COMMUNITY ECOLOGY – ORIGINAL RESEARCH



Ecological and biogeographical drivers of freshwater green algae biodiversity: from local communities to large-scale species pools of desmids

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Abstract

Dispersal limitation, niche-based processes as well as historical legacies shape microbial biodiversity, but their respective influences remain unknown for many groups of microbes. We analysed metacommunity structure and functional trait variation in 148 communities of desmids, freshwater green algae, distributed throughout Europe. We delineated biogeographic modules for both taxa and sites using bipartite network analysis given that the taxa of a module co-occurred more often than expected by chance in sites of the same module. The network analysis distinguished two main acidic and neutral habitats, reflecting environmental filtering, and within each habitat separated species pools with distinct geographic locations, representing a plausible influence of historical biogeography. The geographic differentiation was consistent with a hypothesis of glacial refugia on Atlantic coast. Distance decay in community composition in addition to environmental influence further suggested a role of dispersal limitation. Next, we quantified the variation in cell volume and surface-to-volume of taxa within and among communities, to examine morphological and physiological adaptations of desmids in varying environments. Communities from continental climate contained larger desmids. Conversely, we found a functional convergence of smaller, fast-growing, desmids in oceanic regions. Overall, our findings suggest that niche-based processes, dispersal limitation, and historical legacy together drive the distribution and structure of desmid communities. Combining trait- and network-based analyses can resolve long-lasting questions in microbial ecology and biogeography, and could be successfully used in macrobial ecology too.

Keywords Community assembly · Functional trait · Bipartite network · Biogeography · Green algae

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Introduction

What drives the local and regional biodiversity of microorganisms is a much-debated issue. Do neutral or niche-based processes predominate (Nemergut et al. 2013)? What is the extent of dispersal limitation (Fenchel and Finlay 2004; Foissner 2006; Martiny et al. 2006; Cermeño and Falkowski 2009; Hanson et al. 2012)? Recent evidence supports the early hypothesis of Baas Becking (1934) that environmental filtering selects local assemblages depending on the niche of microbes (Stegen et al. 2012; Wang et al. 2013), but also tend to disprove its hypothesis of unlimited dispersal (Telford et al. 2006; Chytrý et al. 2012; Bates et al. 2013; Zinger et al. 2014). Conversely, several microbial communities show apparent neutrality (Segura et al. 2010) and lack of dispersal limitation. Therefore, it is unclear whether general rules can be derived for microbial communities since microbes encompass various organisms and life strategies

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and occupy very diverse environments (e.g. marine plankton vs. freshwater algae in patchy habitats). Consequently, macroecology of many microbes remains poorly known, which prevents getting a comprehensive picture of their dynamics (Prosser et al. 2007). One of those scarcely explored microbial groups are desmids, Streptophyte green algae (but see Coesel 1996; Neustupa et al. 2009, 2013). They mostly inhabit benthos of non-marine and patchy aquatic ecosystems. Here we investigated the role of ecological and biogeographical processes in shaping biodiversity of desmids across Europe.

The influence of niche-based processes can be grasped by analysing the diversity of key functional traits reflecting the ability of organisms to disperse, establish, survive and reproduce in their local environment (Violle et al. 2007). Addressing the nature and role of functional traits in microbial community dynamics have recently gained momentum (Hall et al. 2008; Fierer et al. 2014; Krause et al. 2014; Nemergut et al. 2014), notably in phytoplankton systems (Reynolds et al. 2002; Litchman and Klausmeier 2008; Kruk et al. 2011). Desmids' cell sizes range from under 10 µm up to 1 mm (Brook 1981) and represent a potentially broad spectrum of ecological niches (Litchman and Klausmeier 2008), given that the size of photoautotrophs is tightly linked to ecophysiological abilities for nutrient and light acquisition (Passy 2007). Size appears to be the key functional trait for unicellular organisms (Margalef 1978; Reynolds et al. 2002). Generally, small cell size is associated with higher population growth rate (Nielsen et al. 1996). High cell surfaceto-volume ratio is expected to increase nutrient uptake in oligotrophic environments (Passy 2007), while a lower ratio limits osmotic stress in highly acidic environments (Černá and Neustupa 2009). Therefore, we hypothesized that variation in cell volume and surface-to-volume ratio within and among desmid communities should reflect the influence of niche-based assembly processes in varying environmental contexts (Cornwell et al. 2006; McGill et al. 2006; Escudero and Valladares 2016).

We addressed the role of assembly processes by deciphering their signature in functional trait distribution (Enquist et al. 2015) within desmid communities. First, the mean trait value of a community (Community-Weighted Mean or CWM) is expected to reflect a collective physiological response to abiotic drivers (Westoby and Wright 2006). Second, environmental constraints can limit the range of trait values that are viable in a community. Third, the relative performance and abundance of coexisting organisms can increase when their trait values are closer to some optimum (trait convergence) (Kraft and Ackerly 2010), which should entail smaller weighted variance of trait values in the community (Community-Weighted Variance or CWV). Such variation in performance and abundance can represent a better adaptation to the physical environment or greater competitive ability (Navas and Violle 2009). Conversely, trait divergence (larger CWV) is expected under the influence of limiting similarity and niche differentiation (Kraft et al. 2008). At a large spatial scale, covariation in functional traits and environmental variables, such as climate, should reveal the imprint of macroecological filters (functional biogeography, Violle et al. 2014). Although analysing the distribution of trait values in communities reveals major drivers of their assembly, the approach is still in its infancy in microbial ecology (but see Courty et al. (2016) for fungi and Kruk et al. (2010) for phytoplankton). We applied the framework to address the imprint of niche-based processes on the functional diversity of desmid communities in Europe.

Apart from the influence of deterministic niche-based processes, historical events can determine species range limits and the structure of contemporary communities (Fukami 2015). Dispersal limitation can entail isolation-by-distance patterns of biodiversity, where distant communities differ in composition despite similar abiotic conditions (Nekola and White 1999). Such limitation can constrain re-colonisation from former glacial refugia and affect taxonomic and functional diversity patterns at large spatial scale (Normand et al. 2011; Klütsch et al. 2012; Ordonez and Svenning 2015). We used a network-based approach to investigate how patterns of desmid co-occurrences deviate from random at a large spatial scale (Carstensen and Olesen 2009; Carstensen et al. 2013a). Network-based analysis has been shown to be more successful in determining biogeographical regions than classically used hierarchical clustering (Bloomfield et al. 2017). This approach allows to classify both sites and taxa into groups-modules characterizing large-scale metacommunity structuring, such that the taxa of a module co-occur more often than expected by chance in the sites of the same module. "Excess" co-occurrence of taxa in modules can be the result of historical biogeography shaping geographically distinct species pools (Carstensen et al. 2013b), or of environmental filtering of taxa with distinct ecological strategies and functional trait values in distinct environmental contexts (functional species pools, de Bello et al. 2012). We assessed the variation in functional traits of taxa and environmental conditions of sites across modules to determine the respective influences of environmental filtering and historical biogeography on large-scale patterns of desmid biodiversity. Therefore, we devised a multiscale approach to decipher: (1) long-term and large-scale signatures of functional and historical biogeography in modules, and (2) niche-based assembly dynamics shaping the trait composition of local communities.

Using a multi-scale (from local to pan-European scale) and multi-tool (trait-based community assembly analysis, network-based analysis) approach, we thus asked: Is there functional variation within and among desmid communities reflecting the role of niche-based assembly processes? At large spatial scale, are these niche-based dynamics enough to explain co-occurrence patterns? If not, what is the relative contribution of niche-based processes, dispersal limitation and historical contingencies to species pool structuring? We hypothesized that desmids with lower surface-to-volume should be better adapted to stressful environments, while smaller desmids should be more competitive, yielding variation in average values of these traits along environmental gradients. Greater abiotic and biotic constraints should also entail a reduction of trait range and variance in communities. Furthermore, we expected distance decay of community similarity and a geographic structure of biogeographic modules reflecting limited dispersal abilities and historical legacies.

Materials and methods

Sampling of desmid communities

We sampled 148 desmid communities (Streptophyta, class Zygnematophyceae, order Desmidiales) distributed throughout Europe (latitudinal limits: 48.92-60.99 and longitudinal limits: - 9.95 to 15.90, see Table A3 in Online Resources). Desmid richness peaks in nutrient-poor and slightly acidic to neutral freshwater habitats; they are missing in limestone areas (Coesel and Meesters 2007). Desmids are typical species of phytobenthos in peat bogs (Brook 1981). Hence, we focused our sampling on peat-forming wetlands and a wide range of climatic, pH and conductivity conditions. Moreover, we selected the main areas where desmid communities were described in Europe (basically on Atlantic side, subarctic region, central European lowland and mountain peat bogs). We sampled the upper layer of the epipelon in 10×10 cm plots, immediately fixated the samples by formaldehyde, and subsequently examined under light microscope. We subsampled approximately 200 cells (from 100 to 328) per community, which we identified at the species level (374 species total). The resulting species \times site matrix included the relative abundance of each species *i*, i.e., the number of cells of species *i* divided by the number of cells in the subsample (dataset provided in Online Resources).

Environmental data

Conductivity and pH are known to be key abiotic drivers of desmid diversity (Coesel 1982; Neustupa et al. 2009). We measured both variables during sampling using a combined pH/conductivity meter WTW 340*i* (WTW, Germany) (for a table of environmental parameters, see Table A3, Online Resources).

Large-scale bioclimatic variation was characterized using the WorldClim database (Hijmans et al. 2005) (2.5 arc-min resolution). We reduced the dimensionality of bioclimatic data by performing a principal component analysis (see Online Resources, Fig A1). The main gradient expressed by the first principal component (PC1) explained 61.6% of the bioclimatic variability, and was positively correlated with precipitation, and negatively with annual range and seasonality of temperature, reflecting a gradient from continental to oceanic climate. PC2 explained 20.9% of the variation and was positively correlated with annual mean temperature and isothermality. We used PC1 and PC2 site scores, pH and conductivity values to compute Euclidean environmental distances among communities.

Desmid trait measurements

We estimated two key morphological traits of desmids: biovolume (volume of the cell) and surface-to-volume ratio (S/V). We used existing data set created by Neustupa et al. (2011) and followed their algorithm to complete information for all species. Desmids have elabourous cell shapes with incisions, lobes, and branchings, therefore it is necessary to adjust computed characteristics of general objects, which are commonly used in biovolume calculations of other photoautotrophs (Hillebrand et al. 1999). First, we calculated volume and surface of standard geometrical object characterizing species' general shape with dimensions obtained from the published literature (mean values for length, width, and thickness). Secondly, we measured frontal area and perimeter of species from microphotograph or where not available illustration from the published literature using the Fiji software (Schindelin et al. 2012). We used this projected area and perimeter to derive actual volume and surface of desmid cell following the protocol developed by Neustupa et al. (2011, 2013) (for details of computations see Online Resources). Desmids have few colonial, filament forming genera. In our samples, we identified 10 filamentous species. We estimated volume and surface for individual cells in filaments and calculated number of cells in filaments. Further in analyses, we treated them as individual cells. The traits were not directly measured in situ; therefore, they represent average volume and surface of the species and neglect intraspecific variability. Trait data were available for 352 species out of 374 and were missing only for some rare species (trait values available in Online Resources, Table A3).

Data analysis

Species turnover

We estimated the Sørensen index of taxonomic dissimilarity between communities (Sørensen 1948) (SorIndex hereafter). We analysed the changes in SorIndex with geographical and environmental distances using Mantel and partial Mantel tests (Legendre and Legendre 1998).

Metacommunity modules

A set of communities (a metacommunity) can be represented as a bipartite network (a.k.a. metacommunity network), in which species and sites are nodes, and the links are the occurrences of species in sites (Carstensen and Olesen 2009; Carstensen et al. 2012). Modularity analysis allows delineating species pools (or modules) based on the distribution of occurrences in this network (Carstensen et al. 2013a). The modules are sub-networks including: (1) species that tend to co-occur more often, and (2) related sites showing more similar composition. Each species and site are thus ascribed to a module so that the modules represent spatially delimited species pools (Carstensen et al. 2012). The modules are robust to sampling heterogeneity and richness variation because they are defined by reference to a null model conserving community richness and species frequencies.

We used the Louvain algorithm (Blondel et al. 2008) to perform a modularity analysis of the sampled desmids metacommunity, and only species with more than 2 occurrences were included. To assess the significance of the decomposition into modules, we calculated the null distribution of the Q statistics of modularity by permuting 999 times the species × site matrix using a swap algorithm (Gotelli and Entsminger 2001, 2003). In addition, we calculated two parameters representing the way each node was connected to the modules: the coefficient of participation (c) represents the frequency of links of a node to other modules compared to its own module, while the within-module degree (z) represents the relative number of links of the node to other nodes from the same module (Guimerà and Amaral 2005; Carstensen et al. 2012). In other words, sites and species with low c and high z values were more "typical" representatives of their module. Species with high c were ecologically more generalist and widespread, and sites with high c included a mix of taxa from different ecological and biogeographical contexts.

To check the robustness of the decomposition into modules, we also performed an alternative delineation based on 'assemblage dispersion field' (Lessard et al. 2012). This probabilistic approach considers that sites with more similar species composition are more likely to provide immigrants to a recipient community. The probability that a given site is included in a species pool is equal to the proportion of species it shares with the recipient community. For each community, we checked whether the source communities defined by dispersion field were more likely to be drawn from the same module as the recipient community. We used 'assemblage dispersion field' to define species pools in following analyses.

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Trait-based community assembly

We calculated trait mean, variance and range values for every community. Traits were log-transformed before computing these metrics. Trait range (max–min) was calculated for each community, without considering species abundances. Community-level trait Mean (CWM) and Variance (CWV) were weighted by the relative abundance of species occurring in the community (Enquist et al. 2015) as:

$$CWM = \sum_{i=1}^{S} A_i \times t_i \tag{1}$$

$$CWV = \sum_{i=1}^{S} A_i \times (t_i - CWM)^2$$
(2)

where t_i is the log-transformed trait value and A_i the relative abundance of species *i*, and *S* is the number of species in a given community.

We performed Kruskal–Wallis tests to compare the trait range, CWM and CWV values of sites among modules.

To test whether the metrics of trait variation (range and CWV) in local desmid communities significantly deviated from random community assembly, we carried out two types of null models (Bernard-Verdier et al. 2012; Taudiere and Violle 2015) For each community, the first null model (NM1) randomly assembled null communities from source communities defined by assemblage dispersion field, while keeping community richness unchanged (Lessard et al. 2012). Reduction in the trait range of local communities was expected under the influence of environmental filtering, compared to null values under NM1. The second null model (NM2) shuffled species abundances within communities. This model thus kept the range of trait values fixed, while changing the distribution of relative abundances in a community. Whenever some optimal trait values conferred greater performance and abundance (trait convergence), or greater abundance was only possible for more dissimilar trait values (limiting similarity yielding trait divergence), we expected a deviation of the community weighted variance (CWV) from null values under NM2 (Bernard-Verdier et al. 2012). Each null distribution was calculated based on 999 randomizations.

We calculated Standardized Effect Size (SES) (Gotelli and McCabe 2002) to quantify the deviation of an observed value from null values as:

$$SES = (I_{observed} - I_{null}) / SD_{null}$$
(3)

where $I_{observed}$ is the observed value of a trait-based statistic, I_{null} is the mean value of the statistic for null communities and SD_{null} is the corresponding standard deviation. Therefore, an observed value that did not differ from the null expectation had an SES value of 0. We performed a Wilcoxon signed ranked test to assess any deviation of SES values from zero (either positively or negatively).

Using the *plsreg1* function of the *Plsdepot* R package (Sanchez 2012), we performed Partial Least Square Regression (PLS) of the trait-based community statistics (CWM, SES of range, and SES CWV) according to the environmental variables. PLS derives from predictors a set of orthogonal latent variables which maximize the explained variance in the dependent variable (Carrascal et al. 2009). We used the full set of bioclimatic variables, conductivity, and pH as predictors. We standardized all predictors prior computation. We selected the number of latent variables for PLS based on cross-validation (Leave-one-out cross-validation). We chose the lowest number of latent variables with highest cumulative Q^2 (cross-validated R^2). For all models, this corresponded to two latent variables.

All the analyses were performed using R (ver. 3.0.3; R Development Core Team).

Results

Species turnover along geographical and environmental gradients

Rarefied richness to minimum sample size (N = 100) ranged between 1.87 and 42.2. It was positively correlated with latitude (Spearman $\rho = 0.55$, P < 0.001) and negatively with longitude (Spearman $\rho = -0.56$, P < 0.001). We detected significant species turnover related to both environmental (Mantel r = 0.20, P < 0.001) and geographical (Mantel r = 0.18, P < 0.001) distances. Partial Mantel test showed a significant distance-decay of community similarity apart from the influence of environmental distances (partial Mantel r = 0.19; P = 0.001).

Metacommunity modules

The metacommunity network was significantly modular (Q statistics of modularity = 0.29, P < 0.001). The first five main modules each included more than 8 communities, summing to 103 communities. The other smaller modules, together 11, included too few communities and were excluded from the detailed description. Based on the c-z metrics, Table A1 in Online Resources shows the most typical sites and species of the modules and their basic ecological requirements. The first five main modules showed distinct geographical (Figs. 1, 2a), environmental (Fig. 2b) and functional separation (Fig. 2c), for the distribution of all 11 modules (see Online Resources, Fig. A2). Modules 2 and 4 were similar in terms of local environment (higher pH and conductivity—Fig. 2b, Tukey's test

P > 0.05) (Tukey's test P = 0.0015), and functional composition (see Fig. 2c, for the distribution of all 11 modules, see Online Resources, Fig. A2). They displayed lower CWM volume (Tukey's test P > 0.05) and higher CWM S/V (Tukey's test P > 0.05, Fig. 2c), and the most typical species of these modules were described in the literature as indicators of the mesotrophic environment (Table A1; Online Resources). However, module 4 was mainly confined to extreme North, while module 2 was in mid-latitude (Figs. 1, 2a; comparison of distribution Tukey's test: latitudinal P = 0.015; longitudinal P = 0.068). This was reflected also in their climatic differences: modules 2 and 4 were similar in climatic PC1 (Tukey's test P = 0.6198) but differed in climatic PC2 (Tukey's test P = 0.0015; module 4 had a lower annual mean temperature. Modules 1 and 3 were similar in terms of local environment and functional composition, with lower pH (Fig. 2b), higher CWM volume and lower CWM S/V (Fig. 2c) compared to modules 2 and 4. They included species associated with oligotrophic habitats (Table A1; Online Resources). While their spatial distribution broadly overlapped, module 3 showed broader longitudinal amplitude (Fig. 1). Module 5 included communities with a broad range of pH values but with restricted geographical distribution to Central Europe and narrow climatic range. This module was also functionally distinct with large CWM of volume. See Online Resources Table A2 for complete results of pairwise comparisons between modules, and Fig A3, PCA analysis of environmental variables showing the environmental envelops of modules.

We tested whether the most probable source communities defined in assembly dispersion fields (ADF) belonged or not to the same module as the recipient site. We found that the average probability of communities forming ADF pools was significantly higher for communities of the same module of the recipient community than for communities of other modules (Wilcoxon signed rank test: P < 0.001). Therefore, the delineation of network-based modules and of ADF pools proved consistent.

Independently of the environmental variation within modules, we found significant distance decay of species composition within each of the four first modules (modules 1–4 Mantel P < 0.05, module 5 P > 0.05).

Trait-based assembly processes

The partial least square regressions (PLS) allowed identifying two latent predictors underlying the most of the variation in community-level trait metrics. The first latent variable was generally related to a climatic gradient from oceanic to continental climate, correlated negatively with bioclimatic variables characterizing temperature; except mean annual temperature (bio2, bio5, bio8) and temperature seasonality (bio7, bio4) and positively with variables related to rainfall amounts (bio12, bio13, bio14, bio16, bio17, bio18, bio19). The second latent variable of PLS was conversely related to mean annual temperature and to precipitation seasonality.

 $R^2 = 2.94\%$, surface-to-volume: 1. PLS axis $R^2 = 19.34$, 2. axis $R^2 = 3.45$), although being steadily negative.

CWM values of cell volume and surface-to-volume varied with climate and to some extent with conductivity. Larger species were found at higher conductivity and in oceanic climate sites with higher annual mean temperature (Fig. 3). Conversely, surface-to-volume ratio did not vary along the continental-oceanic climatic gradient but was negatively correlated to the axis related to mean annual temperature. We did not find any influence of pH on CWM for the two studied traits. We generally detected a significantly smaller range of trait values in local communities, based on null model NM1 (Wilcoxon test P < 0.001). While the standard effect size (SES) of range for surface-to-volume ratio significantly deviated from a random situation for only one community, up to 32% of the communities deviated from random for the SES of the range of cell volume (SES higher than 1.96 or lower than -1.96). The SES of trait range increased along the first axis of PLS from oceanic to continental climate (Fig. 3, volume: 1. PLS axis $R^2 = 8.71$, 2. axis

Based on null model *NM2*, CWV values were generally lower than expected by chance (Wilcoxon test towards lower values P < 0.001; for volume and surface-to-volume), while only four communities had significantly higher (SES > 1.96) variance of cell volume than expected by chance and only two for the surface-to-volume ratio. The SES of CWV also responded to environmental variation, namely, CWV for volume—more convergent communities (lower SES) occurred in oceanic climates (Fig. 3). SES of CWV for surface-tovolume ratio was explained by PLS only marginally, two latent predictors explained only 3.13% of the variance.

Discussion

Disentangling the influence of community assembly dynamics at multiple spatial and temporal scales is a long-standing goal of macroecology and biogeography. The relative importance of biogeography, environmental filtering and dispersal



Fig. 1 Geographical distribution of five main modules. Triangles are representing communities typical for modules, based on their c-z coefficients (c value below the third quartile and z value above the first quartile). Polygons represent minimal convex hulls enclosing modules

Fig. 2 Variation among five main modules of **a** the latitudinal and longitudinal position of the sites of the module; b their local environmental characteristics and **c** of community weighted means (CWM) for volume and surface-to-volume ratio. Values for traits were logtransformed prior analysis. The box indicates the inter-quartile range, the line in the box indicates median, whiskers spread to $1.5 \times$ inner-quartile range and circles represent outliers. Statistics for Kruskal-Wallis test (KW) and groups of pairwise comparison based on Tukey's test are indicated. N = 103





Fig. 3 Correlation circles of Partial Least Square Regression analysis of community-level trait metrics. First two latent variables (axis) are shown. Axes are oriented that, the first one corresponds to the most dominant climatic gradient ranging from continental [high temperature seasonality (4) and temperature annual range (7)] to oceanic climate [high annual precipitation (12)]. The second axis was correlated with mean annual temperature (1) and precipitation seasonality (15). Predicted variables are marked Y. N = 148. Codes for explanatory variables as follows: cond—conductivity, bioclimatic variables (from WorldClim database) are colour coded those linked with Temperature (Precip.) are italicized and blue. Variables linked with Temperature

limitation in microorganisms has been long debated (Baas Becking 1934; Finlay 2002; Green and Bohannan 2006; Martiny et al. 2006; Hanson et al. 2012). Here we used an original combination of network-based and trait-based approaches to tease apart the influences of niche-based assembly dynamics and historical biogeography on desmid diversity in Europe. We found that: (1) morphological functional traits of desmids vary according to environmental conditions across communities at broad scale, (2) species pools identified from the network-based analysis show specific environmental, functional and geographical structuring apart from the broad-scale trait-environment relationships, (3) there is a distance decay of similarity in community composition apart from the influence of species

(Temp.) are red: 1 Annual Mean Temperature, 2 Mean Diurnal Temp. Range, 3 Isothermality, 4 Temperature Seasonality, 5 Max. Temp. of the Warmest Month, 6 Min. Temp. of the Coldest Month, 7 Temperature Annual Range, 8 Mean Temp. of the Wettest Quarter, 9 Mean Temp. of the Driest Quarter, 10 Mean Temp. of the Warmest Quarter, 11 Mean Temp. of the Coldest Quarter, 12 Annual Precip., 13 Precip. of the Wettest Month, 14 Precip. of the Driest Month, 15 Precip. Seasonality, 16 Precip. of the Wettest Quarter, 17 Precip. of the Driest Quarter, 18 Precip. of the Warmest Quarter, 19 Precip. of the Coldest Quarter

pools and environmental variation, and (4) the range and variance of trait values in communities reflect influences of environmental filtering and competition during community assembly. These results thus suggest the joint influence of environmental filtering, dispersal limitation and large-scale biogeographical history in the functional and taxonomic diversity of desmids.

Broad-scale trait-environment relationships

Under the original hypothesis proposed by Baas Becking (1934), weak dispersal limitation entails that "everything is everywhere, but, the environment selects". In this perspective, environmental gradients should determine species

turnover and variation in functional community composition at a broad scale (Violle et al. 2014). We found changes in community-level mean values (CWM) of the desmids' volume and surface-to-volume depending on environmental conditions: cells were larger under a continental climate, as well as in habitats characterized by higher conductivity (Fig. 3). Kruk et al. (2016) similarly showed that phytoplankton cell size decreases towards warmer tropical regions. However, in our study, the strength of these traitenvironment relationships was quite weak (PLS volume: $r^2 = 0.122$ and surface-to-volume: $r^2 = 0.098$), indicating that other biogeographical and ecological processes should determine the variation of community composition.

Biogeographical and environmental segregation of species pools

The analysis of modularity structure revealed strong geographical, environmental and functional structuring among groups (modules) of desmid communities. The five primary modules represented distinct environmental contexts and sets of functional traits, revealing functional species pools (de Bello et al. 2012), but with further spatial segregation of modules covering similar environments, revealing biogeographic species pools (Carstensen et al. 2013b).

The most important natural divisions in peat lands are reflected in pH (Wheeler and Proctor 2000), with a significant contribution of conductivity (Hájek et al. 2006). It is in accordance with the distribution of modules, which largely differed in pH values and to some extent conductivity. Patterns of desmid taxonomic diversity and co-occurrence in modules thus reflected environmental filtering. This filtering was further demonstrated in trait distribution within modules. Specifically, we found communities with higher CWM of volume and small CWM of surface-to-volume in modules characterized by low pH. Previous research already showed that biovolume of desmid communities in Central Europe responded to pH (Neustupa et al. 2013). In acidic conditions, maintaining neutral cytosolic pH is highly demanding (Gerloff-Elias et al. 2005). Consistent with physiological expectations, desmids show lower surface-to-volume in more acidic conditions, which can limit the influx of H⁺ ions (Černá and Neustupa 2009). Therefore, low pH condition may select for species with low surface-to-volume (Černá and Neustupa 2009).

In addition, geographical segregation of modules 1/3 and 2/4 in similar environmental contexts is consistent with an influence of historical biogeography. Geographical separation of modules can be related to previously described biogeographic groups of desmids (atlantic-subarctic, circumpolar, and continental) (Heimans 1969; Coesel 1996; Coesel and Krienitz 2008). Our results support segregation of regional

species pools within Europe apart from environmental differences, which could have emerged as a result of historical legacies. They could be caused by Pleistocene glaciation and lack of suitable conditions for desmids at glacial times over most of Europe. Glacial refugia may have existed on the Atlantic side of Europe, where we found the higher overall richness of desmid communities. The presence of relict habitats and refugia in Western Europe would have allowed subsequent recolonization from West. The presence of refugia has already been suggested in south-western Ireland for desmids (Jurdíková et al. 2014) as well as for land plants (Sinclair et al. 1998) and macroalgae (Provan et al. 2005). Desmids are closely associated with Sphagnum habitats (Brook 1981) for which Szövényi et al. (2007) evidenced refugia along the Atlantic coast of Europe. Current highlatitude distribution of module 4 could also be considered a relict of former widespread distribution of arctic-alpine taxa. Moreover, the module 5 geographically restricted within a wide range of environmental condition supports the hypothesis about different origins of desmid species pools. The role of Pleistocene glaciation creating refugia, with recolonization afterward, and relict distribution of former widespread taxa, is well acknowledged in terrestrial organisms (Normand et al. 2011), but this is less known in aquatic ecosystems (but see Brochmann et al. 2003). Interpreting higher Western species richness as a testimony of former refugia is still under debate. Environmental conditions over the Atlantic side are overall suitable for desmids due to the mild climate, little anthropogenic disturbance, a wide range of habitats and their high connectivity (John and Williamson 2009). Therefore, current biodiversity patterns and variation of richness could reflect a variation in habitat quality (e.g., related to disturbance regimes), this possible influence should be explored in the future.

Role of dispersal limitation

Within modules, partial Mantel tests evidenced a distance decay of community similarity that was not explainable by environmental variation. In a hierarchical conception of ecological processes, such residual pattern of isolationby-distance can reflect the influence of dispersal limitation (Freestone and Inouye 2006). Assessing dispersal limitation is not trivial given the dispersal ability of microbial species (Martiny et al. 2006), but the patchy nature of desmid habitats is likely to limit the exchanges among communities at large scale. The hierarchy of spatial structure among and within modules could then reflect a multiscale influence of dispersal limitation on metacommunity dynamics (Huth et al. 2015), from long-term migration limitation in former refugia, expressed by spatial patterns of module distribution, to more recent effect of dispersal limitation within pools.

Niche-based assembly processes constrain local functional composition

The variation of functional traits within the community is expected to reflect the influence of niche-based community assembly processes, such as environmental filtering and niche differentiation (Ackerly and Cornwell 2007; Kraft et al. 2008). The constraints exerted by assembly processes can be assessed through the Standard Effect Size (SES) of trait range and trait variance in communities, quantifying the deviation from a null model without such constraints (Bernard-Verdier et al. 2012). SES of trait range and SES of CWV were lower than expected by null models, indicating overall trait range reduction and functional convergence in communities, the degree of which varied with climate (Fig. 3).

We found trait range reduction for both volume and surface-to-volume ratio at community-level under continental climate. Trait range reduction is a signature of habitat filtering that excludes individuals with phenotypes not able to thrive under certain conditions (Enquist et al. 2015). Our results support the idea that more continental and low precipitation climate represents severe environmental conditions ('stronger filtering') for desmid establishment and persistence. It echoes previous research, showing that low temperatures create constraints on desmid growth. Epipelic algae occurrence has already been shown to be correlated with temperature (Špačková et al. 2009), and desmids show nearly no growth at temperatures below 15 °C (Coesel and Wardenaar 1990). Under continental climate, growing season is shorter and local abundances are reduced by winter freezing. However, Svoboda et al. (2013) showed that such freezing has no effect on species composition of desmid communities. Reduced trait ranges and shift in CWM could illustrate the ability of large cells with smaller surface-tovolume to better survive and thrive under highly seasonal climate with low precipitation.

Conversely, we found smaller CWV (functional convergence) of biovolume in high precipitation and low seasonality climate. Opposite trends for trait range and variance of biovolume along the climate gradient is consistent with distinctive abiotic and biotic drivers along the gradient. The more stressful environment can entail filtering and trait range reduction at one extreme of the gradient, while more favourable environment can be related to more competitive interactions at the other extreme. Relatively stable and humid climate can, therefore, represent favourable, highly competitive climate, without strong influences of environmental filtering. We found smaller cells in those 'milder' environments. Smaller cells have generally higher surface-to-volume, high nutrient uptake efficiencies and higher growth (Nielsen et al. 1996; Passy 2007). Consequently, larger cells would survive better but display lower growth rates (Reynolds 1987).

Functional convergence, more pronounced under maritime climate, could thus be explained by the exclusion of species having large cell sizes, and slower growth, which appears to be disadvantaged in highly competitive environments. In this perspective, functional convergence can be due to the competitive dominance of certain phenotypes (Chesson 2000; Mayfield and Levine 2010), while trait range reduction can simultaneously represent an influence of abiotic constraints (see also Bernard-Verdier et al. 2012 for similar findings in plant communities). In the other perspective, decreased trait variance could also reflect functional redundancy in more stable environments, as it was shown for phytoplankton in tropical lakes (Kruk et al. 2016). These findings emphasize the entangled influence of niche-based processes on the assembly of desmid communities.

Limitations and perspectives

The studied morphological traits varied along environmental gradients and showed non-random distribution. As hypothesized, biovolume and surface-to-volume could be related to varying physiological responses and community assembly of desmids depending on local environmental conditions. Simple morphological traits are thus likely to provide relevant proxies for the ability of desmids to survive and coexist in response to abiotic and biotic drivers. Cell volume-environment gradient in desmid communities was reported so far at smaller scales (Neustupa et al. 2013) and we here highlighted its ecological meaning over broadscale environmental variation. Although there is apparent determinism of environment on community-level trait distribution, the explanatory power of environmental variables remained low using PLS models. Unexplained variability could be connected to some other unmeasured environmental characteristics, e.g. nutrient availability, the limnological status of locality, and to dispersal and migration limitation (Ordonez and Svenning 2015), stochasticity (Segura et al. 2010) or biotic interactions with other organismal groups (Kruk et al. 2016).

Interestingly, pH did not explain variation in communitylevel trait values (CWM), even though it clearly separated modules 1–5 with different CWM of surface-to-volume values. Communities outside modules 1–5 probably represent a more heterogenous concept, therefore they bring stochasticity, blur the results, and enhance the role of climatic variables. Furthermore, volume and surface-to-volume probably do not capture all ecological strategies of species. Additional functional traits should also be considered to represent other aspects of desmid ecology susceptible to influence their survival, reproduction, and dispersal. For instance, physiological properties could provide complementary information. It was already shown that two desmid species with similar size and surface-area can have different affinities for phosphorus uptake (Spijkerman and Coesel 1996). Creating a global database of microbial (algal) traits is necessary for more detailed studies of microbial functional ecology (Litchman and Klausmeier 2008). Such databases have recently emerged (see Edwards et al. 2015; Klais et al. 2017), however, there is need to broaden their focus for microbes outside phytoplankton.

A single-cell trait-based approach can be very useful in future microbial ecological studies (especially in protists with large body sizes and therefore more reliable and straightforward trait estimation). In addition, the role of intraspecific trait variation in community assembly is now largely recognized in macroorganisms (de Bello et al. 2011; Violle et al. 2012). In desmids, Černá and Neustupa (2009) experimentally confirmed that species can to some extent modify their shape in response to changing pH. Neustupa et al. (2008) also showed changing shape with temperature, although changes were smaller than interspecific shape variations. Accounting for intraspecific variation and direct measuring of biovolume could increase the explanatory power of trait-gradient analyses (Siefert et al. 2015). Our study assumed that interspecific were larger than intraspecific differences, a hypothesis that we suggest testing in future studies [see Kazakou et al. (2014) for a test in plants].

Overall, the combined application of network theory and trait-based community analysis to the distribution of desmid communities provides unique insights into the patterns and drivers of desmid diversity at multiple scales. In turn, it can be considered as a fruitful study case for the relevance of this approach to community ecology and biogeography. Importantly, the application of network theory to different taxonomic groups would be a valuable approach to functional biogeography that aims at integrating multitrophic and multifaceted biodiversity (Violle et al. 2014).

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Author contribution statement

CV and HB originally formulated the idea. CV and FM developed the methodology. HB and PS conducted fieldwork and data sampling. HB, CV, FM performed analyses, and HB, CV, FM, PŠ wrote the manuscript.

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