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Natural forest remnants as refugia for bryophyte diversity in a transformed mountain river valley landscape

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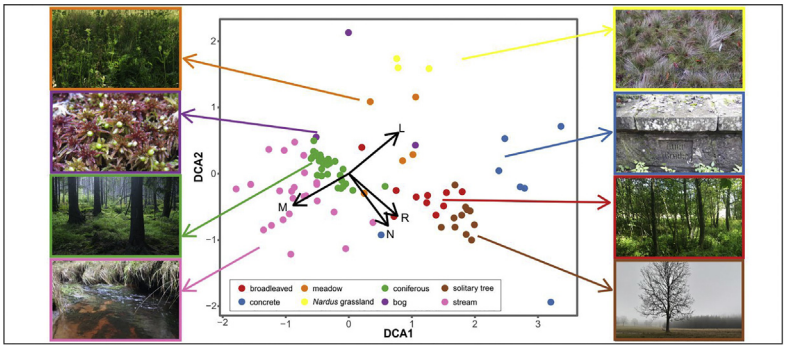
HIGHLIGHTS

- Habitat diversity drives bryophyte species composition.
- We assessed whether rare microhabitats are hotspots of bryophyte diversity.
- Rare habitats contributed to the species pool more than the most abundant habitats.
- Deciduous forests and solitary trees are crucial bryophyte refugia.

GRAPHICAL ABSTRACT



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ABSTRACT

Riparian forests are among the most threatened ecosystem types worldwide. Their exploitation and replacement by coniferous plantations affects species pools and contributes to loss of biodiversity. We aimed to investigate bryophyte species pools within different habitat types in a transformed mountain river valley. We especially focused on the contribution of habitat types (relative to their proportional cover) to the species pool of the whole area. The study was conducted along the Czerwona Woda river – a model stream in the Stołowe Mountains National Park (SW Poland, study area: 91.2 ha) – and an example of coniferous plantations replacing natural broadleaved forest vegetation. Our study revealed the presence of 147 bryophyte species. The most valuable habitats in terms of diversity of bryophyte assemblages were remnants of the natural vegetation – broadleaved forests and streams. These habitats, constituting <5% of the study area, hosted ca 40% of the total species pool (61 and 62 species, respectively), while the species pool of *Picea abies* forests (92 species) was proportional to cover of this habitat type (ca 60%). Remnants of natural vegetation were hotspots of bryophyte diversity within the heavily altered landscape, and may play a future role as sources of recolonization by forest specialists. Our study also confirmed the important role of riparian areas in maintaining bryophyte species diversity at the

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landscape scale. The river valley studied contributes >20-fold more to the bryophyte species pool of the whole national park than indicated by its size. Thus, river valleys require special treatment – conservation based on natural restoration, and should remain reserved from wood production, as areas providing a wide range of ecosystem services.

1. Introduction

Due to history of human impact, recognised mainly as land-use changes (Perlin, 1988; Richardson et al., 2007; Tabacchi et al., 1996), only 0.2% of all deciduous forest communities in Central Europe are thought to possess relatively natural features (Hannah et al., 1995). Natural riparian forests are diverse, dynamic and complex, and as such, together with ecological continuity, are of the utmost importance for biodiversity conservation (e.g. Broadmeadow et al., 2011; Hunter et al., 2017; Naiman et al., 1993; Thomas and Nisbet, 2007). Small riverine ecosystems play functional roles incommensurate with the area they occupy (Broadmeadow and Nisbet, 2004; Hunter et al., 2017), and thus many surveys have concerned protection and ecological restoration of such areas (Leathwick et al., 2010; Morandi et al., 2014; Palmer et al., 2005; Wohl et al., 2015). Riparian ecosystems are one of the most endangered habitat types worldwide. Changing land-use is a major threat to riparian ecosystems. Riverine areas are among the most altered ecosystems by river regulation, settlement, agricultural land use and invasion of alien species (e.g. Dyderski et al., 2015; González et al., 2017; Lapin et al., 2016; Nilsson et al., 2005; Pielech et al., 2015). Broadleaved forests in river valleys have been transformed into agricultural fields or monocultures of coniferous tree species, making them among the most modified and fragmented ecosystems in Europe (Petersen et al., 1987; Sedell and Froggatt, 1984). Human intervention and management practices have led to declines of key ecosystem services such as prevention of soil erosion, improving water quality, controlling floods and maintenance of the riparian vegetation. This cascade of factors corresponds to degradation of the environment, impoverishment and loss of specific features of the river valley (Pielech, 2015).

Bryophytes are a key component within the cryptogams that shape forest diversity (Kriebitzsch et al., 2013). According to their specific ecology linked to certain habitats and substrates (soil, humus, rocks, bark of living trees, rotten wood) and strongly dependent on air humidity (poikilohydric organisms), they are known to respond immediately to alteration (Esseen et al., 1997; Fritz et al., 2009; Glime, 2017), and thus play an important role as useful tools in recognition of environmental changes (Fritz et al., 2009; Herben, 1987; Nascimbene et al., 2014; Wang et al., 2015). Type of forest vegetation, its naturalness, age, and also management practices, together with habitat fragmentation, are the main factors shaping the diversity of cryptogams including substrate-dependent bryophytes (e.g. Frego, 2007; Gustafsson and Hallingbäck, 1988; Paillet et al., 2010). Heterogeneity, together with abundance of species and diversity of different ecological groups of bryophytes, may define a given forest according to natural biodiversity, stand structure and ecological continuity of its integral elements (Frego, 2007).

Both physiological and morphological features define bryophytes as good bioindicators related to ecosystem functioning (Bates, 1992; Friedel et al., 2006; Sun et al., 2013) and as indicators of environmental factors in forest ecosystems (e.g. Cooper-Ellis, 1998; Jagodziński et al., 2018; Sjögren, 1974). In Central Europe, some species of forest specialists, epiphytic bryophytes, are considered relics of the ancient forest (e.g. Cieśliński et al., 1996; Mölder et al., 2015; Peterken, 1974; Stebel and Żarnowiec, 2014). Thus, bryophytes can indicate both degree of naturalness and human impact on different plant communities.

Most of the studies on bryophyte assemblages are conducted in old, well preserved forests (e.g. Gabriel and Bates, 2005; Mežaka et al., 2012, Ódor and Standovár, 2002; Rose, 1992; Söderström, 1988) or in mature managed forests (e.g. Gustafsson and Hallingbäck, 1988; Ódor et al., 2013; Wierzcholska, 2010). Surveys devoted to diversity of mosses and liverworts in riparian forest ecosystems heavily transformed by humans are still in the minority (e.g. Humphrey et al., 2002; Nascimbene et al., 2014). Little is known about bryophytes across habitat-type gradients like those from stream vegetation into the surrounding forest ecosystems, which have variable fluvial-specific widths influenced by dynamics along the length of a stream. Many surveys are devoted to bryophytes as an integral component of aquatic communities (e.g. Vanderpoorten et al., 1999; Vieira et al., 2017; Vitt et al., 1986), and separately to riverine forest (e.g. Heino et al., 2005; Hylander and Dynesius, 2006; Muotka and Virtanen, 1995). Understanding drivers and mechanisms that control relationships between managed forests and bryophyte diversity in river valleys is of great importance for biodiversity conservation. However, at this time there are only a few studies explaining how habitat diversity affects bryophyte species pools in riparian ecosystems influenced by large-magnitude human-induced alterations (e.g. Vanderpoorten and Klein, 1999; Vieira et al., 2012). This knowledge is necessary to improve proper management and conservation of riparian areas. Thus, we aimed to investigate the bryophyte flora of a transformed river valley and assess the impact of habitat and microhabitat diversity on biodiversity of bryophyte flora. We hypothesised that: (1) rare habitats that are relics of the natural vegetation will host more bryophyte species (both all and forest specialists) than dominant secondary forests, (2) contribution of particular habitat types to the total bryophyte species richness is proportional to the area occupied by these habitats, (3) within considerably altered landscapes, river valleys are hotspots of bryophyte diversity.

2. Material and methods

2.1. Study area

As a model study site we chose the Czerwona Woda river valley (Stołowe Mountains National Park; SW Poland; 50.47°N, 16.35°E). Area of the valley was subjectively limited using a digital elevation model of the terrain and covers 91.2 ha. Its elevation ranges from ca 810 (source) to 600 (border of the national park) m a.s.l. Czerwona Woda is the longest (13.4 km) river in the Stołowe Mountains National Park and its width ranges from 0.5 to 3 m (Fig. 1). In the period of 1951–2000 mean annual temperature was 7.1 °C, according to the nearest meteorological station in Kłodzko, ca 20 km from the study site (Trouet and Van Oldenborgh, 2013). Mean annual precipitation for years 1976–2005 was 773 mm, according to Tarka et al. (2011). Forest vegetation in the Stołowe Mountains National Park was strongly transformed by replacement of natural communities (e.g. riverine forest) by coniferous monocultures. In the study area we mean 'riverine ecosystem' as the ecological systems spatially related to river valley. Currently, the study area is mostly covered by artificial stands of *Picea abies* 80 to 120 years old (Table 1). The remnants of natural vegetation (riparian forests from *Alnion incanae* alliance) are represented either by small patches of broadleaved forest stands or by solitary trees of *Acer pseudoplatanus*, *Alnus* spp., *Betula pendula*, *Fagus sylvatica*, *Fraxinus excelsior*, *Salix* spp., *Populus tremula* and *Sorbus aucuparia*. Non-forest vegetation of the study area comprises mostly meadows, bogs and acidophilus grasslands (Table 1). Detailed vegetation survey was presented by Pielech et al. (2018). The forest soils are characterized by