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Rising temperature modulates pH niches of fen species

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Abstract

Rising temperatures may endanger fragile ecosystems because their character and key species show different habitat affinities under different climates. This assumption has only been tested in limited geographical scales. In fens, one of the most endangered ecosystems in Europe, broader pH niches have been reported from cold areas and are expected for colder past periods. We used the largest European-scale vegetation database from fens to test the hypothesis that pH interacts with macroclimate temperature in forming realised niches of fen moss and vascular plant species. We calibrated the data set (29,885 plots after heterogeneity-constrained resampling) with the temperature, using two macroclimate variables, and with the adjusted pH, a variable combining pH and calcium richness. We modelled temperature, pH, and water level niches for one hundred species best characterising European fens using the Generalised Additive Models and tested the interaction between pH and temperature. Fifty-five fen species showed a statistically significant interaction between pH and temperature (adjP<0.01). Forty-six of them (84%) showed the positive interaction manifested by a shift or restriction of a niche to higher pH in warmer locations. Nine vascular plants and no moss showed the opposite interaction. Mosses showed significantly greater interaction. We conclude that climate significantly modulates edaphic niches of fen plants, especially bryophytes. This result explains previously reported regional changes in realised pH niches, a current habitat-dependent decline of endangered taxa, and distribution changes in the past. A warmer climate makes growing seasons longer and warmer, increases productivity, and lowers the water level. These effects prolong the duration and intensity of interspecific competition, support highly competitive *Sphagnum* mosses, and, as such, force niches of specialised fen species towards narrower high-pH ranges. Recent anthropogenic landscape changes pose a severe threat to many fen species and call for mitigation measures to lower competition pressure in their refugia.

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

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-productive 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 part 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 temperature leads to decreases in the water table (Gong et al., 2012; Michel, Brauchli, Lehning, Schaefli, & Huwald, 2020) and accelerates nutrient cycling by the increasing decomposition of soil organic matter (Friberg et al., 2009; Górecki, et al., 2021). Warming climate may narrow realised niches of specialised low-competitive fen species, along with increasing nutrient availability, because the significance of adaptations to environmental stress is reduced while productivity and competition increase.

Regional differences in the realised niches of individual mire species are a well-known phenomenon 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; Kooiijman & 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 two 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 nutrient enrichment, while the opposite held for competitively weak species. Similarly, Kooijman & Westhoff (1995), Graham, et al., (2019), and Peterka, Hájková, et al. (2020) found a niche shift of specialised fen brown mosses of the genus *Scorpidium* to higher pH values in Western and Central Europe when compared to the colder and less polluted areas of

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

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

Methods

Data set selection and its calibration with pH and water level

For the modelling of realised niches of fen species, we used data from large phytosociological databases aggregated in the European Vegetation Archive (Chytrý et al., 2016), most of them being already utilised in Peterka et al. (2017). As in Peterka et al. (2017), we selected only georeferenced plots of a size of 1–100 m^2, for which a complete list of moss and vascular plant taxa was reported. Peterka, Syrovátka, et al. (2020) demonstrated that plot sizes of at least 1 m^2 sufficiently describe the broad-scale pattern in the representation of fen specialists and may be safely merged in broad-scale analyses with larger plot sizes, without introducing substantial bias. Restriction to a narrower plot size range would have resulted in a considerable loss of essential data from several regions. For details on the procedure of data filtering see Hájek, Těšitel, et al. (2021); 10.5281/zenodo.4915753).

We selected 35.984 vegetation-plot records (Figure 1). To reduce the effect of oversampling in specific regions on niche modelling, we resampled the data set by selecting a maximum of five plots per grid cell of 1 km x 1 km. When the number of plots exceeded this number, we used heterogeneity constrained resampling (Lengyel, Chytrý, & Tichý, 2011) to maximise internal beta-diversity based on the Sørensen distance metric over a random selection of 50 plots per grid cell. The resampling reduced the number of plots to 29,885.

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

Based on direct measurements and imputations (see data repository for details on the procedure and testing; Hájek, Těšitel, et al. (2021); we calculated, for the entire data set (i.e. 29,885 plots), the variable combining pH and calcium into a single value (the *adjusted pH*; Plesková, et al., 2016; Horsáková, et al., 2018). The *adjusted pH* refers to the joined effects of pH and calcium, e.g. in the uptake of toxic ions to mosses, ultimately affecting the bryophyte layer (Plesková, et al., 2016), which in turn affects the composition of vascular plants (Singh et al., 2019). As the first step, conductivity was transformed to calcium concentration values (in mg l^{-1}) using the equation $y = 0.153x$, where y is Ca^{2+} concentration in mg l^{-1}, and x is conductivity in $\mu S\ cm^{-1}$. The equation is based on the regression relationship between Ca^{2+}

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

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

Data analysis

Selection of climate predictors

From the available set of macroclimate variables, we selected the two that best address the effects of an ongoing climate warming on vegetation: the length and temperature of the growing season (Fridley, Lynn, Grime & Askew, 2016) and the minimum winter temperature, which is particularly significant to fen communities (Horsáková et al., 2018; Küttim, et al., 2019). To address the length of the growing season, we calculated the effective temperature sum (growing degree days) at the baseline of 5°C (GDD5). GDD5 was calculated from monthly temperature data available in the CHELSA database (Climatologies at high resolution for the earth's land surface areas, Karger, et al., 2017) for the 1979-2014 period. We further extracted the minimum temperature of the coldest month from the same database to capture the winter thermal regime. These two macroclimate variables were intercorrelated (Pearson $r = 0.716$). Therefore, we applied a principal component analysis (PCA) on the climate variables and then used the scores of the first PCA axis (accounting for 85.8% of variability) as a combined variable named “*relative climate temperature*” (from now on referred to as *temperature*), scaled to zero-mean and unit-variance, where high values relate to warm and long growing seasons and warm winters. This variable did not correlate with adjusted pH in the resampled data set (Pearson's product-moment correlation; t = 0.08, df = 29883, p-value = 0.93).

Analysed taxa

We limited the study to the prominent vascular plant and moss taxa (species or aggregates of closely allied species) that frequently occur in European fens, except for taxa with a narrow climate or pH range, and simultaneously show their ecological optimum either in fens or in wet, acidic mires in general (i.e., poor fens, bog hollows and bog lawns) (see Appendix S1 in Supporting Information). From now on, we refer to them as *fen species*. Their list is based on the consensus list of European-scale diagnostic species of sedge-moss vegetation that grows in fens and bog hollows (the *Scheuchzerio-Caricetea fuscae* class). The kernel of the list is the species classification used in the current overview of European vegetation (Mucina, et al., 2016), updated by Peterka et al. (2017) and Horsáková et al. (2018). Hepatics were not considered because they are not always reliably recorded in the database data. Notably, the selected fen species are not always strict indicators of fens, and approximately one-quarter of them characterises, according to Mucina et al. (2016), also other vegetation classes in some parts of the study area, most often ombrotrophic raised bogs, and nutrient-enriched or seasonally desiccating fen wetlands, such as alder carrs or wet grasslands. We limited the analysis to common taxa, i.e. those occurring in at least 200 vegetation plots. In order to exclude taxa showing narrow niches to temperature or pH, preventing meaningful testing of the interaction between temperature and pH, we calculated the 10^{th}-90^{th} percentile range for each fen species. We included only fen species for which this range was higher than one-quarter of the entire range of the variable in the data set (i.e., > 0.099 for temperature and > 1.625 for pH). These criteria have led to selecting 100 fen species (37 bryophyte and 63 vascular plant species) that best characterise European fens (at least in a part of the study area) and are frequent enough.

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

Generalised Additive Models

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

Species abundance data were transformed to presence/absence. Thus GAMs with binomial error distribution were used. Before niche modelling, we trimmed 0.5% extremes of all the gradients (961 records) to prevent the excessive effects of extreme values on the resulting models. This step reduced the data set size to 28,924 plots.

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

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

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

Taxonomic nomenclature

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

Results

Niche modelling and testing

Fifty-five taxa (55%) showed a significant interaction between pH and temperature in forming their realised niche (adjusted $p < 0.01$). Out of these fifty-five taxa, forty-six (84 %) taxa showed positive interaction (Figure 2, Figure 3). The total deviances explained by interaction were generally higher for positive than for 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 (*E. scheuchzeri, P. squarrosa, S. obtusum, S. 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 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 the optimum outside warm areas (Appendix S1, Figure S1.1), showing only isolated relict occurrences here (*Comarum palustre, Eriophorum scheuchzeri, Ligularia sibirica, Menyanthes trifoliata*).

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

Discussion

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

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

More than half of one hundred specialised and frequent European fen species showed a statistically significant interaction between pH niche and macroclimate temperature at the European scale. Many species of base-rich fens can occur in more acidic conditions, and some species of acidic fens can occur in more alkaline conditions when the climate is colder. The interaction between climate and pH niches explains niche shifts reported by previous comparisons between Scandinavia and Western or Central Europe (Kooijman & Westhoff, 1995; Graham, Farr, Hedenäs, Devez & Watts, 2019, Peterka, Hájková, et al., 2020), or between the two Central-European regions differing in nutrient status (Plesková et al. 2016), or between cold mountains of the Balkans and warmer Central-European fens (Hájková et al., 2008). The same explanation may apply to observations that the occurrences of some fen mosses had become more limited to the most base-rich fens during recent decades across Europe (Hájek et al., 2015; Kolari, Korpelainen, Kumpula, & Tahvanainen 2021). Nevertheless, the effects of temperature *per se* and nutrient availability may not be easily disentangled; they likely act in concert (Jeppesen et al., 2010; Sperle & Bruelheide, 2021).

Competitive release as the leading cause of observed niche shifts?

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

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

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

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

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

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

Negative interactions between pH and temperature niches and bimodal responses

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

Bimodal responses to *temperature* might be caused by the uneven occurrence of some habitats (e.g., quaking fens) across Europe or even only by their uneven sampling. Nevertheless, because all species showing bimodal responses but *S. squarrosum* are considered to be glacial relicts in Central Europe (Dítě et al., 2018; Peterka, Hájková, et al., 2020), the bimodality might arise from uneven distribution of long-term stable, refugial habitats that had not experienced Middle-Holocene wood encroachments or shifts to acidic bogs (Hájková et al., 2018).

A need to protect and manage fen refugia in warm areas

The pattern of positive pH-climate interaction has important implications for explaining the past and current distribution patterns and habitat affinities of endangered calcicole rich-fen species in Central and Southern Europe (Dítě et al., 2018; Hájková et al., 2018; Peterka, Hájková, et al., 2020; Sperle & Bruelheide 2021). These species are expected to have had much wider niches and distributions in cold and wet periods of the Quaternary (Jiménez-Alfaro, Garcia-Calvo, Garcia, & Acebes, 2016; Dítě et al., 2018), as evidenced for *Carex dioica, C. limosa, Cinclidium stygium, Eriophorum gracile, Ligularia sibirica, Paludella squarrosa, Primula farinosa* agg.*, Pseudocalliergon trifarium, Saxifraga hirculus, Scorpidium scorpioides* and *Sphagnum obtusum* (Hájek et al., 2011; Dítě et al., 2018). Their pH niches might be broader during the colder climate phases, and their current distributional restriction results from a narrowed pH niche. Indeed, palaeoecological studies sometimes report their co-occurrence, at the scale of square centimetres, with the acidophytic species (Drzymulska & Jadwiszczak, 2020), while recently such combinations are rare, being observed especially in cold high-mountain or arctic habitats (Dierssen, 1996; Pérez-Haase, & Ninot, 2017) or in the Baltic region under specific conditions (Pakalne, 1994). Woodland or *Sphagnum* expansions to fens during Middle-Holocene warming (Hájková, et al., 2018) or even fen-to-bog transitions (Hughes, 2000; Väliranta, et al., 2017) had likely increased competition pressure and restricted relict species to refugia, where their niches still may have remained much broader than they are today (Hájek, et al., 2015). Although deforestation and anthropogenic disturbances since late prehistory and Middle Ages gave a second chance to these light-demanding relict species (Hájková, et al., 2018), current changes in the landscape down them again. The recent retreat of low-competitive fen species is probably more profound than the retreat during the Middle Holocene because of the unprecedented anthropogenic transformation of landscapes. It has decreased connectivity of fen habitats and, thus, disrupted metacommunity and metapopulation structures that are important for insular habitats such as fens (Soomers, Karssenberg, Verhoeven, Verweij, & Wassen, 2013; Jamin, Peintinger, Gimmi, Holderegger, & Bergamini, 2020) and made fens highly endangered (Janssen et al., 2016).

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

Ongoing warming may trigger the negative development of rich fens in cold areas, such as the Alps, Southern-European high mountains or Fennoscandia, and endanger fen species in their last low-elevation refugia even if they are legally protected (Sperle & Bruelheide 2021). The increasing competition seems to play an essential role in this process, suppressing habitat specialists more than generalist species (Denelle, Violle, DivGrass 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.

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

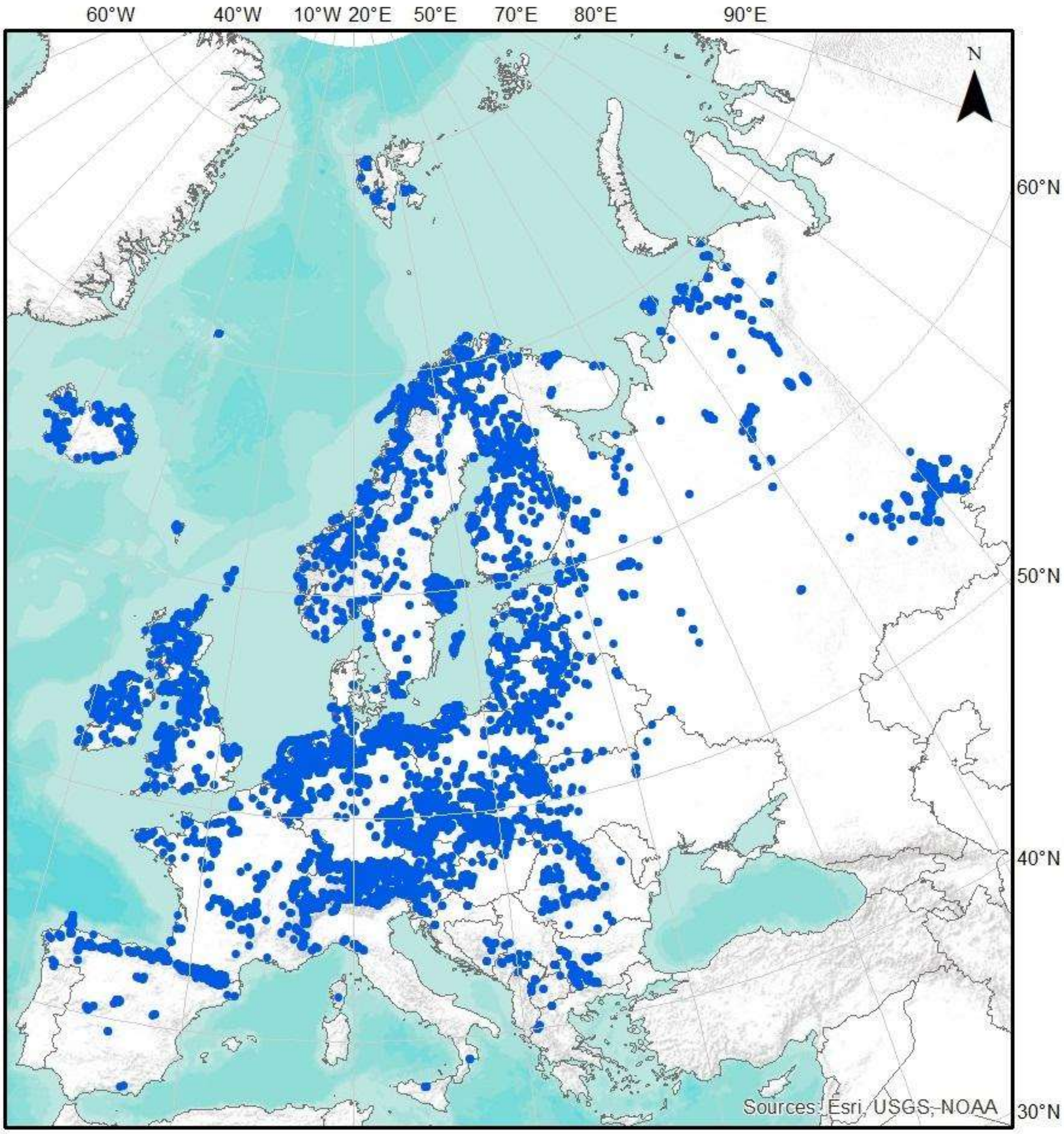


Figure 2. Total deviances explained by the interaction between macroclimate temperature and pH in generalised additive modelling of realised niches of one hundred European fen species plotted against standardised interaction coefficients. Each circle represents one taxon. For the full names of taxa,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

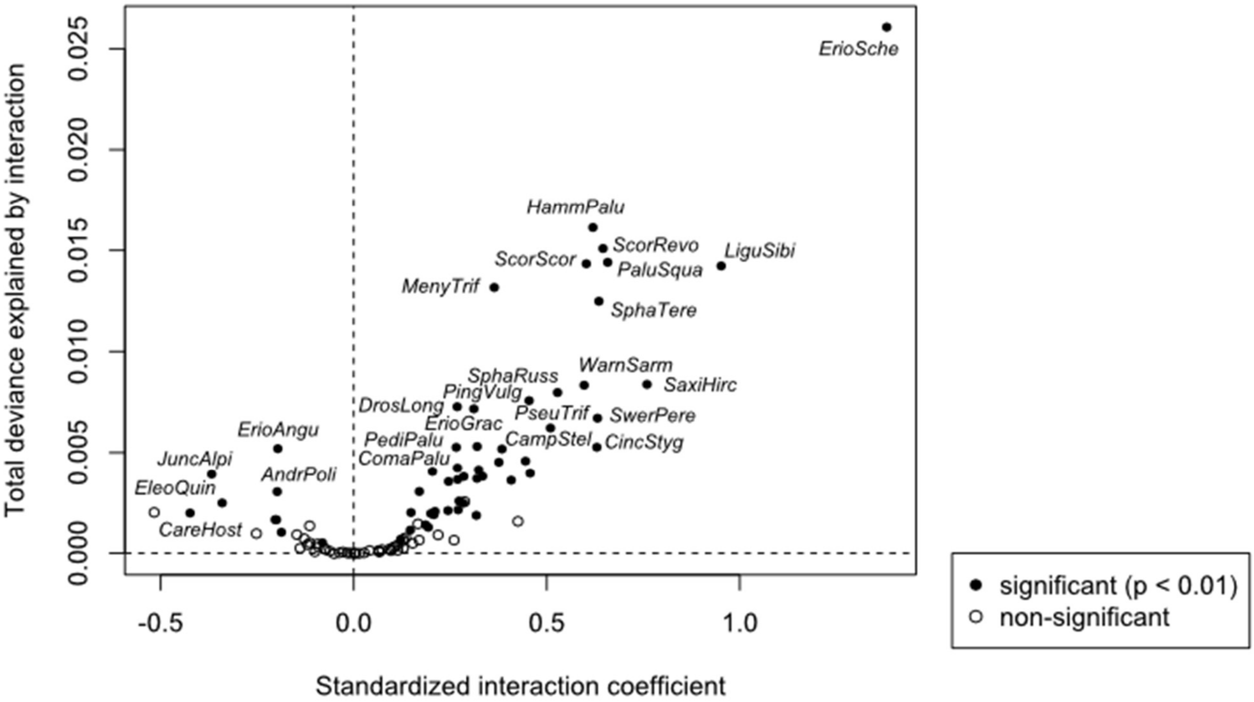


Figure 3. Contour plots representing GAM models of fen species to pH and macroclimate temperature. Species with a positive parametric effect of the interaction between the two gradients are displayed (significant at $p < 0.01$ after Holm correction).

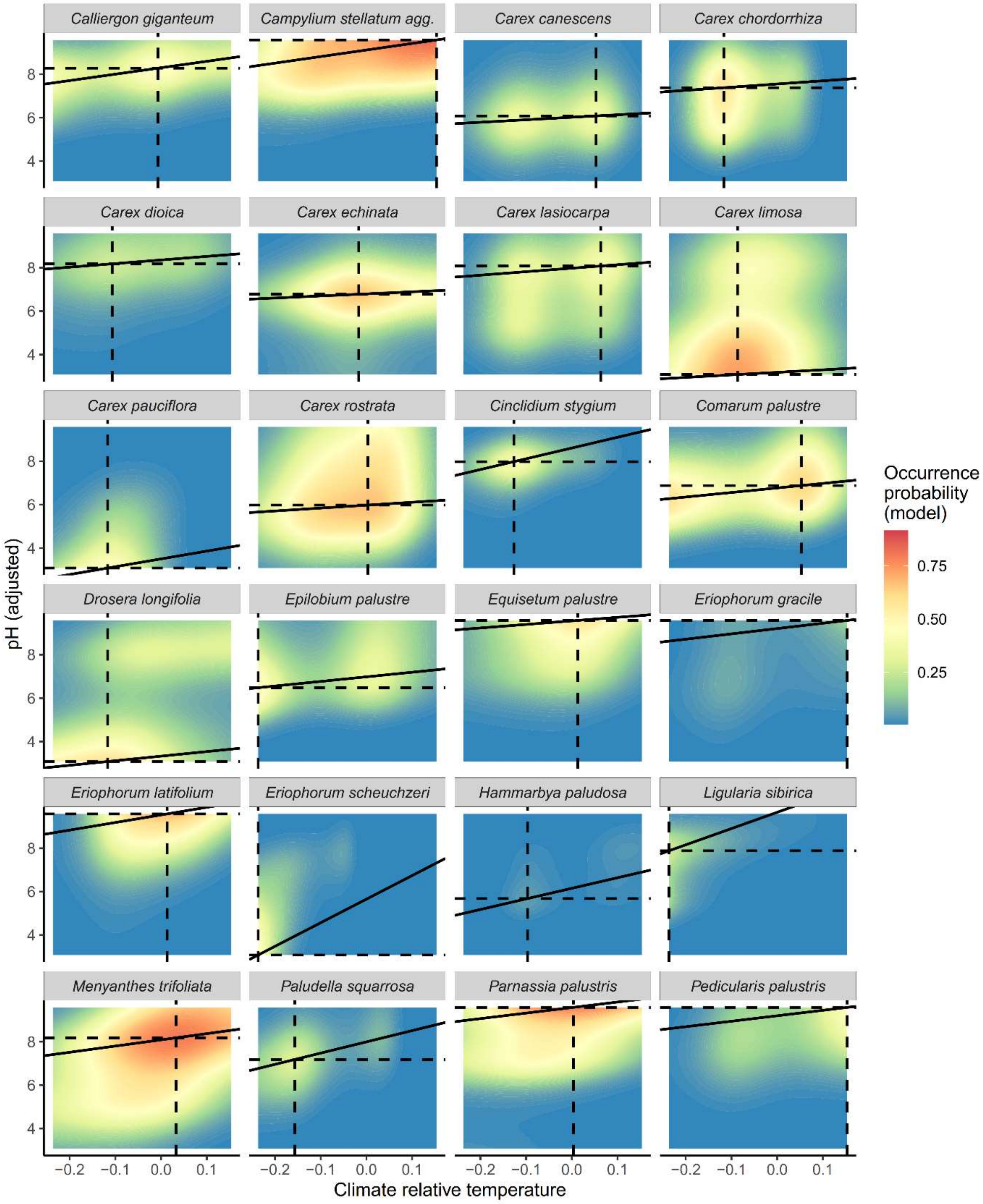


Figure 3, continuation

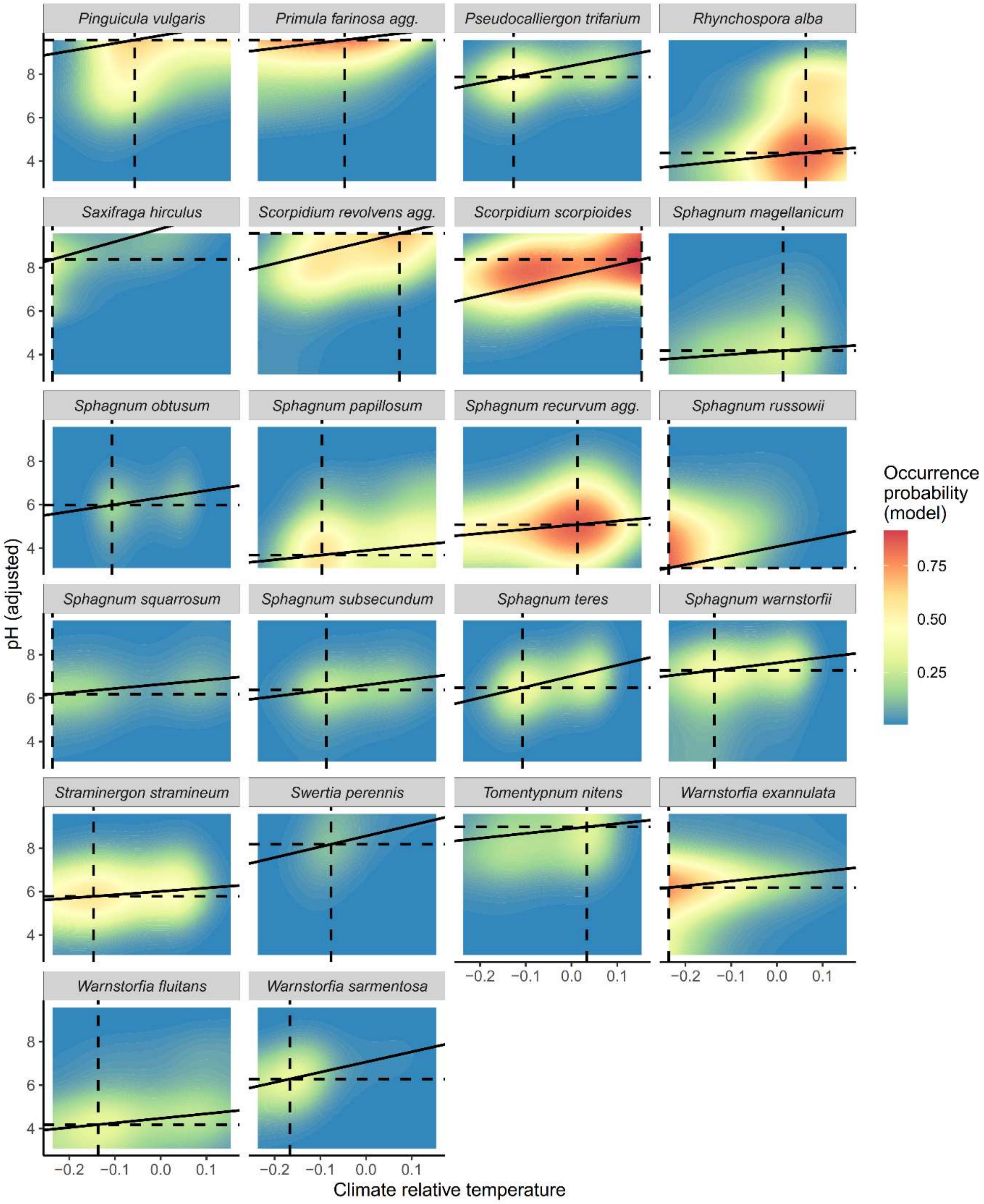


Figure 4. Contour plots representing GAM models of fen species to pH and climate temperature. Species with the negative parametric effect of the interaction between the two gradients are displayed (significant at $p < 0.01$ after Holm correction).

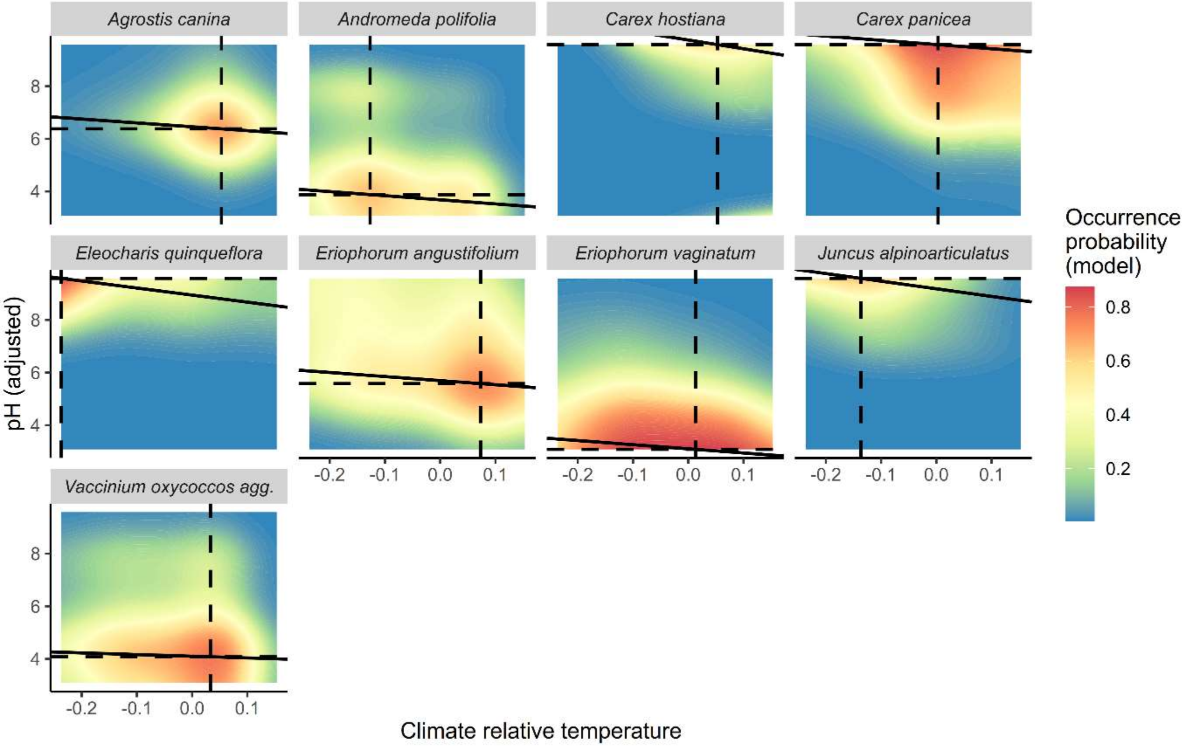


Figure 5. Contour plots representing GAM models of fen species to pH and climate temperature. Ecological niches of species displayed here show an apparent bimodal pattern to either temperature or pH, without significant interaction between the two gradients ($p > 0.05$ after Holm correction).

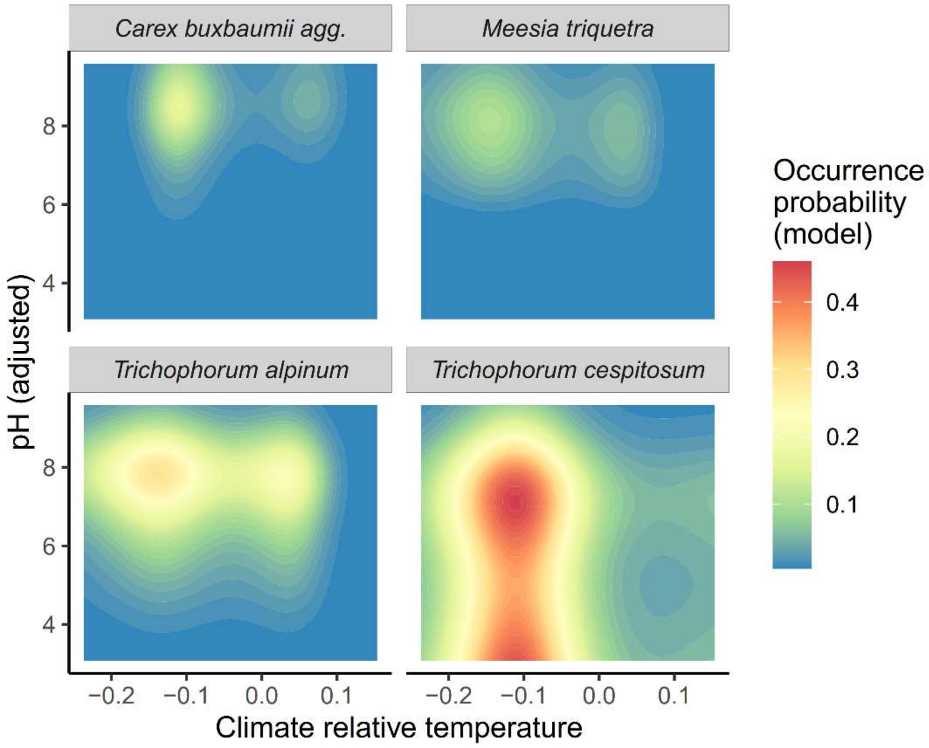
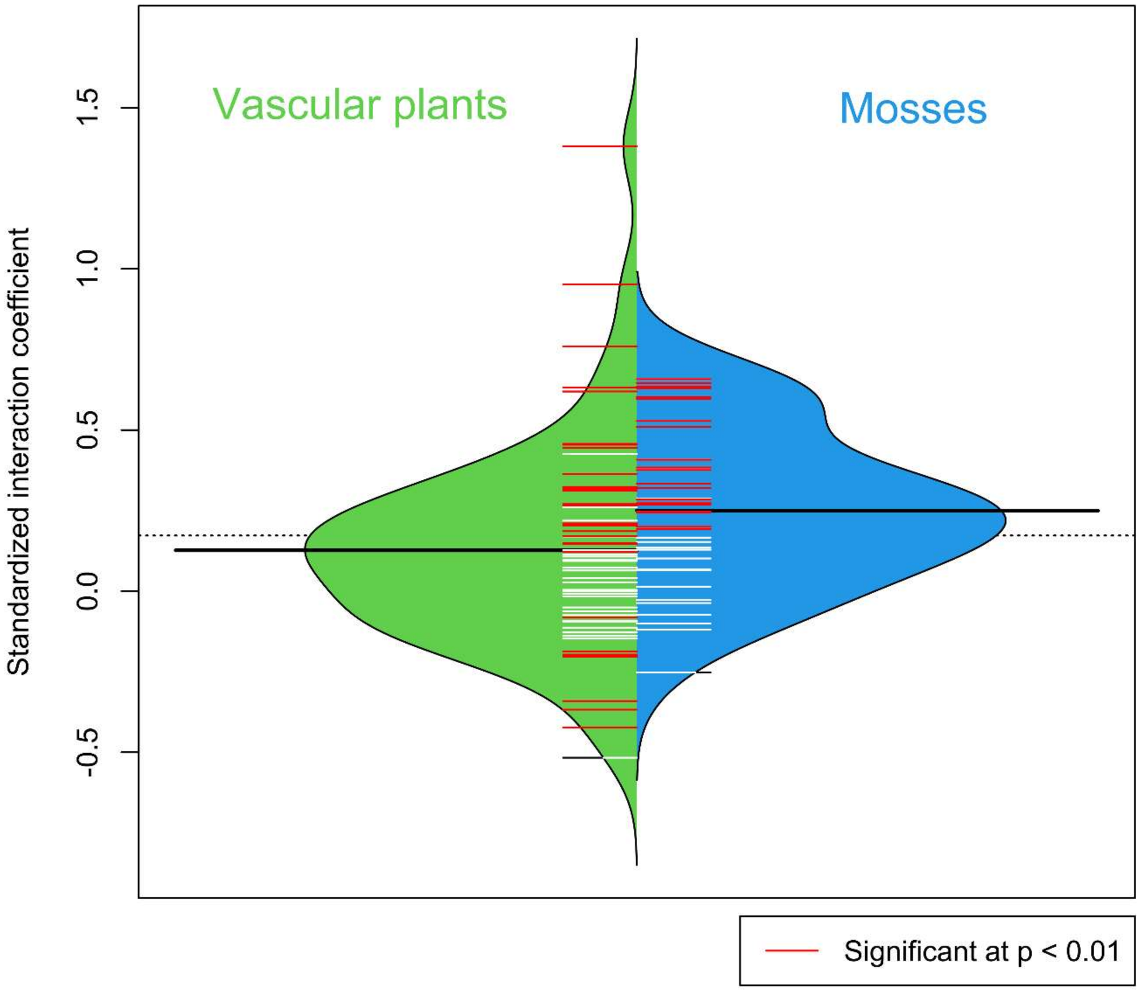


Figure 6. The bean plot showing the difference in standardised interaction coefficient (interaction between temperature and pH in Generalised Additive Models) between mosses and vascular plants. Each taxon is represented by the line, with statistically significant interaction indicated by the red colour.



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.