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Changes in the structural and functional diversity of macrophyte communities along an acidity gradient in softwater lakes

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ABSTRACT

We present a new approach to the diversity of macrophyte communities based on species richness (S), Simpson's diversity index (SD), Rao's functional diversity (FD), functional attribute diversity (FAD) and the share of life history traits along a gradient of acidity in softwater lakes. On the basis of 10,800 cover-plant samples (squares with an area of 0.1 m^2) collected from 241 sections of the bottom (depth belts) of 38 lakes, four communities were identified using the TWINSPAN algorithm: moss carpet (median water pH 4.7), isoetids with acidophytic mosses (pH 5.5), isoetids with neutrophytic mosses (pH 6.3) and neutrophytic vascular plants with charophytes (pH 7.1). Along a gradient of increasing pH, the diversity of communities increases and the species composition and share of life history traits are subject to significant changes. Evergreen, plagiotropic and unanchored plants with small, thin leaves (mosses) are replaced by evergreen, rosette forms (isoetids), which are replaced by non-evergreen charophytes and broadleaf vascular plants, especially pondweeds, in addition to an increasing fraction of plants with generative reproduction. A strong relationship was found between plant traits (leaves and shoots) and environmental factors (pH and calcium content). The regulator of diversity in macrophyte communities is the calcium concentration in water.

1. Introduction

Species composition at a given site is determined by environmental, biological and historical factors and is thus a complex ecological problem to evaluate. A community contains the individuals of species that potentially interact within a single patch or local area of a habitat (Leibold et al., 2004). One of the challenges in the study of communities is disentangling the principal environmental factors that regulate the distribution and abundance of species (Chase, 2003) and influence the diversity of communities (Chmara et al., 2013). New research tools, especially statistical approaches, allow in-depth analyses of the community structure and diversity as well as their relationships with environmental factors. In water bodies, such analyses are frequently performed along the environmental gradients, e.g., along the direction of increasing depth, lighting (Chambers, 1987; Duarte and Kalff, 1990; Madsen and Sand-Jensen 1994), alkalinity or trophic state (Arts et al., 1990; Rørslett, 1991; Srivastava et al., 1995; Vestergaard and Sand-Jensen, 2000).

We focused on softwater lakes that are abundant in the northern part of the Northern Hemisphere and are acidic, poor in calcium and nutrients, and represent an important component of the freshwater biodiversity (Murphy, 2002). The vegetation of such lakes consists of species that tolerate only part of a wide range of water pH values, from very acidic peatland lakes with acidophytic mosses (Banaś et al., 2012), through slightly acidic with isoetids (Szmeja, 1987a,b; Riis and Sand-Jensen, 1998; Szmeja and Bazydło, 2005) to neutral waters with different species, including some stoneworts (Vestergaard and Sand-Jensen, 2000). An important group of plant species in these lakes are isoetids, such as *Lobelia dortmanna*, *Littorella uniflora* and *Isoëtes* spp. They are evergreen perennials with the lowest growth and mortality rates among aquatic species (Nielsen and Sand-Jensen, 1991). While these traits are essential adaptations to clear-water lakes that are low in inorganic carbon and nutrients, they make the vegetation susceptible to alkalinization, acidification, eutrophication and excessively low light intensity resulting from human impact (Arts, 2002). Isoetids have small leaves in a rosette with well-developed roots on a short stem and extensive air channels allowing for efficient intra-plant transport of O_2 and CO_2 between the roots and leaves (Pedersen et al., 1995; Pulido et al., 2011). Plant communities in softwater lakes are also created by acidophytic mosses, such as *Sphagnum denticulatum* (Gacia et. al., 1994; Szmeja, 2010; Riis and Sand-Jensen, 1997)

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Table 1
Selected characteristics of 38 studied lakes.

Trait	Mean ± s.d.	Range
Area (ha)	23.6 ± 33.1	1.5–154.0
Max. depth (m)	11.3 ± 6.9	5.0–33.2
Secchi depth (m)	4.3 ± 1.4	1.5–9.0
pH	5.8 ± 1.0	4.1–7.9
Water conductivity ($\mu S\,cm^{-1}$)	48.7 ± 18.1	13.1–95.4
Calcium ($mg\,l^{-1}$)	5.4 ± 4.0	1.0–18.6
Tot-*N* ($mg\,l^{-1}$)	1.3 ± 0.2	0.6–3.5
Tot-*P* ($mg\,l^{-1}$)	0.09 ± 0.02	0.003–0.9

and *Warnstorfia exannulata* (Ilyashuk, 2002; Szmeja et al., 2010) deriving from peatland lakes (Banaś et al., 2012), as well as some stoneworts from semi- hardwater lakes (Pukacz et al., 2013). Thus, to better understand and predict the impact of acidity and depth on macrophyte communities, we combined a structural and functional approach. Using functional trait composition to account for the diversity of macrophyte communities reveals a much broader aspect of diversity and better explains ecosystem functioning than does species richness (Díaz et al., 2007; Hu et al., 2014).

Finally, if acidity changes the structural and functional composition of communities, we can test whether this gradient affects the diversity of macrophyte communities in softwater lakes. Previous studies found that macrophyte diversity changes with varying environmental conditions, such as biogenic resources, depth, light intensity or climate. Recent studies report that functional traits composition predicts macrophyte communities along a water depth gradient in lakes (Fu et al., 2014).

We hypothesize that the diversity of communities changes along a gradient of acidity and is modified by depth as a factor that is associated with light intensity. We expect that along the environmental gradient there is an exchange of species and life history traits between the communities, and there is an increasing functional diversity of communities due to the larger number of species growth forms. We also expect directional shifts in communities along the acidity gradient.

2. Material and methods

2.1. Study area and sampling

The studies were conducted in 38 lakes that were clearly free from any signs of human pressure and are situated along the southern coast of the Baltic Sea in NW Poland (Supplementary Table 1). They are small; acidic or neutral; poor in calcium, nitrogen and phosphorus (Table 1); and typologically belong to the shallow softwater lakes. These include: (1) peatland lakes, which are very acidic (median water pH 4.7) and poor in calcium (1.0–3.0 $mg\,Ca\,l^{-1}$; (2) less acidic (pH 5.5) and calcium- deficient (1.3–5.2 $mg\,Ca\,l^{-1}$); and (3) slightly acidic (pH 6.3), moderately calcium-rich (2.4–15.3 $mg\,Ca\,l^{-1}$) and (4) neutral lakes (pH 7.1) with relatively high concentrations of calcium (4.0–18.6 $mg\,Ca\,l^{-1}$).

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We collected 10,800 cover-plant samples (squares with sides = 0.33 m, area = 0.1 m^2), including 1200 samples from very acidic lakes (median water pH 4.7), 3430 samples from less acidic (pH 5.5), 4366 samples from slightly acidic (pH 6.3) and 1804 samples from neutral waters (pH 7.1). Samples were taken at random from 241 sections of the bottom (depth zones at 1.0 m), each of which had a length of 250 m (Supplementary Fig. 1). The bottom sections were parallel to the lake shore. The number of cover-plant samples in the lake depended on the maximum depth of macrophyte occurrence and the number of depth zones. The samples were collected by SCUBA diving. The material was collected during the vegetation seasons (in June and August) from 2010 to 2013. Moreover, 241 water samples were collected in the depth zones, each of which was 500 ml. The water pH, conductivity ($\mu S\,cm^{-1}$), Secchi depth (m), calcium content ($mg\,l^{-1}$), Tot-N ($mg\,l^{-1}$) and Tot-P ($mg\,l^{-1}$) were determined. The measurements were performed using the methods suggested by Wetzel (2001) and Eaton et al. (2005). The statistical significance of the differences between measures of water quality was calculated with Tukey's post-hoc test (Sokal and Rohlf, 1995). For the post-hoc test we used 241 transect data nested in 38 lakes.

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2.2. Classification of the macrophyte communities and data analysis

Samples were grouped into similar communities by means of TWINSPAN analysis (Hill and Šmilauer, 2005). The classification of the macrophyte communities was undertaken using six pseudo-species cut-levels (0, 2, 5, 15, 30 and 50% cover of species). Plant names follow The Plant List (2013).

To detect changes in trait composition in the macrophyte communities, we organized the data into a single number of species × trait attributes matrix, based on the 241 transect nested in 38 lakes. We submitted the matrix to a principal component analysis (PCA) based on the correlation matrix of variables. We ran separate PCAs for leaf traits (leaf distribution, leaf area, leaf type), reproduction and clonality and shoot traits. Principal Component Analysis were performed using CANOCO, version 4.5 (ter Braak, 2008). The correlations between the eigenvector scores of the macrophyte traits on the PCA axes and acidity gradient were tested with the Spearman rank correlation coefficient.

2.3. Diversity and trait metrics

For each community, the following indices were calculated:

(i) Species richness (S),
(ii) Simpson index of diversity (SD),

$$SD = 1 - \sum_{i=1}^{S} p_i^2$$

where p_i is the proportion of the *i*th species, i.e., $p_i = N_i/N$ and $N = \Sigma N_i$. Originally, N_i was used as the number of individuals of the *i*th species. We used species relative abundance.

(iii) Functional diversity (FD),
(iv) Functional attribute diversity (FAD).

We chose easily measurable traits ("soft" traits) that are considered to be reasonable surrogates for more functional, but difficult to measure ("hard"), traits (McIntyre et al., 1999). The calculations of FD and FAD take into account 7 macrophyte life history traits: (1) plant life span, (2) shoot growth form, (3) leaf type, (4) leaf area, (5) leaf distribution along the stem, (6) reproduction, and (7) clonality with according to Willby et al. (2000) and Kleyer et al. (2008) and the LEDA-Traitbase (www.leda-traitbase.org). The subdivision of these traits produced a total of 28 attributes (Table 2). The FD index was calculated according to Rao's formula (Ricotta, 2005; Lepš et al., 2006):

$$FD = \sum_{i=1}^{S} i \sum_{j=1}^{S} id_{ij} p_i p_j$$