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Functional diversity, succession, and human-mediated disturbances in raised bog vegetation

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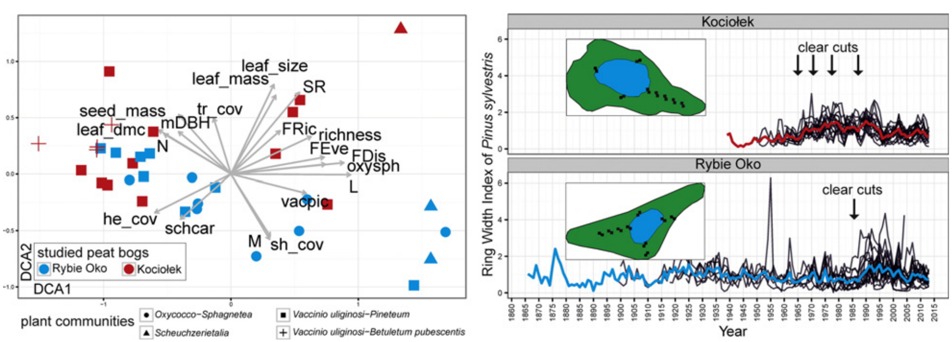
HIGHLIGHTS

- We assessed impact of neighbourhood clear cuts on raised bog vegetation.
- We expected its influence on vegetation patterns and functional diversity.
- We analyzed vegetation patterns and functional diversity, and tree ring widths.
- There were no relationships between functional diversity and successional dynamics.
- Raised bogs are resilient to consequences of neighbourhood clear cuts.

GRAPHICAL ABSTRACT



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ABSTRACT

Raised and transitional bogs are one of the most threatened types of ecosystem, due to high specialisation of biota, associated with adaptations to severe environmental conditions. The aim of the study was to characterize the relationships between functional diversity (reflecting ecosystem-shaping processes) of raised bog plant communities and successional gradients (expressed as tree dimensions) and to show how impacts of former clear cuts may alter these relationships in two raised bogs in 'Bory Tucholskie' National Park (N Poland). Herbaceous layers of the plant communities were examined by floristic relevés (25 m^2) on systematically established transects. We also assessed patterns of tree ring widths. There were no relationships between vegetation functional diversity components and successional progress: only functional dispersion was negatively, but weakly, correlated with median DBH. Lack of these relationships may be connected with lack of prevalence of habitat filtering and low level of competition over all the successional phases. Former clear cuts, indicated by peaks of tree ring width, influenced the growth of trees in the bogs studied. In the bog with more intensive clear cuts we found more species with higher trophic requirements, which may indicate nutrient influx. However, we did not observe differences in vegetation patterns, functional traits or functional diversity indices between the two bogs studied. We also did not find an influence of clear cut intensity on relationships between functional diversity indices and successional progress. Thus, we found that alteration of the ecosystems studied by neighbourhood clear cuts did not affect the bogs strongly, as the vegetation was resilient to these impacts. Knowledge of vegetation resilience after clear cuts may be crucial for conservation planning in raised bog ecosystems.

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1. Introduction

Raised and transitional bogs are ecosystems typical for boreal, subboreal and northern nemoral zones (Ellenberg, 1988; Klinger, 1996; Montanarella et al., 2006; Parish et al., 2008). In Central Europe most of the raised bogs formed as a result of terrestrialization of lakes. As peat bogs grow in height, the water regime may at some point undergo transition from groundwater supply to precipitation supply and subsequent formation of ombrotrophic bogs (Hughes and Dumayne-Peaty, 2002; Parish et al., 2008; Schumann and Joosten, 2008). Some raised bogs formed as a result of quaking fen growth. This process starts as a floating mat near the lakeshore, composed of sphagna and vascular plants typical for transitional bogs, which then tends to overgrow the whole lake. Then, due to peat accumulation, the lake is filled in with peat and the bog grows in height. Extreme habitat conditions – high moisture and acidity as well as very low nutrient availability – cause these ecosystems to be suitable for only a limited number of species. With continued progress of dystrophic lake terrestrialization, peat thickness increases and its moisture content may decrease (Ellenberg, 1988; Namura-Ochalska, 2007).

Peat bogs are ecosystems both precious and endangered, mainly due to drainage for purposes of agriculture, forestry and peat mining. Moreover, raised bogs have been destroyed as a result of eutrophication caused by agricultural activities and atmospheric nitrogen deposition (Limpens et al., 2003; Tomassen et al., 2004; Herbichowa et al., 2007; Kollmann and Rasmussen, 2012). Due to a high proportion of strongly specialized plant species, peat bog vegetation is the most sensitive element of these ecosystems to anthropogenic transformation. Therefore, floristic composition of peat bog vegetation may indicate their state of preservation (Gunnarsson et al., 2002; Joosten and Clarke, 2002; Herbichowa et al., 2007; Dyderski et al., 2015). Due to specific environmental conditions, functional diversity of raised bog vascular plant communities reflects low levels of competition and high levels of habitat filtering, expressed by prevalence of stress-tolerant species among competitors (e.g. Glaser, 1987; Gunnarsson et al., 2002; Rydin and Jeglum, 2006; Parish et al., 2008). However, vascular plants and sphagna compete for light, space and nutrients. This competition is asymmetric, as vascular plants are able to shade mosses, being better competitors for light, while sphagna are able to take up nutrients throughout the whole plant, and intercept nutrients in rainwater more quickly (by capitula) than vascular plants can take up by their root systems (Rydin and Jeglum, 2006; Vile et al., 2011). Functional diversity is defined as the sum of functional richness (FRic), evenness (FEve), divergence (FDiv) and dispersion (FDis), as proposed by Mason et al. (2005) and Laliberté and Legendre (2010), and is usually associated with species richness and increases as succession progresses (Bu et al., 2014).

Succession is both a natural element of peat bog ecosystem development and a threat to their persistence. Especially in ecosystems strongly transformed by humans, particularly where hydrological conditions have been disturbed, the rate of successional processes is increasing. This leads to quicker encroachment and development of forest plant communities, which causes extinction of specialized, light-demanding plant species by shading (Kollmann and Rasmussen, 2012; Woziwoda and Kopeć, 2014). Growth of tree stands also causes increasing water deficiency by higher transpiration rates than on open bogs, which in turn increases tree stand development, causing further drainage (Macdonald and Yin, 1999; Fay and Lavoie, 2009; Talbot et al., 2010). This chain of feedbacks between tree stand occurrence, increased transpiration and drainage, and increased survival of natural tree regeneration otherwise limited by high groundwater levels (Holmgren et al., 2015), is most often connected with climate fluctuations, e.g. periods with high or low precipitation (Eckstein et al., 2011). In the cases of peat bogs untouched by human activities, rate of woody species encroachment is relatively slow and their contribution to peat bog biodiversity is rather positive, by creating microsites with conditions typical of late-successional stages (Gunnarsson et al., 2002). Thus, succession dynamics, both natural or altered by human activity, may be described by dimensions of trees, such as tree stand basal area or tree stand volume (Laine et al., 1995; Dyderski et al., 2015). However, all ecosystems have some inertia, which allows them to resist both natural and anthropogenic disturbances and regenerate after these perturbations. This response, called resilience, may be defined both as amount of disturbance after which an ecosystem may return to a stable state or return time to a stable state (Holling, 1973; Gunderson, 2000).

The aim of this study was to recognize the relationships between functional diversity of plant communities, successional dynamics (expressed as trees dimensions) and impact of former clear cuts on raised bog plant communities. We hypothesised that: (1) functional diversity indices will be correlated with successional progress (Lohbeck et al., 2012; Bu et al., 2014), expressed by median tree diameter at breast height (DBH), as the role of competition (expressed as high values of FDiv and FEve) will increase and that of habitat filtering (expressed by low values FRic and FDis) will decrease; (2) former clear cuts affected growth of tree stands around the peat bogs studied by increasing their annual radial growth, independently of climate fluctuations; (3) clear cutting a tree stand on the shore of one of the partially bog-covered lakes caused nutrient leaching (Nieminen, 2004) into the lake, which we hypothesize will affect the plant community species composition by increasing cover of species with higher trophic requirements; and (4) this cutting will influence the relationship between functional diversity indices and successional progress, expressed by median DBH.

2. Materials and methods

2.1. Study area

'Bory Tucholskie' National Park (BTNP) is located in northern Poland, in the Pomerania region (53°48′N; 17°33′E). The National Park was established in 1996 and was designated as a UNESCO Biosphere Reserve in 2010. The area of BTNP is 4613 ha, including 82.9% forests (mostly *Pinus sylvestris*), 11.1% water and only 1.1% organogenic habitats, mostly wetlands (Szmeja, 2000; Matuszkiewicz et al., 2012). This study examined undrained (pristine) peat bogs around two strictly protected dystrophic lakes: 'Rybie Oko' and 'Kociołek' (Fig. 1). The strict protection area 'Rybie Oko' covers 1.5 ha, including a lake area of 0.2 ha. Average lake depth is 1.6 m, and pH is 4.6. The strict protection area 'Kociołek' covers 1.5 ha, including a lake area of 0.8 ha. Average lake depth is 7.2 m, and pH is 4.3 (Kraska et al., 2000; Szmeja, 2000). Tree stands around the shore of the 'Kociołek' lake were clear-cut in the 1950s, whereas tree stands around the 'Rybie Oko' lake were not cut, although there was a clear cut in the neighbourhood (nearest forest subcompartments, up to 100 m from the bog studied) in ca. 1986 (Fig. 1). Before forest management activity considered in this study, both bogs were covered by *Pinus sylvestris* forest, according to a historical map (Wojskowy Instytut Geograficzny, 1932).

2.2. Study design

Two perpendicular transects were established across peat bogs around each of the study lakes. Each transect covered only the area with organic soil. The first transect was placed to cross the longest axis of the lake, and the second was perpendicular to the first. In each transect, starting from the lake shore, 10×10 m plots were established, with 10 m spacing between plots (Fig. 1). On the each of 17 plots two floristic relevés (25 m^2) were established. A list of vascular plants in the herbaceous (<0.5 m height) layer, with their abundances using the Braun-Blanquet scale, was compiled for each relevé. These relevés were located systematically, in the upper-right and lower-left corners of the plots. In each plot, diameters at breast height (1.3 m; DBH) of all trees were measured. We used median DBH of trees in the plot as an index of successional progress instead of basal area, as the small area of the bogs studied did not allow establishment of larger plots