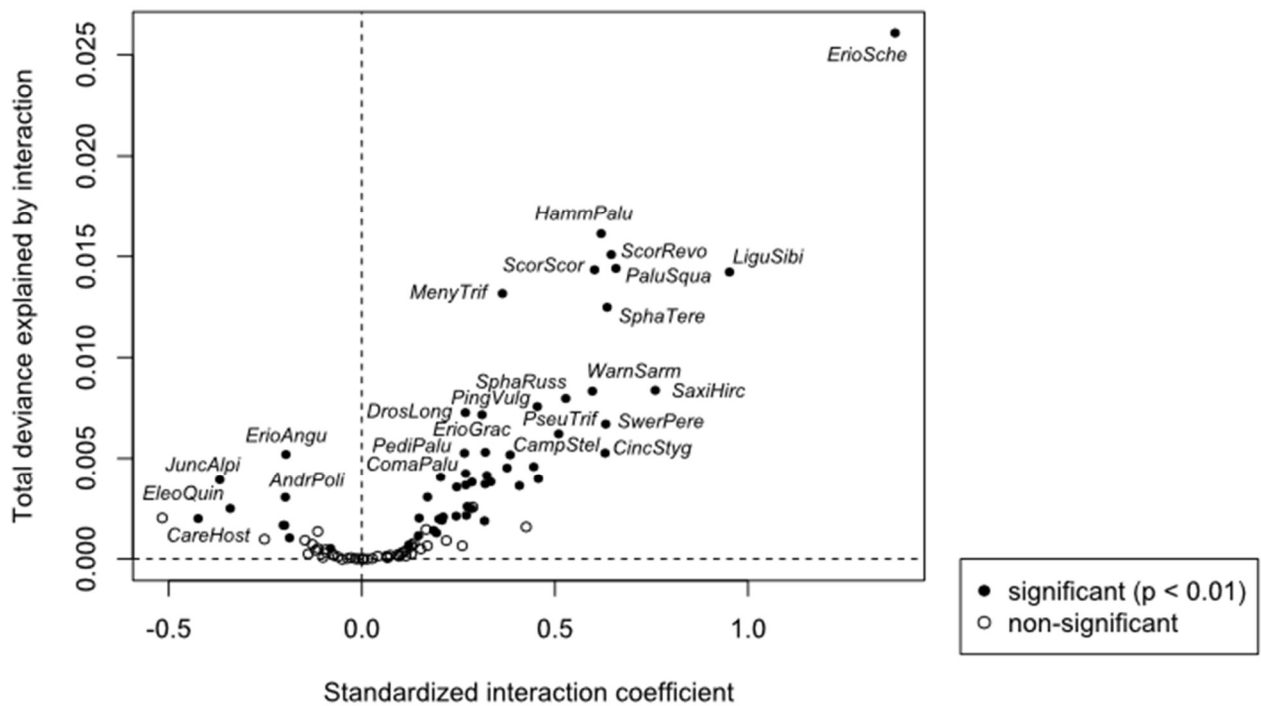
811 **Figure 1.** Distribution of fen vegetation-plot records in Europe selected for this study.



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814 **Figure 2.** Total deviances explained by the interaction between macroclimate temperature and
 815 pH in generalised additive modelling of realised niches of one hundred European fen species
 816 plotted against standardised interaction coefficients. Each circle represents one taxon. For the
 817 full names of taxa, see Table S1.1. in Supporting Information.
 818



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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).

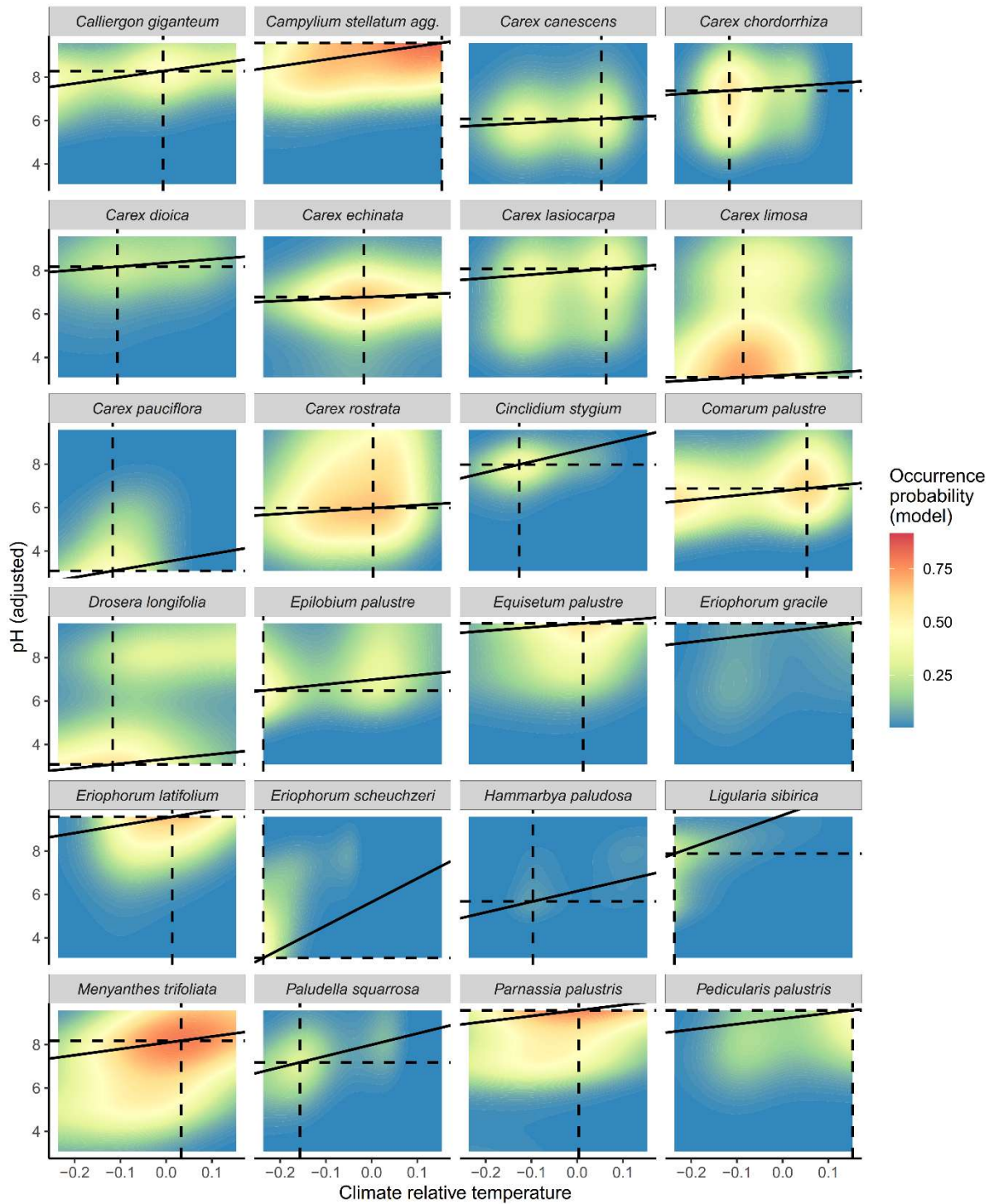


Figure 3, continuation

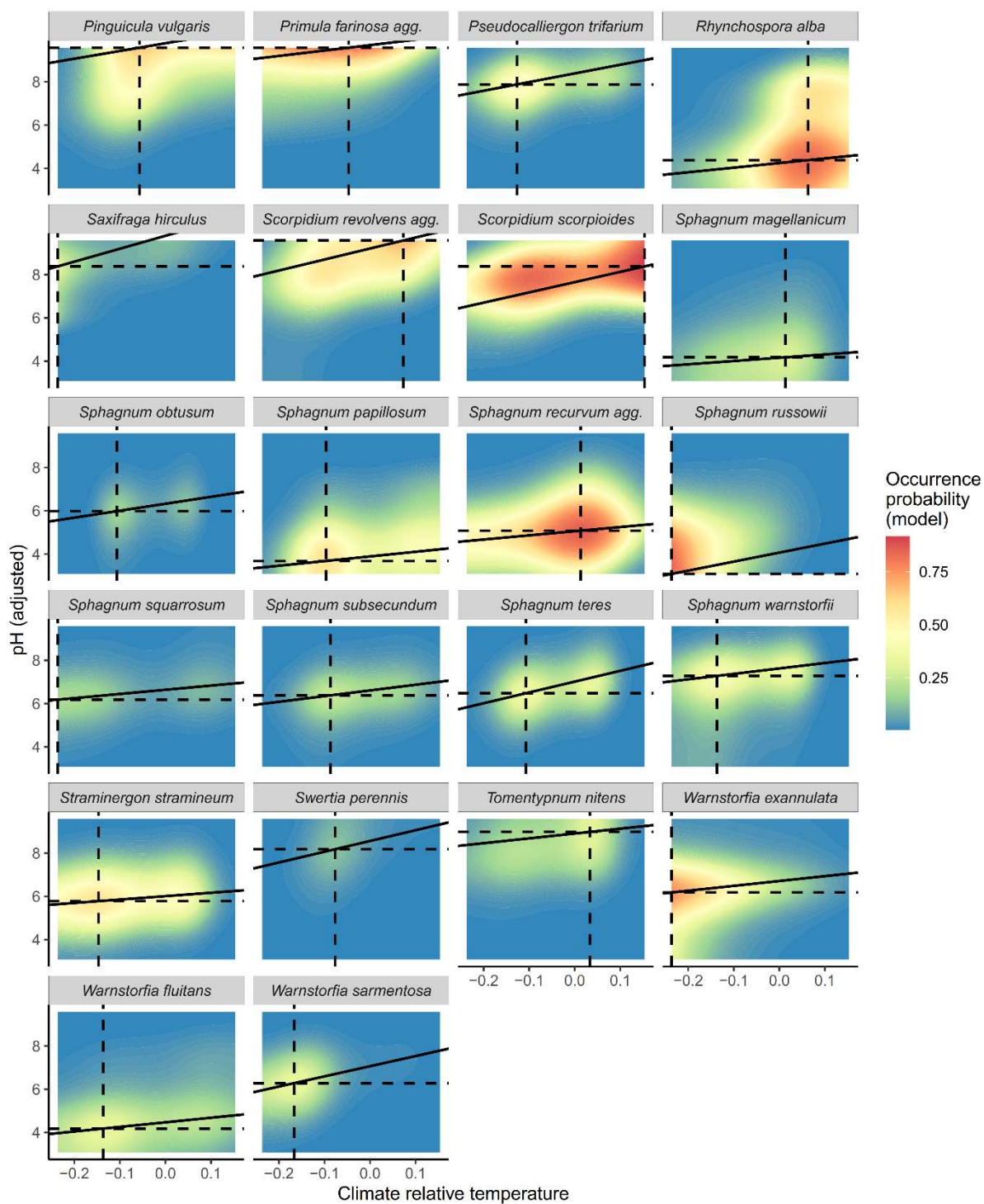


Figure 4. Contour plots representing GAM models of fen species to pH and climate temperature. Species with the negative parametric effect of the interaction between the two gradients are displayed (significant at $p < 0.01$ after Holm correction).

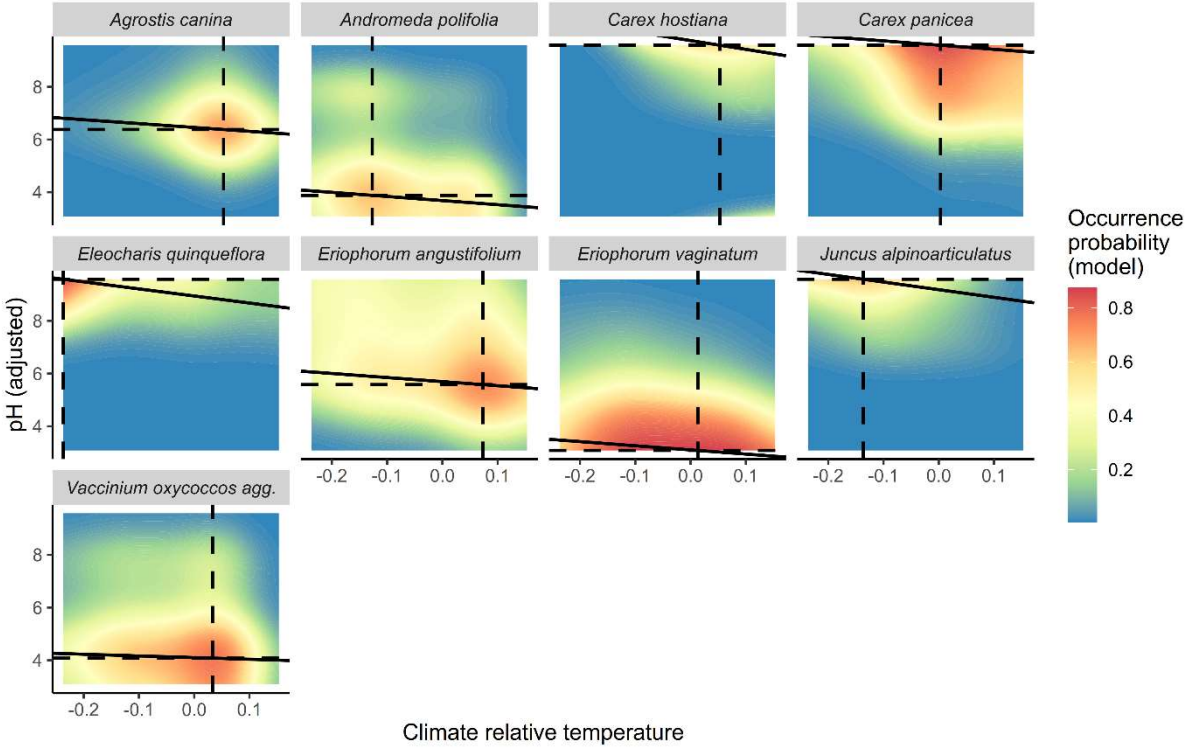


Figure 5. Contour plots representing GAM models of fen species to pH and climate temperature. Ecological niches of species displayed here show an apparent bimodal pattern to either temperature or pH, without significant interaction between the two gradients ($p > 0.05$ after Holm correction).

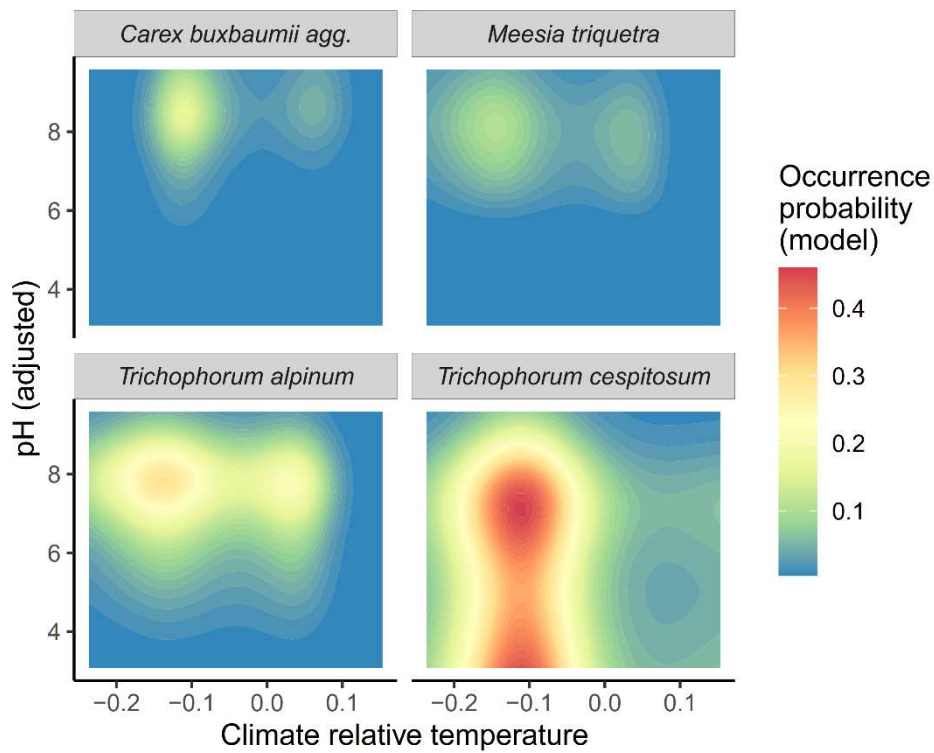
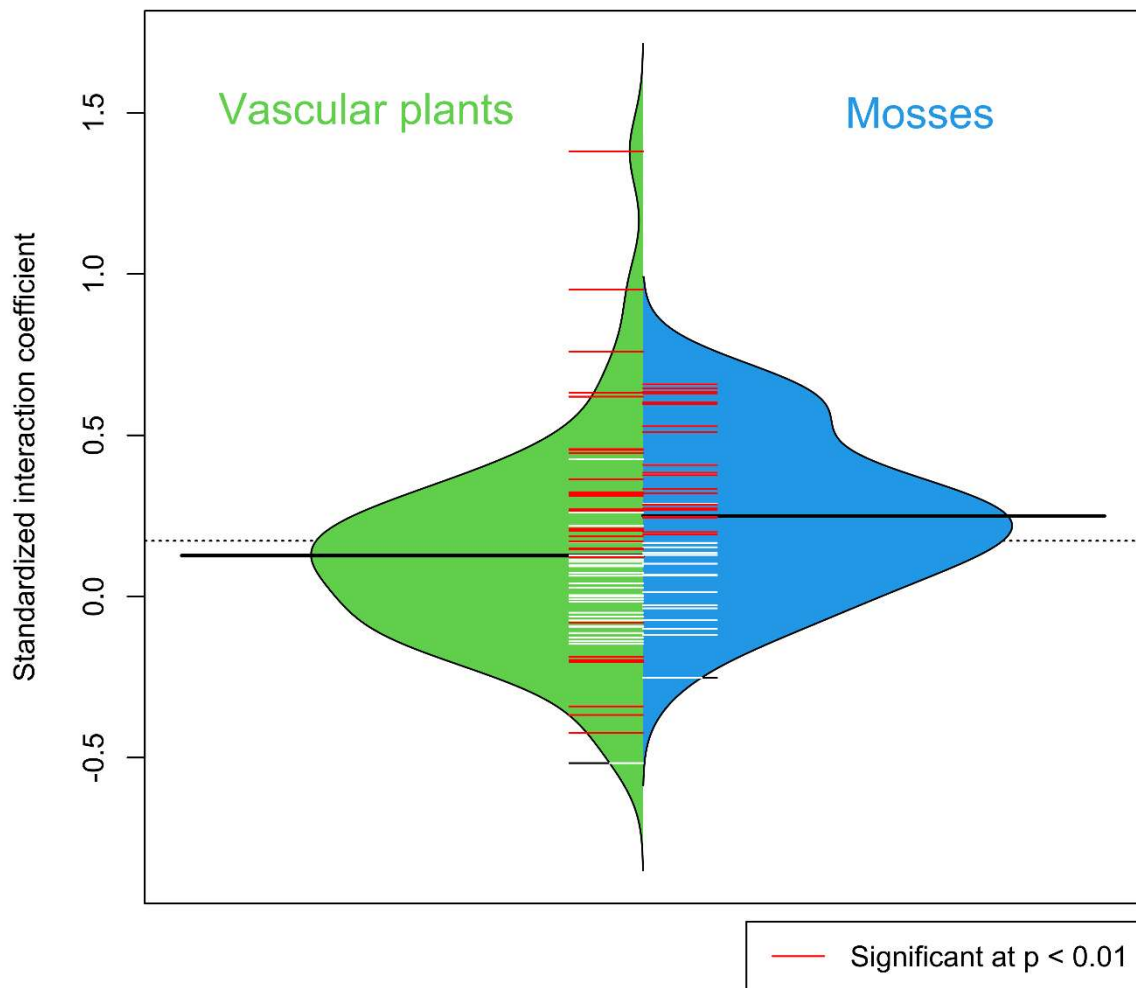


Figure 6. The bean plot showing the difference in standardised interaction coefficient (interaction between temperature and pH in Generalised Additive Models) between mosses and vascular plants. Each taxon is represented by the line, with statistically significant interaction indicated by the red colour.



Author contributions

M.H., J.T., T.T. and T.P. conceived the ideas and designed research; M.H., T.P. and B.J.-A. prepared the working datasheets, J.T. designed analytical methodology, analysed data and prepared most figures, L.T. contributed to data imputation using calibration subset, E.M. supervised bryophyte data, M.H. led the writing of the manuscript, and B.J.-A. prepared the map. T.P., AP-H, MC, T.H.M.K., P.H., LA, P.P., BJ-A, T.I., MT, D.D. and Z.P. provided unpublished data. T.P., E.G., F.J., U.J., and AP-H managed, selected and prepared data from public vegetation databases. All authors contributed critically to the drafts and gave final approval for publication.