Coexistence and niche differentiation at large spatial scale in a West-European softwater plant community

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Abstract There is growing evidence that species are able to coexist in communities through niche separa- tion, and that consistent community structuring can take place at the biogeographical scale, as the same biotic interactions can determine species’ fate at large scales. In this study, we document niche differentia- tion at a larger scale within a specific plant community of softwater lakes in Western Europe. Five species were selected for their relative frequency and wide geographical distribution within the dataset that we collected. Their niches were modelled both from

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presence–absence data and from ordinal abundance data, using mixed regression techniques (generalized linear mixed models and proportional odds mixed models, respectively). The modelled realized niches differed among the species on the West-European scale, although strict separation was not shown and geographical coverage is not complete. Plant strategy characterization of the species supported the assump- tion that functional traits underpin the niche differen- tiation among the species through fitness trade-offs. Mechanistic experimental research at a range of spatial scales is needed to test the importance of different community structuring mechanisms at the biogeographical scale, such as biotic interactions and environmental filtering.

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Abbreviations

GLMM Generalized linear mixed model POMM Proportional odds mixed model VIF Variance inflation factor

Introduction

Niches are a convenient instrument to describe conditions under which species survive, reproduce and coexist in a community (Mueller-Dombois and Ellenberg 1974; Austin and Smith 1989; Amarasekare 2003; Silvertown 2004). Following the view of Hutchinson (1957) and Silvertown (2004) the niche is described as the abstract hypervolume defined by axes of conditions and resources within which popu- lations of a species can maintain a long-term average net reproductive rate C1. The concept is especially used to visualize how biotic interactions shape the species’ realized niche, in relation to its physiological capabilities, also known as its fundamental niche (Austin 1990; Keddy 2001). Why species can be the ‘winner’ only in a *part* of their fundamental niche, is supposed to be linked to an inherent trade-off (Kneitel and Chase 2004; Silvertown 2004), e.g. a high ability to quickly take advantage of new light and nutrient supplies would not be compatible with a high ability to compete in a more resource-limited environment.

There is growing evidence that species are able to coexist in communities through niche separation (McKane et al. 2002; Levine and HilleRisLambers 2009), often referred to as resource partitioning in the case of resource gradients (Tilman 1982). Niche separa- tion, then, is typically the result of changing competitive interactions among the same species along environmental gradients in a community (Keddy 2001). Also, growing evidence exists of consistent community structuring at the biogeographical scale, as the same biotic interactions can determine species’ fate at large scales (Wisz et al. 2013), and hence coexistence. On the other hand, coexistence in a community can occur through neutral processes, i.e. as a result of local stochastic dispersal and demographic events (Hubbell 2001; Kneitel and Chase 2004; Tilman 2004; Leibold et al. 2004).

We present a study on the realized niches of five semi-aquatic plant species within a West-European vegetation type of nutrient-poor softwater lake shores: the *Eleocharition multicaulis* Vanden Berghen 1969 alliance. The niches of its characteristic species have not been subject to much quantitative research (but see Vanderhaeghe et al. (2005) on the realized niche of *Eleocharis multicaulis,* the most characteristic species of the community). Actually testing community struc- turing mechanisms in nature is difficult (Amarasekare 2003) and we did not consider testing them as a goal. Nevertheless we explored niche separation at the biogeographical scale, between these specific species and within the vegetation type, though geographical balance was not complete. By maintaining focus on one vegetation type and not extending to the species’ niches outside this community, we expected to observe a more consistent outcome of the same (or similar) community assembly mechanisms, that operate in this community throughout the investigated area. Within this vegetation type, several characteristic species are present that are competitively suppressed or replaced by other species (Vanderhaeghe et al. 2013). Among the five investi- gated species were two characteristic species and three potentially dominant species. As competitive trade-offs are related to functional trait trade-offs (Kneitel and Chase 2004; Westoby and Wright 2006), we also looked at whether large-scale niche differentiation coincides with functional species classification.

In the current study, we (1) determine the realized niche, in terms of occurrence and ground cover, of five selected amphibious perennials, within one vegetation type, the *Eleocharition multicaulis*; (2) seek for the existence of niche differentiation and resource sepa- ration between these species at larger scale; (3) compare niche differentiation with strategy types, in order to seek a competitive trade-off for resource acquisition between neighbouring species.

Methods

Studied community and location of plots

To describe the realized niche of an entire species with niche models (species distribution models or habitat models), the ideal approach is to sample along the whole biogeographical and environmental distribution range (Austin 2007; Thuiller et al. 2008;

Franklin and Miller 2009; Elith and Leathwick 2009). However, to verify niche differentiation within one vegetation type, it is necessary to focus only on sites and areas where this community is present. 46 softwater lakes with characteristic species of the *Eleocharition multicaulis* alliance were therefore selected within the geographical range of the alliance (Fig. 1), which is Atlantic (Schoof-van Pelt 1973; Dierssen 1975; Pietsch 1977, 1985; Arts and Den Hartog 1990; Szmeja and Cle´ment 1990; Schamine´e et al. 1992; Rodriguez- Oubina et al. 1997). This alliance is often brought into synonymy with the somewhat broader *Hydro- cotylo*-*Baldellion* Tu¨ xen & Dierssen 1972, and is part of the European habitat 3130 of Atlantic softwater lakes (European Commission 2007). The *Eleocharition multicaulis* is characterized by *Eleo- charis multicaulis* (Smith) Desv., *Hypericum elodes*

L. and *Scirpus fluitans* L. Within each lake, mostly one or two plots of 2 m2 were investigated. Their location was chosen based on the on-site variation in species composition. In this way, data were col- lected from 79 plots, all representing an *Eleochari- tion multicaulis* community, with an internal gradient from ‘pristine’ (low productivity) to more or less ‘degraded’ (high productivity). More details on the locations of lakes and plots are given in Online Resources 1 and 2.

Data collection

In each plot, ground cover was visually estimated for all plant species during the summer of 2001 using the ordinal Londo cover-abundance scale (Londo 1984). For the current study, we selected five species for further examination, based on their frequency and geographical spread in the dataset (frequency of 58, 32, 46, 58 and 71 % of the sampled plots, respec- tively): *Eleocharis multicaulis* and *Hypericum elodes*, both characteristic of the *Eleocharition multicaulis* alliance, and *Agrostis canina* L., *Hydrocotyle vulgaris*

L. and *Juncus bulbosus* L. The latter three can dominate over characteristic species of the *Littorel- letea* (Lucassen et al. 1999; Arts 2002), and are less confined to the environment of softwater lakes alone. Consequently, the dataset contains both presences and absences of the targeted species, necessary to define their realized niches. The original cover classes were merged for analysis: 0 % (absent), 0–4.99 and

5–100 % ground cover. This is because the frequency of the higher cover classes was too low.

Both in summer of 2001 and during the following winter in 2002, surface water and soil samples were collected in each plot. In this way we captured different seasonal states to characterize a species’ environment. Furthermore, we used four bioclimatic variables extracted from the WorldClim 1.3 grid, supplemented with mean height of the water layer above the plot (see Table 1; Hijmans et al. (2005)). More explanations on soil, water and climate variables are given in Online Resource 2.

Species association

In order to assess local (plot)-scale coexistence between the selected species in the dataset, gamma was used as a non-parametric measure of ordinal association between species. It was applied both to presence–absence and to ordinal cover responses. The same statistic was used to assess discriminative accuracy of the ordinal niche models (see Online Resource 2 for further information). Ordinal association measures are based on the concor- dance between two variables, of which at least one is ordinal (Gonzalez and Nelson 1996; Guisan and Harrell 2000; Harrell 2001; Vaughan and Ormerod 2005). More specifically, each possible pair of sites is evalu- ated. If the ranking orders of both variables are the same, the pair of sites is counted as a concordance. If the ranking orders between both variables are opposite, it is counted as a discordance. Three further cases can be distinguished, based on ties (in which case both sites have an equal value): i.e. for ties on one, on the other or on both variables. We used gamma as the association measure because it does not penalize ties in either of both variables, as this would introduce artefacts for ordinal cover and in bootstrap model evaluations (Gonzalez and Nelson 1996). Gamma is defined as (*C* - *D*)/(*C* ? *D*), where *C* is the number of concor- dances and *D* the number of discordances, when comparing the ranks between both variables for all possible pairs of sites. Its values are between -1 and

?1.

Niche models

For the objective of niche comparison, we selected 39 environmental variables (Table 1) out of all initially

Fig. 1 Geographical location of the sampled softwater lakes (see Online Resource 1 for more details). The *shaded zone* is the area where all three characteristic species of the *Eleocharition multicaulis* occur: *Eleocharis multicaulis*, *Hypericum elodes* and *Scirpus fluitans* (after Fitter (1978), Hulte´n and Fries (1986) and the GBIF data portal, data.gbif.org)

measured environmental variables. This selection was based both on the assumed primary importance of several variables for the physiology and fitness of plant species (Austin and Smith 1989; Austin 2007; Franklin and Miller 2009), and on additional variables that had previously been shown to predict the cover of one characteristic species (Vanderhaeghe et al. 2005). A preliminary correlation analysis led to the predictors shown in Table 2, in which subsequent selection steps are shown. As a proxy of diffuse competition, we also included total cover of the neighbouring species as a predictor. More explanations on variable selection are given in Online Resource 2.

Comparison between species needs to be done in the same niche hyperspace. Therefore, the fitted niche models of different species contained the same predictors (species distribution models or habitat models, see Guisan and Zimmermann (2000), Austin (2007), Thuiller et al. (2008), Elith and Leathwick (2009)). Models were fitted to the data with as few predictors as possible, in order to minimize the degree of overfitting, using the Akaike Information Criterion (AIC) as the main criterion for model selection (Johnson and Omland 2004; Ginzburg and Jensen 2004; Zuur et al. 2009). We used generalized linear mixed models (GLMM; Raudenbusch and Bryk 2002;

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Soil Soil Soil Soil Soil Soil Soil Soil Soil Soil Soil Soil Soil | C C C C C C C C C C C C P | S S S S S S W W W W W W S | Ammonium NaCl extraction (lmol/kg DW) Nitrate water extraction (lmol/kg DW) Phosphorus digestion (lmol/kg DW) Orthophosphate lactate extraction (lmol/kg DW) Phosphorus NaCl extraction (lmol/kg DW)Total N content (lmol/kg DW)Ammonium NaCl extraction (lmol/kg DW) Nitrate water extraction (lmol/kg DW) Phosphorus digestion (lmol/kg DW) Orthophosphate lactate extraction (lmol/kg DW) Phosphorus NaCl extraction (lmol/kg DW)Total N content (lmol/kg DW) Moisture (%) | S\_AMMS S\_NO3W S\_PD S\_PO4L S\_PS S\_TOTN W\_AMMS W\_NO3W W\_PD W\_PO4L W\_PS W\_TOTN S\_MOIS |
| Surface water Surface water Surface water Surface water Direct gradientsAir | C C C CP | W W W WS | Ammonium (lmol/L) Carbon dioxide (lmol/L) Nitrate (lmol/L) Orthophosphate (lmol/L)Max. Temperature of Warmest Month | AMM CO2 NO3 PO4BIO5 |
| Air | P | W | Min. Temperature of Coldest Month | BIO6 |
| Air | P | S | Mean Temperature of Warmest Quarter | BIO10 |
| Air | P | W | Mean Temperature of Coldest Quarter | BIO11 |
| Soil Soil Soil | C C C | S W S | Calcium NaCl extraction (lmol/kg DW) Calcium NaCl extraction (lmol/kg DW) N/P ratio (NaCl extraction) | S\_CAS W\_CAS S\_NP |
| Soil | C | W | N/P ratio (NaCl extraction) | W\_NP |
| Surface water Surface water Surface water | C C C | W W W | Alkalinity (leq/L) Calcium (lmol/L) pH | ALK CA PH |
| Surface water | C | W | NH4/NO3 ratio | ANI |
| Indirect gradients |  |  |  |  |
| Soil Soil Soil Soil Soil | C C C C C | S S S W W | Iron NaCl extraction (lmol/kg DW) Loss on ignition (LOI) (%)Silicon digestion (lmol/kg DW) Iron NaCl extraction (lmol/kg DW) Loss on ignition (LOI) (%) | S\_FES S\_LOI S\_SID W\_FES W\_LOI |
| Soil Soil | C P | W– | Silicon digestion (lmol/kg DW) Thickness of organic soil layer (cm) | W\_SID OS\_THIC |
| Surface water | C | W | Ion Ratio (Ca/(Ca ? Cl)) | IR |
| Surface water | P | S | Mean thickness of water layer (cm) | WATLATHS |
| Surface water | P | W | Mean thickness of water layer (cm) | WATLATHW |

Table 1 The 39 environmental variables that were originally selected for analysis

Compartment Type Season Variable Abbreviation Resource gradients

*C* chemical, *P* physical, *S* summer, *W* winter

Table 2 Pearson correlation between 24 environmental covariates of ecological interest (after transformation)



Boldface coefficients are higher than 0.5 (as absolute values); for abbreviations of variables, see Table 1. To get this subset, several variables were removed from the list in Table 1, based on correlations between summer and winter variables and chosen according to strongest univariate response pattern. The variables are ordered according to environmental compartment and plant ecological role (R: resource gradients, D: direct gradients, I: indirect gradients). Further predictor selection steps are explained in the legend

Bolker et al. 2009) for the presence–absence response as well as proportional odds mixed models (POMM; Guisan and Harrell 2000; Harrell 2001) to distinguish between cover classes. We considered the use of cover classes as ecologically more appealing as, under the assumption of equilibrium with the environment (Guisan and Zimmermann 2000), it reflects perfor- mance, and therefore fitness, a property preferred to describe a species’ niche (Austin 1999; Thuiller et al. 2010). Furthermore, cover classes are relatively stable over the year. The results were plotted as probabilities of occurrence (GLMM) or of cover classes (POMM), separately for each predictor, setting the other predictors at constant values. We opted for the use of the outer and central border (Heegaard 2002) to set the lower limits of the visualized species niche.

Regarding the models’ predictive accuracies, we report apparent performance (trained model), test performance (bootstrap evaluation) and overfit (of the trained model) for each accuracy statistic. As a discrimination statistic, we selected the non-paramet- ric concordance index, which we derived from gamma (*c*-index; Harrell (2001)). As a calibration statistic, we calculated mean calibration, which we define as the mean predicted response divided by the prevalence of the species. Furthermore, for GLMM and for each cover threshold in POMM, we inspected calibration

plots of the trained model (Harrell 2001; Vaughan and Ormerod 2005) to assess calibration conditional on the predicted response.

More explanations on model building and model evaluation are given in Online Resource 2.

Species’ functional characterization

Several approaches are available for the functional classification of macrophytes: Grime’s (1979) trian- gular strategy scheme (Rørslett 1989; Murphy et al. 1990), a rectangular modification for macrophytes (Kautsky 1988) or starting from numerical classifica- tion of an elaborate trait dataset (Willby et al. 2000). We applied the functional classification system for macrophytes by Kautsky (1988). It is an extension of the triangular scheme of Grime (1979) with a fourth ‘stunted’ strategy, occurring in an environment that combines disturbance *and* stress. The strategies are competitive (C), ruderal (R), biomass storer (B) and stunted (S), in which biomass storer is the equivalent of the stress-tolerant strategy of Grime (1979). Several functional traits of the considered species were determined using the LEDA database (Knevel et al. 2003; Kleyer et al. 2008) and literature (Grime 1988; Willby et al. 2000). The species were then assigned to

one or more strategies applying Table 2 in Kautsky (1988).

Software

All data exploration, variable selection and modelling steps were written in the free and open source statistical package *R version 2.14.0* (R Development Core Team 2011), additionally making use of func- tions from the packages *lme4* for GLMM (Bates et al. 2011), *ordinal* for POMM (Christensen 2012), *boot* for bootstrap resampling (Davison and Hinkley 1997; Canty and Ripley 2012) and *Hmisc* for the calculation of the c-index (Harrell and with contributions from many other users 2012). For graphical presentation, the *ggplot2* package was used (Wickham 2009).

Results

Both the GLMM and POMM final models ended with the same variable subset, consisting of five variables: the four surface water variables ammonium, calcium (second degree), orthophosphate (second degree) and ammonium/nitrate ratio, plus the total soil silicon content in winter. *Juncus* didn’t respond to most variables, except to the ammonium/nitrate ratio to which it had a positive presence response (Fig. 2). On the contrary, *Eleocharis* was the most ecologically separated species compared to the remaining three species, and performed better at high ammonium concentrations but at a low ammonium/nitrate ratio (\1), and at low orthophosphate concentrations and high silicon content. This species showed these responses both for its presence as for its high cover class, while the low cover class was non-specific.

The predictive discriminatory ability of the models,

i.e. the test performance of the concordance index, was moderate (though rather poor for *Juncus*) and compa- rable between GLMM and POMM (Table 3). The predictive calibration as well as the calibration plots (not shown) were very good for the POMM models and slightly less for the GLMM models (however poor for *Hypericum* GLMM). The degree of overfitting was much less in the POMM models than in the GLMM models, both for the concordance index and the calibration index. For the concordance index this was due to the higher apparent performance in the GLMM models, which is, as such, misleading.

*Hypericum* and *Agrostis* showed a negative response to ammonium and a positive response to ammonium/nitrate ratio and orthophosphate, at least in their response based on presence and high cover class, and with *Agrostis* always having a larger niche width for these variables. *Hypericum*, *Agrostis* and *Hydrocotyle* all showed a negative response to silicon for their presence response and low cover class, with *Hypericum* having the smallest niche width and *Hydrocotyle* the largest. All three showed an optimum for calcium, for which they can be ranked as *Hypericum* \ *Agrostis* \ *Hydrocotyle* (both for presence response and low cover class). Contrary to *Hypericum* and *Agrostis*, *Hydrocotyle* responded to orthophosphate in a negative way for all response types.

The species association analysis indicated that *Hypericum*, *Agrostis* and *Hydrocotyle* tend to grow together on the plot scale. They showed a positive intercorrelation for their cover response (Table 4). *Eleocharis* had a weaker, but positive plot-scale association with *Juncus*. No further association was found between both groups, so sometimes species from both groups co-occur, and sometimes they don’t. All species have a mixed strategy (Table 5).

*Eleocharis* is functionally distinct from the other species, especially because it neither has lateral spread, nor is vegetative reproduction important in the species. *Hypericum*, *Agrostis* and *Hydrocotyle* share many functional traits. Finally, *Juncus* has the widest functional characterization.

Discussion

Species patterns and niche differentiation

The realized niches for the tested species differed on the large (West-European) scale, although strict separation was not shown as *Juncus bulbosus* showed no clear pattern, and *Agrostis canina* and *Hypericum elodes* showed overlaps for every predictor. The species often coexisted in a plot, as no negative correlations between species were revealed (Table 4). Three species showed positive association, coinciding with a similarity of their modelled niches at the biogeographical scale. Interestingly, the two species entitled ‘characteristic’ of the vegetation alliance (*Eleocharis multicaulis* and *Hypericum elodes*)



Fig. 2 The modelled realized niche of the five species. Predicted probabilities of occurrence (GLMM; *first row*), and of high and low cover classes (POMM; *second* and *third row*, respectively) are shown separately for each predictor. The probabilities are shown above a specific value (see ‘‘Methods’’ section for further details). For each predictor, all other covariates are kept constant at their median observed value,

unless stated otherwise. Because for several variables, working with median values results in predictions outside the niche of some species (near-zero probabilities), some graphs are for other than median values of the other covariates, i.e. at their first (Q1) or third quartile (Q3). EM *Eleocharis multicaulis*, HE *Hyper- icum elodes*, AC *Agrostis canina*, HV *Hydrocotyle vulgaris*, JB *Juncus bulbosus*

showed an opposite response to several predictors. This had also been noted in a univariate analysis of a subset of the same data (Vanderhaeghe et al. 2005).

*Juncus bulbosus* clearly had a wider niche width than the other species within the sampled environ- mental range. It was present in 71 % of the plots. Therefore, the rather poor predictive performance of

this species’ model is not surprising, as the higher the presence of a species in an investigated sample or area, the more difficult it becomes to model its niche due to less absence records (Jime´nez-Valverde et al. 2008; Franklin and Miller 2009).

It must be remarked that measuring environment at a plot resolution of 2 m2, although matching the scale at

Table 3 Predictive accuracy evaluation of the binomial mixed GLM models (GLMM) and the proportional odds mixed models (POMM)

|  |  |  |  |
| --- | --- | --- | --- |
| GLMMa |  | Concordance index | Mean calibration |
| *Eleocharis multicaulis* |  | 0.885/0.766/0.210 | 1.006/1.020/-0.016 |
| *Hypericum elodes* |  | 0.967/0.768/0.222 | 0.944/0.614/0.359 |
| *Agrostis canina* |  | 0.848/0.770/0.209 | 1.000/1.028/-0.028 |
| *Hydrocotyle vulgaris* |  | 0.974/0.888/0.105 | 1.012/1.028/-0.024 |
| *Juncus bulbosus* |  | 0.707/0.663/0.310 | 1.000/1.144/-0.127 |
| POMMb | Concordance index | Mean calibration of first threshold (high cover class) | Mean calibrationof second threshold(high ? low cover class) |
| *Eleocharis multicaulis* | 0.776/0.753/0.051 | 1.013/0.993/0.018 | 1.015/1.011/0.000 |
| *Hypericum elodes* | 0.803/0.763/0.078 | 0.984/1.001/-0.013 | 0.986/0.988/-0.001 |
| *Agrostis canina* | 0.764/0.738/0.068 | 1.021/1.044/-0.013 | 0.994/0.987/0.012 |
| *Hydrocotyle vulgaris* | 0.860/0.832/0.049 | 0.968/1.018/-0.032 | 0.994/1.000/-0.003 |
| *Juncus bulbosus* | 0.643/0.631/0.096 | 1.016/1.039/-0.023 | 1.005/0.993/0.011 |

Values are presented in the following order: apparent performance/test performance/overfit. For a definition of concordance index and mean calibration, see Online Resource 2. Apparent performance compares the original data with the fitted model (how well does the model perform for the data?), test performance compares the original data with the bootstrap model (how well do the bootstrap models perform for the data on average?), and overfit compares the difference between bootstrap performance and test performance (the degree to which the original model is overfitted according to the bootstrap method; see text for more details). The model’s performance is to be assessed by its test performance (Verbyla and Litvaitis 1989)

a Generalized linear mixed models for a binomial response

b Proportional odds mixed models

Table 4 Association analysis between the five species within the plant community, using the gamma coefficient

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| *Eleocharis* | 0.05 | -0.20 | 0.13 | *0.50* |
| -0.06 | *Hypericum* | 0.59 | 0.71 | 0.19 |
| -0.19 | 0.51 | *Agrostis* | 0.66 | 0.30 |
| 0.13 | 0.60 | 0.53 | *Hydrocotyle* | 0.17 |
| *0.47* | 0.05 | 0.07 | -0.07 | *Juncus* |

Top-right represents gamma for presence–absence response; bottom-left for cover response. Bold values: *P* \ 0.05, italicized values: *P* \ 0.10, in Pearson correlation tests

which population performance (cover) can be well estimated, integrates within-plot environmental hetero- geneity that may coincide with fine-scale, unmeasured niche differentiation between coexisting species (Mou- quet and Loreau 2002; Miller et al. 2005). Hence, the obtained ‘niche overlaps’, i.e. where species coexist and are positively associated at plot scale, represent results of measuring the environment (niche) at plot scale and not environmental variation within plots. This demonstrates the difficulty to detect the presence of actual niche differentiation in a community. On the other hand, by measuring many different sites, it

should be expected that species-specific niche patterns emerge and can differ, which was the case in this study and which is consistent with the paradigm of coexis- tence at regional level through niche differentiation (Amarasekare 2003; Kneitel and Chase 2004; Silver- town 2004).

Apart from unmeasured fine-scale resource heterogeneity, other mechanisms can also be at work that have led to coexistence within plots: niche separation along unmeasured gradients, including functional ones such as spatial resource partitioning (e.g. rooting depth) or partitioning in time (McKane et al. 2002); moderate local-scale dispersal in an environmentally homogeneous environment (Hub- bell 2001; Kneitel and Chase 2004); coexistence through cyclic patterns in resource consumption (Huisman and Weissing 1999). Also, frequent regional dispersal may in principle lead to local coexistence, but between-lake dispersal is probably unimportant, as this habitat is highly fragmented in space and several softwater macrophytes do not succeed to quickly recolonize sites after habitat restoration (Brouwer et al. 2002).

Table 5 Traits and strategies of the investigated plant species

Plant trait Corresponding challengea *Eleocharis multicaulis*

*Hypericum elodes*

*Agrostis canina*

*Hydrocotyle vulgaris*

*Juncus bulbosus*

‘?’ meaning: Interpretation

of ‘?’ in PESS contextb

Plant morphology

Lateral spread Persistence (space acquisition) ? ? ? ? Present to extensive Competitive/

biomass storer Height Persistence (competitive ability) ? ? ? ? ? Higher than 15 cm Competitive

Specific leaf area Establishment (relative growth rate) &

Persistence (competitive ability)

? Higher than 40 mm2/mg Competitive

Heterophylly Persistence (plasticity) ? Present Competitive

Carbon capture from air

Life history

Persistence (competitive ability) ? ? ? ? Prevailing Competitive

Evergreen leaves Persistence (stress tolerance) ? Present Biomass storer/ stunted

Onset of flowering

Persistence (disturbance avoidance) Early Ruderal

Seed investmentc Dispersal, establishment, persistence

(disturbance avoidance)

? ? Higher than 100 mm3 of seeds per shoot

Ruderal

Vegetative reproduction

Life strategy (Kautsky 1988)

Persistence (disturbance tolerance) ? ? ? ? Important Ruderal

CS CR CR CR CBRS

All species are perennials with anchored leaves

a Gaudet and Keddy (1988), Tilman (1988), Westoby (1998), Weiher et al. (1999), Knevel et al. (2003)

b PESS = Plant Ecology Strategy Scheme. Interpretation after Grime (1988), Kautsky (1988), Maillette and Keddy (1989), Rørslett (1989), Murphy et al. (1990), Westoby (1998), Willby et al. (2000), Grime (2001), and using terminology of Kautsky (1988)

c Based on the product of estimated seed number per shoot and seed volume (LEDA database)

Practical constraints in this study led to an unequal geographical sampling intensity, with a larger weight of Belgium and The Netherlands (Fig. 1). We there- fore assessed the degree of representativeness of the presented niche models for the West-European range (Online Resource 3). These results confirm that the representativeness is considerable but not high, and this should not surprise given the unbalanced dataset. Consequently, the presented niche results should not be considered as conclusive for the West-European scale, although from the spatial variation of the predictors it can be seen that important parts of the modelled realized niches were effectively provided by the large geographical extent of the sampling scheme (see Online Resource 2).

Interpretation of the predictors

Considering the predictors retained in the models, we notice that both ammonium and the ammonium/nitrate ratio were selected, meaning that nitrate would have been equally informative in the model as the ammo- nium/nitrate ratio, in the presence of the predictor ammonium. Orthophosphate was a third resource that was effective in defining the realized niches.

It could be that other correlated environmental variables, discarded in an earlier stage or not even measured, have an actual causal relationship to the species’ response. This may for example be the case for surface water calcium, which strongly refl cts pH and alkalinity in our dataset. Apart from nutrients, alkalinity and pH are known to explain much variation when considering the diversity among aquatic macrophyte communities (Bloemendaal and Roelofs 1988; Wetzel 2001; Smolders et al. 2002; Lacoul and Freedman 2006). Total soil silicon content was the only soil variable in the niche models. It is the silicon concentration made available after digestion with a HNO3–H2O2 solution. This variable is not an expected explaining variable according to macrophyte ecology literature (Smolders et al. 2002; Lacoul and Freedman 2006; Bornette and Puijalon 2011). Soil silicon, however, was negatively correlated with surface water pH. It is possible that pH is an actual causal variable, and that soil silicon better integrates past pH variability and was therefore more informative to the models than a one-time pH mea- surement. Soil silicon was highest in countries with more agricultural activity. In such areas, acidification is more likely to have occurred in isolated lakes due to

atmospheric nitrogen deposition (Roelofs et al. 1996; Vanderhaeghe et al. 2005; Bobbink et al. 2010).

It can be hypothesized from our findings that atmospheric ammonium deposition favours *Eleocharis multicaulis* at first, but eventually leads to its decline and disappearance. *Hypericum elodes* did not prefer high ammonium concentrations. It can be expected that these characteristic species will profit from restoration measures against acidification.

Support for competitive trade-offs

It is very remarkable that opposite dominance hierar- chies were observed depending on the resource gradient considered (e.g. ammonium compared to orthophosphate). A possible explanation is that com- petitive trade-offs exist for access to these different resources, conferring competitive advantage of one species over another for one resource, whilst the opposite is true for another resource. A similar trade- off between different resources was shown for two grass species, in a competition experiment by Ven- terink and Gu¨sewell (2010). They found that one species was a stronger competitor under phosphorus limitation while the other species was strongest under nitrogen limitation. The patterns we found within most gradients are compatible with assumptions of the competitive hierarchy model (Keddy 1989, 2001), in which dominant species with higher competitive ability outcompete subordinant species from a part of their fundamental niche, resulting in a competitive ranking along the resource gradient. In contrast with earlier studies however (Gaudet and Keddy 1988; Keddy et al. 1994; Ro¨sch et al. 1997; Keddy et al. 2000) our observed ranking changed and even reversed depending on the resource.

The mixed ecological strategy of the five species makes hypothesizing a ranking from traits not at all straightforward. The distinct strategy of *Eleocharis multicaulis* coincides with its observed pattern of niche separation. On the other hand, the three species that had a rather similar niche pattern also share many functional traits. Further, the broad characterization of *Juncus bulbosus* in terms of functional traits coincides with its wider realized niche. These findings support the assumption that functional characteristics under- pin, at least in part, niche differentiation among species through fitness trade-offs.

Needs for further research

In this study we investigated niche differentiation in a specific system, between specific species and at a specific resolution and extent. It must therefore be seen as a contribution to observed community struc- tures in nature at large scale, rather than being designed to distinguish between the actual mecha- nisms. It must be kept in mind that multiple mecha- nisms may lead to a similar observed pattern. Ideally, the study of patterns is done at multiple spatial scales in order to capture relevant mechanisms and to achieve generality (Levin 1992; Kunin 1998; Crawley and Harral 2001; Hartley and Kunin 2003; Rahbek 2005). Moreover, experiments are the ultimate means of testing the relevance of a proposed mechanism. Hence, mechanistic experimental research at a range of spatial scales is needed to test the importance of different community structuring mechanisms at the biogeographical scale, such as biotic interactions and environmental filtering. Following Wisz et al. (2013), we suggest that this research path would greatly benefit insights in community biogeography.

The characteristic isoetid species that grow deeper in these softwater lakes than the *Eleocharition mul- ticaulis* alliance have received much more attention by researchers (Arts 2002; Brouwer et al. 2002; Murphy 2002; Smolders et al. 2002). More ecological knowl- edge on target species of the *Eleocharition multicaulis* would be very useful for their conservation. Models like the ones in this paper can be used to support restoration of their abiotic environment. Our models may be refined by collecting more data. Furthermore, several experiments could be set up in order to test the expectations on species’ performance in different environments, and in order to elucidate physiological mechanisms.

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