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Water temperature and acidity regime shape dominance and beta-diversity patterns in the plant communities of springs

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Abstract. The processes underlying species' dominance patterns and community composition are insufficiently investigated for springs, yet these systems, which are believed to be very stable environments, represent an important interface between aquatic and terrestrial habitats contributing significantly to local and regional diversity. We studied the dominance patterns and plant community composition of 238 springs in Central Europe. According to the conventional ecological belief we hypothesized (1) a positive relationship between local abundance and regional distribution of spring plant species, as well as between species commonness and species' realized breadth and (2) the occurrence of oligarchic species similar to other stable environments like tropical forests. Based on previous studies on these springs, we furthermore hypothesized (3) that water pH—essentially a proxy for nutrient availability—is the major driver of spatial compositional dissimilarity, i.e. beta-diversity. We tested these three hypotheses by using species commonness estimates, realized niche space and generalized dissimilarity modelling based on hydrochemistry. In line with conventional wisdom, we report a positive relationship between local abundance, species commonness and regional distribution for the majority of the species. In contradiction to other systems, we found both specialist and generalist species to be locally dominant and regionally widespread, thus common, while species with intermediate niche breadth showed the lowest commonness values. However, we detected three oligarchic species, exceeding all other species in local abundance and regional distribution, which did not follow these relationships. Both dominance relations (oligarchy) and community composition were mainly driven by water temperature and concentration of elements related to acidity regime (Al, Cd, Ca and Mg), although much of the variation in both remained unexplained. Thus, further research should focus on biotic interactions, which are likely to be important drivers of plant community composition in springs.

Keywords. beta-diversity, community composition, generalized dissimilarity modelling, helocrenic forest springs, hierarchical variation partitioning, niche space hyper volume, realized niche breadth, species commonness

Introduction

The organisation of ecological communities and ecosystems has been a central topic in ecology and biogeography for decades (Brown 1984, Condit et al. 2002, Legendre et al. 2005). The extent and direction of community responses to a changing environment in space and time strongly depend on the initial species composition, species cover and abundance (Grime et al. 2000, Potts et al. 2006). In general, communities consist of a set of interacting species, where relative success in the competition for resources shapes dominance relations within these communities (Whittaker 1965). Species are unequally successful, so natural

communities are often characterized by a few species that repress other co-occurring species (Whittaker 1965, McNaughton and Wolf 1970). Whereas these species dominate in terms of structure and productivity, numerous additional species comprise the majority of species diversity (McNaughton and Wolf 1970).

Local abundance and spatial distribution have been shown, in numerous studies, to be intimately positively related (Brown 1984 and references therein, Gaston et al. 1997, Gregory and Gaston 2000). A high local abundance means a large number of individuals of a species at a given site (Gaston et al. 1997). Whereas most species

are both rare and regionally restricted, a few species show local hyper-dominance and a wide regional distribution. We call these hyper-abundant, widespread species ‘oligarchic species’ (Pitman et al. 2001). The occurrence of oligarchic species, which is known for many tropical forests (Arenallo et al. 2013), may be especially favoured by stable environmental conditions (Pitman et al. 2013). Several authors argue that oligarchic species occupy the widest ecological niches, leading to their local hyper-dominance and wide distribution (e.g., McNaughton and Wolf 1970, Brown 1984, Pitman et al. 2001). In contrast, species with narrow ecological niches might reach high local abundance under certain appropriate conditions but are commonly denied a wide spatial distribution (Pitman et al. 2013).

The realized niche of a given species is defined as a set of abiotic as well as biotic environmental parameters, which enable or limit the survival and reproduction of the species (Hutchinson 1957). Spatial variation in both abiotic conditions (e.g., climate or geology) and biotic conditions (including interspecific differences in dispersal ability, competitive strength and historical effects), drives patterns of compositional dissimilarity within a given type of ecosystem (Condit et al. 2002). This can be quantified as compositional dissimilarity between communities or beta-diversity (*sensu* Whittaker 1960, 1972). Although community composition and beta-diversity patterns have been popular subjects for ecologists and biogeographers for more than three decades, underlying processes and environmental drivers are still not entirely understood, and have been insufficiently investigated, in particular for less ‘popular’ systems like springs.

Despite their importance for clean water supply and local as well as regional biodiversity, springs are underrepresented in ecological research (Cantonati et al. 2012a,b). Springs are often very small ecosystems but at the same time very numerous, both regionally and globally (Glazier 2012). As an interface between aquatic and terrestrial habitats, springs harbour numerous specialized species which strongly respond to changes in water chemistry and thus the biogeo-

chemistry of the catchments feeding them (Beierkuhnlein and Gollan 1999, Cantonati et al. 2006, Kapfer et al. 2012, Kubíková et al. 2012). Among all the morphological types of springs described by Thienemann (1924), ‘helocrenic’ springs (seepage springs) host the most specialized and taxon-rich communities (Cantonati et al. 2012a). These springs are characterized by a spatially diffuse emergence of slow-flowing water, which causes a constantly water-saturated, swampy zone (seepage area) with a spatial extent of several to a few hundred square metres (Thienemann 1924, Cantonati et al. 2012a).

Most previous studies of springs focused on the zoological legacy of the groundwater (see Cantonati et al. 2012a for review). In consequence, springs are understudied in terms of plant communities, although they typically harbour an extraordinary diversity of specialized plant species in very small areas (Cantonati et al. 2006, Spitale et al. 2012). Studies of the plant community composition of springs are a prerequisite for understanding what determines the biodiversity and abundance patterns of these vulnerable systems.

In this study, we investigate the spatial patterns of dominance and beta-diversity of 238 helocrenic springs in the lower mountain ranges of Central Germany and the north-west Czech Republic. We focus on two research questions: (1) How are these spring plant communities organized in terms of species’ local abundance and regional distribution? (2) What are the major environmental drivers of compositional dissimilarity and thus beta diversity patterns in these systems?

Pristine springs are commonly believed to be characterized by very stable environmental conditions (including water temperature, acidity regime and nutrient availability). We therefore hypothesized that the dominance patterns of spring plant communities should be characterized by oligarchic species, similar in this respect to tropical communities. We further hypothesized a positive relationship between local abundance and regional distribution of spring plant species, as well as between species commonness (as a combination of local abundance and regional distribution) and the volume of the species’ realized

niche. Based on previous studies about abiotic drivers of plant community composition (Audorff et al. 2011), we hypothesized that water pH (essentially a proxy for nutrient availability) is the major driver of spatial compositional dissimilarity.

Methods

Study region

We studied dominance relations and compositional dissimilarity of spring plant communities for 238 springs from five mountainous landscapes of east-central Germany and the north-west of the Czech Republic (Thüringer Schiefergebirge n=48 springs, Thüringer Wald n=41, Frankenwald n=50, Fichtelgebirge n=41 and Erzgebirge n=58, Fig. 1). The springs studied represent the helocrenic spring type (Thienemann 1924, Cantonati et al. 2012a), with continuously water-saturated seepage areas of a few to some hundred square metres. The individual discharge rates are mostly low (mean discharge = 0.3 L s^{-1}) but relatively constant throughout the year. Springs of this kind occur at high spatial density in the study region, allowing investigation of community responses at the landscape scale.

We chose predominantly forested catchment areas, mainly characterized by Norway spruce (*Picea abies*, L. H.Karst.) but also partly by European beech (*Fagus sylvatica*, L.). The altitude of the springs sampled ranges from 270 to 1240 m a.s.l. The climatic conditions are transitional between oceanic and continental climates. Detailed regional characteristics are provided in Audorff et al.

(2011). The dense siliceous bedrock does not allow groundwater to penetrate. Instead, water is transported mainly as interflow close to the surface, in Pleistocene solifluction layers covering the whole area, which was not glaciated (Kleber et al. 1998). Thus, retention time of precipitated water in the catchments is rather short: a magnitude of weeks to months. Therefore, hydrochemical spring water characteristics are expected to be directly coupled to biogeochemical processes in the catchments (Beierkuhnlein and Durka 1993).

Data collection

We investigated abundance/dominance relations of spring plant communities and hydro-chemical water characteristics for all springs between 1989 and 1996. For the vegetation surveys we determined all vascular plants, mosses and liverworts of the spring communities during July or August of the study years. Because previous studies on these springs have shown that bryophytes do not significantly differ from vascular plants in their response to interannual environmental changes (pH, electric conductivity, water temperature and discharge; Kapfer et al. 2012), we pooled all three groups for our study. As a result of seasonal frost heaving in winter, the helocrenic seepage area is well differentiated from the forest floor, which allows easy delimitation of the spring site from the surrounding area. We quantified local abundance of each plant species by estimating the cover using a modified Braun–Blanquet method (Reichelt and Willmanns 1973), where the Braun–

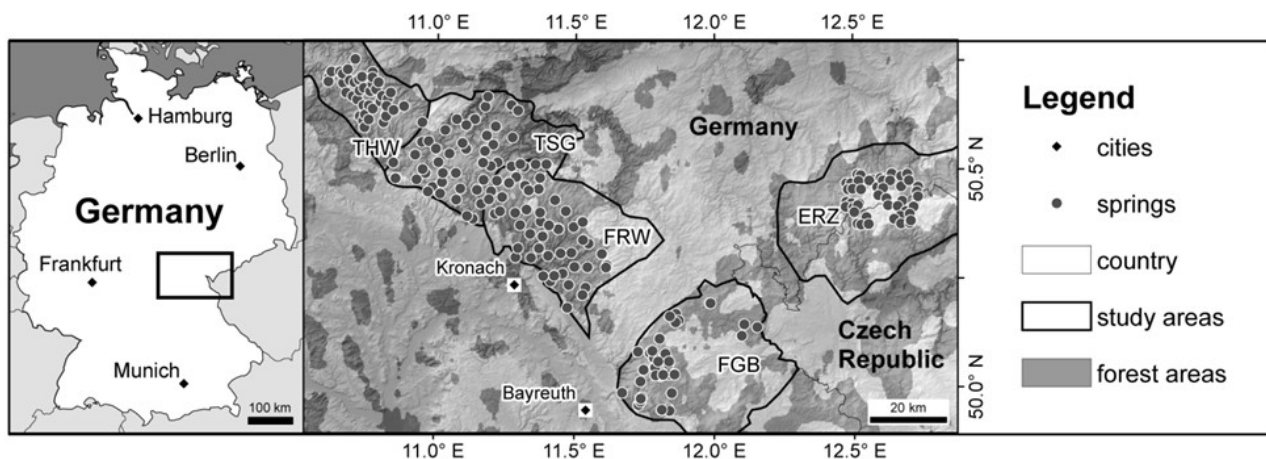


Figure 1. Locations of the helocrenic springs investigated in central Germany and the north-west Czech Republic (THW: Thüringer Wald, TSG: Thüringer Schiefergebirge, FRW: Frankenwald, FGB: Fichtelgebirge, ERZ: Erzgebirge).

Blanquet scores: r, +, 1, 2m, 2a, 2b, 3, 4 and 5 were transformed for analysis to mean percentage covers of: 0.01, 0.2, 2, 3, 10, 20, 37.5, 62.5 and 87.5, respectively.

Surveys of water hydro-chemistry took place in late September and October of the corresponding years. To avoid any kind of distorting effect caused by physico-chemical atmosphere–water interactions, we sampled spring water at the uppermost point of the seepage area with above-ground flow. We measured water temperature, electrical conductivity and pH *in situ* using a portable pH–conductivity multimeter with a liquid electrolyte pH-probe/conductivity probe (WTW pH/Cond 340i with WTW SenTix 81/WTW Tetra-Con 325, Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany). Because water temperature of springs is very stable at least within a timeframe of hours to days, we did not account for the time differences between the different measurements at the different spring sites. We visually estimated water discharge based on a seven-point ordinal scale, ranging from 0 to $>1.5 \text{ L s}^{-1}$. We determined acid neutralisation capacity (ANC) in the laboratory using titration (0.01 M HCl to pH 4.3). Concentrations of nutrient and toxic elements / compounds (Ca, K, As, B, Be, Ba, Co, Cr, Cu, Fe, Hg, Mo, Ni, NO_3 , SO_4 , PO_4 , NH_4 , DOC, Al, Pb, Se) were determined *ex situ* in the laboratory using filtered (0.45 μm cellulose acetate filters, Satorius Stedim Biotech GmbH, Goettingen, Germany) and partly acidified (HNO_3 , distilled) water samples. Additionally, we quantified light regime at the particular spring site by estimating the percentage tree cover. Elevations of the spring sites were derived from a digital elevation model. Subsequently, we used this set of 36 environmental variables to quantify species' realized niche breadth and compositional dissimilarity.

Data analyses

We quantified species' commonness as a parameter representing both local abundance and spatial frequency of occurrence, based on the h-index of academic productivity, using the r-command provided by Arenallo et al. (2013). For each species, a proportional index (h_p) was assigned when the spe-

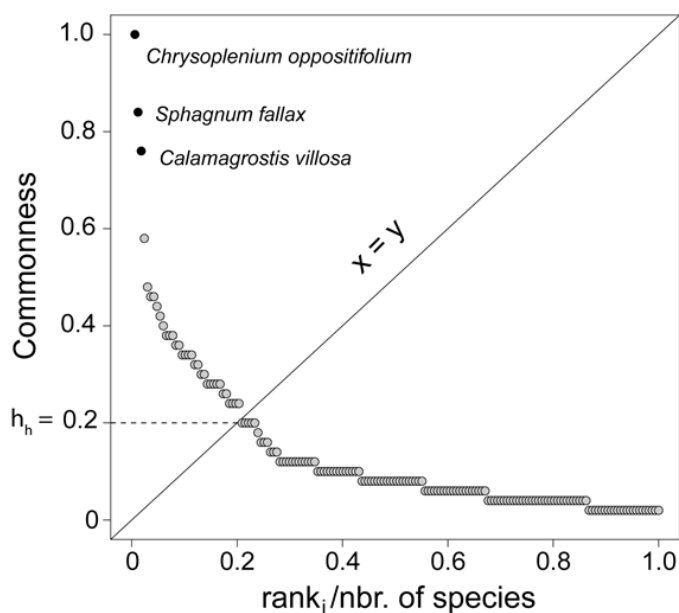


Figure 2. Commonness of helocrenic spring plant species in Central Europe. Commonness is measured as proportional commonness based on the commonness value of the most common species. Species are sorted by commonness (horizontal axis). Common and rare species are separated at $h_h = 0.2$ (see Methods). The three 'oligarchic species' are highlighted by black points and named.

cies was present in h_p percentage of the 238 spring sites with h_p percentage or more cover in each of the studied spring sites (for details see Arenallo et al. 2013). Afterwards, we divided all the h_p -indices by the maximum h_p -index observed among the considered species. We used this relative h-index to quantify the commonness of the spring plant species. Based on their calculated commonness values, we categorized all species into three groups: oligarchic, common and rare species, following Arenallo et al. (2013). Common species were separated from rare species based on the intersection of the $x=y$ (1:1) line with the proportional commonness–rank curve (see Fig. 2). Therefore we used the commonness-value (y-value, h_h in Fig. 2) of this intersection as a threshold to separate common ($>h_h$) from rare species ($\leq h_h$; see Arenallo et al. 2013).

Furthermore, we quantified the extent of each species' realized niche space. To ensure statistically robust niche space estimates, we only considered species occurring in more than 50 springs. Our definition of niche space

followed Hutchinson (1957), who defined a species niche as an n -dimensional hypervolume of environmental characteristics in which the species/population can maintain a positive net growth rate. To calculate the Hutchinsonian hypervolume of individual niche spaces we conducted kernel-density estimations based on relevant environmental variables ('hypervolume' package for R, v.0.9.9.7, Blonder 2014). Relevant environmental variables were selected based on knowledge from previous studies conducted in this region about the environmental drivers of spring plant community composition (Audorff et al. 2011, Kapfer et al. 2012) and spatial coverage (available for more than 75% of all springs). Thus, a set of 16 environmental variables was used: elevation, water temperature, discharge, pH, electric conductivity, ANC as well as the concentrations of K, Na, Ca, Mg, Cd, Mn, Al, NO_3 , SO_4 , PO_4 and NH_4 . To reduce the number of dimensions and to minimize distorting effects caused by co-linearity between the variables we *a priori* performed a principal components analysis (PCA) based on all 16 variables. To quantify the species' Hutchinsonian hypervolume we used the first three PCA axes, which accounted for more than 99.9% of the total variation.

Additionally, we analyzed the effect of abiotic environmental conditions on compositional dissimilarity by using generalized dissimilarity modelling (Ferrier et al. 2007). This statistical technique, which can be used to analyse and predict beta-diversity patterns across large spatial scales, is an extension of matrix regression, which is capable of handling non-linearity in large-scale ecological datasets. We included geographical distance between sites (Euclidean distance based on spring site coordinates) as an additional term in the model. We quantified compositional dissimilarity by calculating the Bray–Curtis dissimilarity between all investigated communities/springs. Dissimilarities between the spring plant communities were modelled by the abiotic variables based on l-spline

basis function fits to the environmental predictors in combination with a maximum-likelihood estimation of model coefficients. We used the percentage of deviance accounted for by the fitted model as a goodness-of-fit estimate. We selected relevant environmental variables, a subset of the 16 variables mentioned above, *a priori* by a stepwise forward and backward model approach. For both approaches, addition or removal of variables was stopped when percentage of explained deviance decreased after a maximum was reached. The final set of relevant environmental variables was selected by considering both forward and backward model selection. Based on these selection criteria, a set of 10 environmental variables was used for the analysis: water temperature, ANC as well as concentrations of Al, Mn, Ca, Mg, Cd, PO_4 , NH_4 and NO_3 . As we were particularly interested in the relative importance of single variables in explaining species composition we did not use the previously mentioned principle components which can be used to avoid co-linearity among the variables under consideration, although we detected moderate co-linearity among the chosen variables. We quantified the relative importance of the selected environmental variables in terms of accounting for the compositional dissimilarity between the investigated springs, using the hierarchical partitioning approach of Chevan and Sutherland (1991). This approach is considered adequate to quantify relative importance of single variables for non-linear models (Murray and Conner 2009). The goodness-of-fit measure was percentage of explained deviance and not R^2 (which is implemented in the `hier.part` R package v.1.0-4; Walsh and Mac Nally 2013), so we had to adjust the algorithms to our approach. We conducted all analyses in the R environment (v.3.0.2, R Development Core Team 2013) with the add-on package `vegan` (v.2.0-10; Oksanen et al. 2013). Generalized dissimilarity modelling was performed using the GDM R Distribution Pack¹. We conducted all analysis based on inferential statistics with a level of significance of $\alpha = 0.05$.

1 v.1.1, available at <https://sites.google.com/site/gdmssoftware/>, last accessed 18/09/2014.

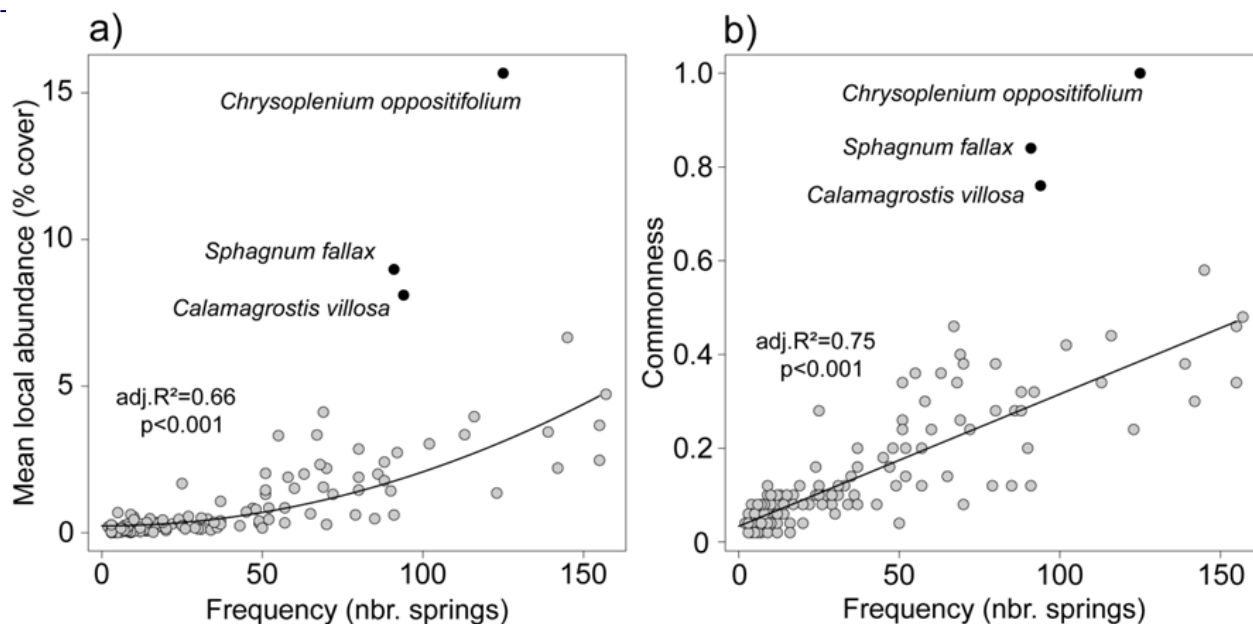


Figure 3. Relationship between species' spatial distribution, quantified by the number of occupied springs, and (a) mean local abundance, i.e. mean local cover, and (b) commonness of helocrenic spring plant species in Central Europe. The three oligarchic species are highlighted by black points and were not included in the regression models.

Results

Dominance relations

Species' commonness varied greatly; only 34 (20%) of the species were classified as 'common' (including the three oligarchic species, see Fig. 2), the rest as 'rare' (133 species). We classified the herbaceous species *Chrysplenium oppositifolium* L. and *Calamagrostis villosa* (Chaix ex Vill.) J. F. Gmel. and the moss *Sphagnum fallax* H. Klinggr. as 'oligarchic species'. All three species had considerably higher commonness values (> 0.7) than the other common species.

We found a significant positive relationship between extent of spatial distribution (frequency of occurrence) and mean local abundance of the spring-inhabiting species, expressed as the arithmetic mean of species cover classes (Fig. 3a). We also found a significant positive relationship between extent of distribution and commonness (Fig. 3b). However, the three oligarchic species showed much higher local abundance (and thus commonness) than expected from their extent of distribution on the basis of the other species (see black points in Fig. 3).

Species' realized niche breadth

Excluding the three oligarchic species, we observed a weak U-shaped relationship between species' niche volume and commonness (Fig. 4). The lowest com-

monness values were associated with intermediate niche volumes, with commonness increasing for both smaller and larger niche volumes. The three oligarchic plant species, *Chrysplenium oppositifolium*, *Sphagnum fallax* and *Calamagrostis villosa* were again far removed from the main trend. Neither local abundance nor the extent of distribution were significantly related to realized niche breadth.

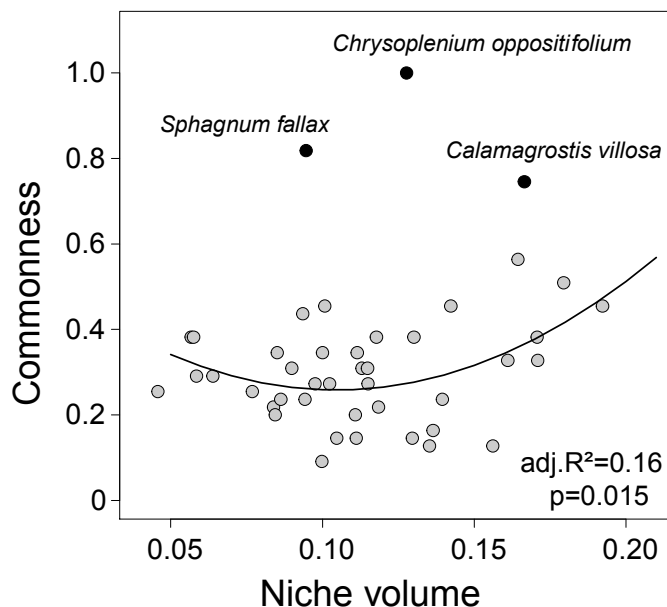


Figure 4. Relation between species' commonness and the volume of the realized ecological niche for helocrenic spring plant species in Central Europe. The three oligarchic species are highlighted by black points and were not included in the regression model.

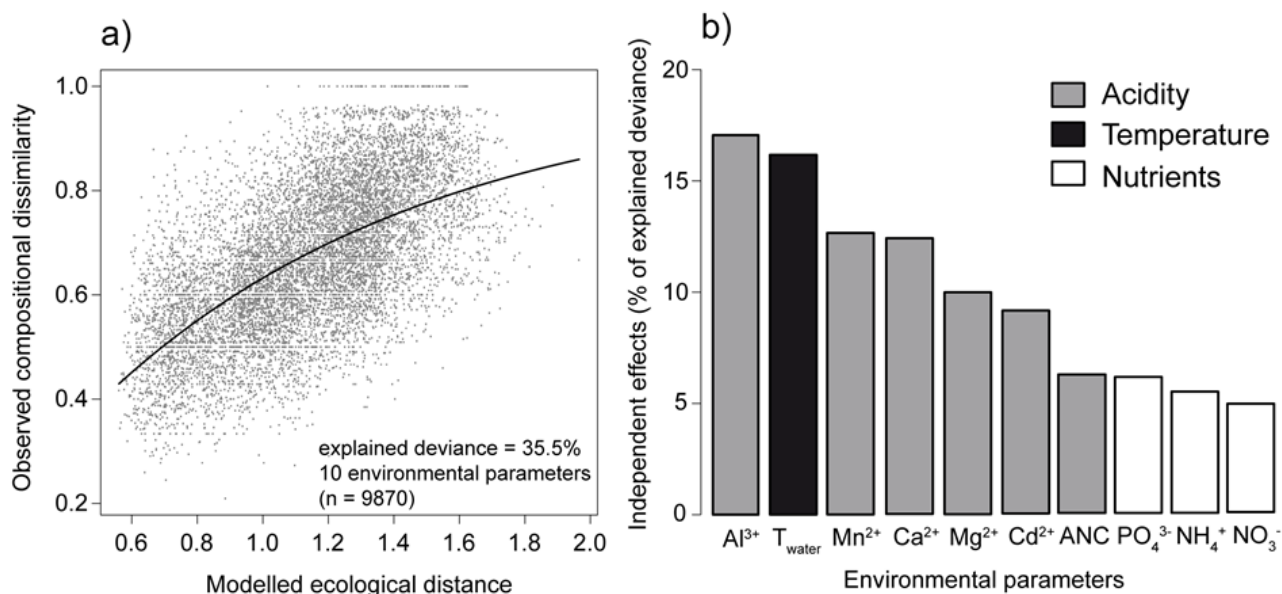


Figure 5. Abiotic environmental drivers of compositional dissimilarities between the helocrenic spring plant communities. a) Generalized dissimilarity model (gdm) fit between observed compositional dissimilarity and modelled ecological distance. Each point represents a pairwise comparison between springs. b) Relative importance (independent effects) of the 10 most influential environmental variables (based on hierarchical variation partitioning applied to the gdm). Different colours represent different groups of variables (black: temperature regime, grey: acidity regime, white: nutrient availability).

Compositional dissimilarity

Using the 10 environmental variables selected *a priori*, and geographic distance as co-variable, we could account for 35.5% of the total deviance in compositional dissimilarity (Fig. 5a). Aluminium concentration and water temperature had the highest explanatory power (independent effects: 17.1% and 16.2% of total explained deviance, respectively; Fig. 5b). Element concentrations of Mn, Ca, Mg and Cd showed relative importances (independent effects) between 12.6% and 9.1%. Concentrations of nitrate, phosphate and ammonium, as well as acid neutralisation capacity (ANC), showed low relative importance (between 6.1% and 4.9%). Geographic distance considered as an explanatory variable showed a relative importance of 7.1% of total explained deviance.

Increasing geographic distance among the spring sites promoted compositional dissimilarity in a largely linear manner (Fig. 6a). Increase in water temperature had minimal independent effects on the dissimilarity in community composition for lower water temperatures (below 8°C), but its effect increased rapidly with tem-

peratures above this value (Fig. 6a). Environmental variables associated with the acidity regime of the springs affected compositional dissimilarity in a similar fashion to each other (Fig. 6b,c): we observed strong independent effects of ANC when this was low (below 0.1 mmol L⁻¹), and the same for concentrations of Ca, Mg and the heavy metal Cd (below 7.0 mg L⁻¹, 2.0 mg L⁻¹, 0.1 µg L⁻¹, respectively). However, increasing values of these variables above these levels were associated with minimal additional effects. We found no such saturation in the independent effects of increasing concentrations of Al and Mn (Fig. 6c), both of which showed monotonic, decelerating effects; the overall effect size was smaller for Mn than for Al. Chemical compounds associated with the nutrient regime of the springs showed relatively small independent effects on compositional dissimilarity (Fig. 6d), with saturation behaviour for NH₄ and PO₄. The independent effect of increasing concentrations of NO₃ showed striking similarities to the effect size behaviour of water temperature and was more prominent than for the other two nutrient compounds.

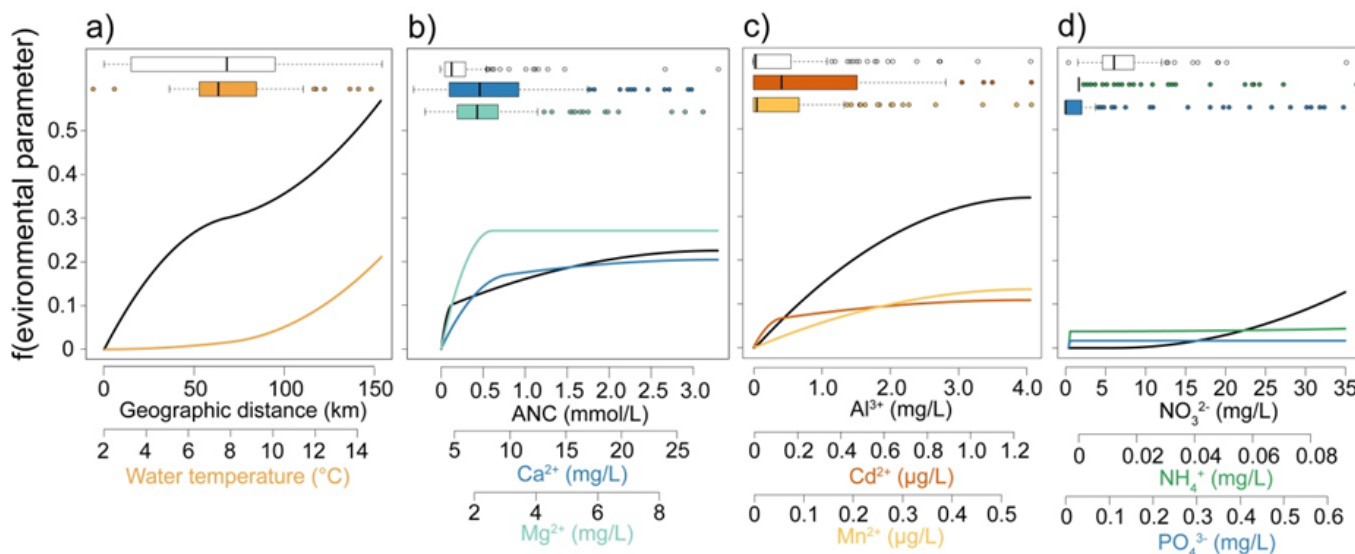


Figure 6. Effects of the 10 most influential abiotic drivers of compositional dissimilarities between the helocrenic spring plant communities. a) Geography and water temperature, b) and c) variables associated with acidification, d) nutrient elements. The slope and total values of each function (vertical axis) depict the rate and amount of compositional turnover, which is associated with the gradient of each environmental variable by holding all other parameters constant. Distributions of the measured values along the total gradient of each variable on which the fits are based, are depicted as boxplots correspondingly coloured in the upper part of the plots (box: first quartile, median and third quartile, whiskers: 1.5 times interquartile distance, points: individual values outside the whiskers).

Discussion

We found that oligarchic species, often associated with environmentally stable ecosystems like tropical forests (Arenallo et al. 2013, Pitman et al. 2001, 2013), also characterize Central European spring plant communities. In support of the conventional belief in ecological literature (e.g., Gregory and Gaston 2000), we also found positive relationships between local abundance, species commonness and regional distribution for the majority of the species analyzed. However, the three oligarchic species were strikingly different from all other species, with much higher local abundance; they did not follow the relationships we found between local abundance, regional distribution and commonness for the other species.

In general, two mechanisms have been proposed to explain positive relationships between local abundance and regional distribution: meta-population dynamics and differences in species' niche breadth. Regarding the first mechanism, species-specific differences in extinction and colonization rate (carrying capacity) are assumed to cause the positive relationship between local abundance and regional distribution, which shapes the meta-population structure. Following

the carrying capacity hypothesis (Nee et al. 1991) locally abundant species are assumed to have lower extinction and/or higher colonization rates and, thus, are more widespread, especially when extinction events are frequent among meta-populations. As extinction events can be considered very rare in spring ecosystems (because of the very stable abiotic conditions), we assume this first mechanism to be negligible for spring plant communities. Regarding the second mechanism (niche breadth), it is argued that more abundant and widespread species can use a broader range of resources and, thus, have broader realized niches (McNaughton and Wolf 1970, Brown 1984). This would mean that oligarchic species occupy the widest ecological niches, leading to their local dominance and wide distribution (Pitman et al. 2001). This was not the case for our spring plant communities: the niche spaces occupied by the oligarchic species were intermediate compared with the co-occurring species. Furthermore, we found no linear increase of species' commonness with increasing realized niche space but rather a weak U-shaped relationship for the non-oligarchic species (and no relationship if the oligarchic species were included). In other words, non-oligarchic species with intermediate niche breadth were

least common in the spring plant communities, whereas species with relatively narrow or wide niches were slightly more common.

Although a positive relationship between niche breadth and commonness can be inferred from theoretical models, various studies have failed to find any such relationship, or have found negative relationships (see Gaston et al. 1997 for review). According to Gaston et al. (1997) the main reason for this inconsistency is that most studies do not cover a spatial extent which is appropriate to cover the full range of environmental conditions under which species occur in a certain system. As a consequence most studies are not able to correctly determine species' realized niches. Furthermore, considering species that co-occur in the same system but have quite distinctive ecological characteristics and, thus, might occur in the same system but because of different reasons, might also lead to wrong conclusions (Gaston et al. 1997). We argue that neither problem affects our study. Although our study is confined to a regional scale, the narrow amplitude of environmental conditions characterizing the studied springs allowed us to cover the full range of environmental conditions under which the species occur in these systems. Furthermore, most spring plant species are specialized to the stable environmental conditions that characterize these systems and, thus, show quite similar ecological characteristics (Cantonati et al. 2012a). This quite narrow amplitude of environmental conditions to which species are especially adapted is not regionally restricted but characterizes springs of this type over large geographical extents. This may allow species with narrow ecological niches not only to reach high local abundance under certain, appropriate conditions (Pitman et al. 2013) but also to have wide regional distributions, causing the high commonness values we observed for these specialized species. So the common assumption, that generalist species will be more widespread than specialized species, seems only partly true for springs, where abiotic conditions are very similar and stable on long time scales and relatively large spatial scales. Thus, specialists with narrow ecological niches seem not to be disadvantaged compared to species with wider ecological niches.

Abiotic environmental conditions are commonly considered to shape dominance relations among co-existing plant species, and thus plant community structure (Ellenberg and Leuschner 2010). Consulting the extensive amount of phytosociological work which was done for the studied springs during the 1990's, all three oligarchic species we detected in our study clearly reflect the predominant environmental gradients of the springs, which are characterized by acidity (modern acidification and/or historic precipitation regime) and water temperature (elevation). The perennial *Chrysplenium oppositifolium* is known to characterize neutral springs whereas the moss *Sphagnum fallax* characterizes acidified springs in the studied region (Audorff et al. 1999, Beierkuhnlein 1999, Beierkuhnlein and Schmidt 1999, Peintinger and Beierkuhnlein 1999, Riedel and Beierkuhnlein 1999). *Calamagrostis villosa* is a typical species of helocrenic springs in the cooler, higher elevations of this region above 700 m a.s.l. (Audorff et al. 1999). In a previous study of the environmental parameters shaping spring plant community composition in this region (Audorff et al. 2011), hydrochemical variables related to the acidity regime (Al, Cd, Mn, Ca and Mg) played a fundamental role while spatial and hydrophysical variables (e.g., water temperature) were less important. Spring water chemistry, especially variables related to acidity and nutrient availability, has been shown in numerous studies to strongly affect plant community composition in Central European springs (Beierkuhnlein 1994, Hájek et al. 2002, Hájková and Hájek 2003, Hájková et al. 2004, 2008, Cantonati et al. 2012a). Furthermore, water temperature is known from several studies on benthic pro- and eukaryotic algae, diatoms and invertebrates to shape spring community structure (Cantonati et al. 2012b, 2012c, Glazier 2012). However, the actual shape of community response to abiotic factors has not been considered so far.

In our study, we can confirm the importance of temperature and acidity regime in shaping spring plant communities in Central Europe. Compositional dissimilarity between the springs was best explained by water temperature and concentrations of elements related to the actual

acidity regime (Al, Mn, Cd, Ca, Mg). Although we observed a small effect of water temperature below 8°C, effect size increased strongly with increasing temperature. Low temperatures are known to limit the metabolic rates and, thus, the competitive ability of species (Brown et al. 2004). With increasing temperatures, species' metabolic rates are no longer limited, which might enhance competition among species and, thus, cause higher rates of community turnover (Glazier 2012). This seems to be especially the case for spring plant communities, where compositional dissimilarity between the different sites, and thus spatial community turnover, is strongly affected by temperature regime.

For the heavy metals Al and Mn, we observed increasing community responses over the full range of observed element concentrations. Both elements are known to be toxic for plants at high concentrations. Species' susceptibility to Mn clearly depends on the acidity regime prevalent at the site (Mahmoud and Grime 1977). The occurrences of species along a pH gradient also strongly depend on their Al tolerance. Among all elements affected in solubility by acidification, Al is one of the most cytotoxic, and thus most restricting, factors in terms of species' establishment and occurrence (Cantonati et al. 2006, Abedi et al. 2013). Although the bioactive concentrations of both elements are driven by the present acidity regime of the spring sites (Audorff et al. 2011), element concentrations rather than acidity itself (meaning the activity of H⁺ ions) influence species' performance and, thus, drive the compositional dissimilarity between the springs. This indirect effect of acidity regime on spring plant community composition is confirmed by the high independent effects of Ca, Mg and Cd. Although all three elements are strongly affected by the prevalent acidity regime of the catchment/spring (Hruška et al. 2002), independent effects were visibly higher than the explanatory power of acidity itself (quantified as pH and ANC).

In this study we can support the notion that acidity and temperature regime are the predominant environmental factors directly and indirectly shaping plant community composition of Central

European helocrenic springs. Considering the 10 most relevant environmental variables, we were able to account for 35.5% of the total variation in compositional dissimilarity. This exceeds the overall explanatory power which was reported by Audorff et al. (2011). By analysing springs from the same region but using a different analytical approach (partial correspondence analyses and multiple response permutation procedure) they were only able to account for 18.8% of total variation in spring plant community composition using 18 abiotic variables. Reporting similar low predictive power of abiotic variables in explaining spatial variation in spring community composition (<17% of total variation), Spitale et al. (2012) assumed biotic interactions to be more important than generally perceived for these systems. Furthermore, neutral processes like interspecific differences in dispersal ability, which clearly depend on the geographic distance between the different spring sites, could account for the large portion of unexplained variation in compositional dissimilarity (Audorff et al. 2011). Although the importance of geographic distance in explaining community composition between the spring sites was higher than in the study of Audorff et al. (2011) (7.1% vs. 3.6% of total variation), this obviously important factor cannot account for the large portion of unexplained variation. Thus, unaccounted-for biotic interactions more than neutral processes are likely to be the reason for the relatively large portion of unexplained variation of compositional dissimilarity.

Conclusions

Understanding the patterns and underlying drivers of dominance relations and beta-diversity patterns of plant communities is one fundamental goal in ecology and badly needed to adequately assess future climate change effects on biodiversity and ecosystem functioning. This is especially relevant for springs, which house numerous species that are especially susceptible to a changing environment (e.g., climate change, acid rain) but are still underrepresented in ecological research. In this study we showed that species with narrow ecological niches, which are known from other

systems to be locally dominant only under certain environmental conditions and, thus, restricted in regional distribution, are regionally widely distributed in springs. We also showed that oligarchic patterns in community composition occur in these helocrenic springs. Both circumstances seem to be caused by the relatively stable environmental conditions that characterize these semi-aquatic systems. Furthermore, we showed that water temperature (linked to elevation) and acidity regime (representing a combination of acidic deposition and bedrock traits), are major drivers of dominance relations and compositional dissimilarity between helocrenic spring plant communities in Central Europe. By identifying the patterns and important environmental drivers, we filled some of the important knowledge gaps regarding these understudied systems. However, further research should unravel in more detail the biotic interactions and responses to changing abiotic conditions which are projected for the future.

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