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Mollusc and plant assemblages controlled by different ecological gradients at Eastern European fens

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ABSTRACT

Ecological patterns of mollusc assemblages and vegetation in relation to water chemistry, water regime, nutrient availability and climate were studied in eastern Polish lowland fens. Our goal was to examine if major compositional changes differ for molluscs and vegetation under the joint influence of multiple ecological gradients. Altogether 32 fen sites were investigated in 2010–2011, and analyzed using metric multidimensional scaling, cluster analysis and generalized additive models. Two major gradients driving the differences in mollusc species composition were revealed. The main direction of compositional changes was associated with the water table gradient, governing a species turnover from inundated and strongly water-logged sites occupied mostly by aquatic mollusc species, to moderately wet sites with the predominance of fen and meadow species. The second most important gradient for molluscs was that of mineral richness. For vegetation, three major gradients explained the changes in species composition. The highest importance was assigned to the nitrogen-to-phosphorus availability gradient (defined as a shift from N-limited to P-limited vegetation), followed by the water table gradient, and the mineral richness gradient. Our results demonstrate that the impact of mineral richness gradient, which has been often reported as the major determinant of compositional changes of fen molluscs and vegetation, can be exceeded by other ecological gradients of comparable variation. We also document for the first time that the main species turnover of fen vegetation is not accompanied by the analogous change in species composition of mollusc assemblages, due to a different sensitivity of these taxa to particular environmental factors (i.e. water level dynamics and type of nutrient limitation).

1. Introduction

Disentangling the relationships between environmental conditions and compositional changes of mire communities has long been an important objective of studies in ecology and conservation of mire habitats (e.g. Malmer, 1986; Wheeler and Proctor, 2000; Økland et al. 2001; Hájek et al. 2006; Horsák and Cernohorsky, 2008). A substantial number of ecological gradients have been described, among which three seem to have the broadest experimental support: the mineral richness gradient, the fertility gradient and the water table gradient. The mineral richness gradient encompasses the changes in biotic and abiotic conditions from poor fens dominated by *Sphagnum* species to calcareous tufa-forming fens dominated by brown-moss vegetation (Hájek et al., 2006). In many different regions this gradient has been proved to have a crucial importance for the compositional variation of vascular plants and bryophytes (e.g. Waughman, 1980; Malmer, 1986; Hájek et al., 2002; Nekola, 2004). As a second, the fertility gradient is related to the availability of limiting nutrients, primarily phosphorus and nitrogen, and it is mostly independent of the gradient of mineral richness (Bridgham et al., 1996; Wheeler and Proctor, 2000; Rozbrojová and Hájek, 2008). The fertility gradient operates at the rich end of the mineral richness gradient (Hájek et al., 2006), and when focusing on low-productive brown-moss rich fens only, Pawlikowski et al. (2013) recently suggested

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replacing this gradient with the nitrogen-to-phosphorus availability gradient, defined in terms of the biomass N:P ratio. The third, water table gradient reflects the position of fen surface relative to water level and governs the floristic variation both among and within the fen sites (Bragazza and Gerdol, 1996; Nekola, 2004; Jabłońska et al., 2011). However, evaluating the relative importance of ecological gradients strongly depends on scale of the study (Hájková et al., 2004; Nekola, 2004) and also regional characteristics of fen ecosystems in relation to their evolution (Hájek et al., 2006; Hájková et al., 2006).

As already outlined, most studies dealing with the ecological gradients in fens have focused on plant communities. However, in recent years, other groups of organisms have received attention as well. The importance of the mineral richness gradient has been well established, based on the results obtained for the algal, testacean, mollusc, clitellate and dipteran assemblages (Horsák and Hájek, 2003; Opravilová and Hájek, 2006; Fránková et al., 2009; Bojková et al., 2011; Omelková et al., 2013). The existence of the fertility gradient was recorded for molluscs and testate amoebae, which probably relates to the fact that these two groups have been extensively studied in fens (e.g. Mitchell, 2004; Hájek et al., 2006). Large number of researches also pointed out the role of the water table depth for testate amoebae (e.g. Charman and Warner, 1992; Mitchell et al., 2008). For molluscs only fine-scale changes in species composition along transects from the moistest part of spring fen to dry grassland surrounding the fen have been documented (Hettenbergerová et al., 2013). The large-scale importance of the water table gradient has not been evaluated for molluscs so far.

In this study we compare the ecology of mollusc assemblages and vegetation of the low-productive eastern Polish fens. In previous studies from other regions, molluscs and vegetation were found to have analogous responses to mineral richness, though being trophically independent on the species level (Horsák and Hájek, 2003; Horsák et al., 2011a). In these studies the variation in calcium richness was usually higher than in other environmental predictors, and the mineral richness gradient therefore accounted for the major compositional changes in both mollusc assemblages and vegetation. As for the water table gradient, we can expect a tight response of mollusc assemblages, as only a few wetland land snails are able to climb up the plant stems and dwell there during the periods of increased water levels (Boycott, 1934). On the contrary, vegetation composition should be less affected by small changes in water level than mollusc species composition. Many wetland plant species are able to withstand the short-term shallow flooding (Casanova and Brock, 2000), whereas most land snail species are strongly affected by only few centimeters of above-ground water. As our study sites vary substantially in water regime, from seasonally inundated to moderately wet fens, we tested the hypothesis that the major compositional gradients differ for molluscs and vegetation. Primarily, we focus on the patterns in mollusc assemblages, as the ecology of fen mollusc fauna has never been extensively studied in lowland Polish fens.

2. Materials and methods

2.1. Study area and study sites

The study was carried out at 32 fen sites of the eastern Poland situated between 50°29′–54°22′N and 20°22′–23°36′E (Fig. 1). Large proportion of Polish fens has been seriously damaged by human activities, such as drainage, agriculture, forestry, infrastructure development and peat extraction. At present, fens occur frequently in northern and eastern parts of the country, whereas in central and southern Poland only few fen remnants have been preserved (Wołejko et al., 2012). Thus, the distribution of our study sites is spatially aggregated, following the current distribution of preserved fen areas (Fig. 1). The study area falls within the nemoral and boreo-nemoral zones and its climate is distinctly continental, with the mean annual temperatures varying between 5.8 and 7.9 °C and the mean annual precipitations between 515 and 639 mm.

Both the landscape relief and bedrock geology of Poland were predominantly formed by the Pleistocene glaciations. Northern and north-western Poland represents a young post-glacial landscape, characteristic with moraines, outwash plains, meltwater valleys, glacial lakes and wetland complexes. Most of the area is covered by glacial deposits, such as gravel, sand and clay. In central and central-eastern Poland glacial landforms are older and have been extensively denudated. Toward the south-eastern and southern Poland, older bedrock layers, often rich in calcium, are exposed to the surface (Kondracki, 2002). Groundwater seeping to the surface through the calcareous bedrock or young glacial deposits gives the origin to mineral rich fen types with basiphilous plant communities (Wołejko et al., 2012).

Our sample sites covered the entire mineral richness gradient in fens, from mineral poor fens dominated by *Sphagnum* spp. to calcareous fens with tufa precipitation (see Hájek et al., 2006). Along the water table gradient, seasonally inundated, occasionally inundated, strongly waterlogged, wet and moderately wet fen sites were represented, as indicated in the field according to the vegetation composition (i.e. presence of the aquatic or meadow plant species). The range of the water table gradient was broader than in previous studies of fen mollusc assemblages across Europe (Horsák and Hájek, 2003; Horsák et al., 2011a), but always complying with the definition of "fens" sensu Hájek et al. (2006).

2.2. Field sampling and explanatory variables

The 32 sites were surveyed during July 2010 (pilot sampling of 4 sites) and June 2011 (sampling of 28 sites). To record mollusc assemblages, a sampling plot of 4 × 4 m^2 was defined in the central part of each site, from which one sample of 12-L volume was collected, comprising the upper soil layer, litter, bryophytes and herbaceous vegetation. This sample volume was proved to sufficiently estimate the whole site's species pool (Cernohorsky et al., 2010). Shells were extracted from samples using the wet sieving technique in the field (Horsák, 2003), to remove coarse plant matter and fine soil particles. After drying, shells were separated from the remaining material under a dissecting stereo microscope, identified and counted, including live individuals and empty shells with entire periostracum. Species nomenclature follows Horsák et al. (2013).

Species composition of vascular plants, bryophytes and macroalgae (*Chara vulgaris*) was recorded in the same 4 × 4 m^2 plots. The occurrence and cover of plant species were recorded on the nine-grade Braun–Blanquet scale for both vascular plants and bryophytes (Van der Maarel, 1979). Vascular plant identifications were mostly conducted in the field, whereas the bryophyte identifications were verified under a microscope in the laboratory. Species nomenclature follows Flora Europaea database (2013) for vascular plants and Hill et al. (2006) for bryophytes.

Geographic coordinates and altitude were measured with GPS device in the field (using a WGS84 system, GARMIN GPSmap 60C/CS, with the accuracy <15 m). Water conductivity and water pH were measured at microsites best supplied by water in the central parts of each sampling plot, using Greisinger GMH 3410 Conductivity meter and Greisinger GPRT 1400 AN pH-meter (Greisinger Electronic GmbH, Regenstauf, Germany). Water conductivity strongly positively correlates with the amount of calcium and magnesium ions in fens (Sjörs and Gunnarsson, 2002; Hájek et al.,