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Contrasting responses of millipedes and terrestrial isopods to hydrologic regime changes in forested montane wetlands

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ABSTRACT

Forested montane wetlands are subject to changing disturbance regimes. The factors responsible for their hydrologic degradation include drainage for forestry. Few studies have explicitly addressed the effects of changing hydrologic regimes linked with artificial drainage and disruption of these drainage systems on soil fauna communities. Because millipedes (Diplopoda) and terrestrial isopods (Oniscidea) are an important components of the soil macro-decomposer community and exhibit a wide range of ecological requirements, we examined their response to regimes changes in mountain fen sites of *Caltho-Alnetum* demonstrating different degrees of alteration of hydrologic conditions and classified into three categories: natural, semi-natural and degraded. Our results showed that hydrologic alteration of mountain fens affected terrestrial isopod and millipede communities much less strongly than soil physico-chemical properties. However, the increasing hydrologic disturbances, due to drainage and lowering of groundwater level also led to differential responses of these two groups of soil macro-decomposer communities, and induced significant change of terrestrial isopod community composition in semi-natural conditions but no response of millipede communities. The observed differences in the responses of these two groups correspond to differences in their sensitivity, resistance and resilience to hydrologic changes in mountain fens. We conclude that the significant response of terrestrial isopod community composition documented in semi-natural conditions reflects their low ability to return to the pre-drying state and indicates their higher sensitivity and limited resilience to disturbances related to groundwater withdrawal compared to communities of millipedes. Besides, our results also suggest that in mountain areas altitude acts as a stronger environmental filter on community composition of terrestrial isopods and millipedes than hydrologic conditions.

1. Introduction

Many ecological components, populations, communities and ecosystems are maintained by natural and human driven disturbances [1], but the responsiveness of biological entities to environmental changes is still poorly understood, particularly in the context of their sensitivity to different environmental disturbances [2]. The variety of alterations of natural disturbance regimes allows for quantifying two separate processes, community resistance and recovery rate in terms of ecological resilience [3]. Resilience is often defined as the capacity of an ecosystem to absorb disturbance without shifting to an alternative state [4], or the ability of a community or an ecosystem to return to a pre-disturbed state [5]. In highly variable wetland ecosystems, invertebrates are well adapted to cope with a wide range of habitat conditions, such as flooding and drying conditions: however, their response to environmental change may be very resilient or highly sensitive [6]. The impact of ecological and human disturbances on soil biota has been widely documented, including flooding, as reviewed in detail by Plum [7], and drainage [8]. Although there is broad understanding of the isolated impact of disturbances, possible changes caused by transient dynamics in a hydrologic disturbance regime are not well known and understood. The responses of soil fauna to changes in the hydrological regime have only been investigated in selected groups of soil mesofauna in peatlands drained for forestry in

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Finland [8] and in fluvial forests of the Latorica River floodplain [9,10].

Wetlands in mountain areas are unique and very diverse ecosystems exhibiting exceptional climatic, geological, geomorphological, hydrographical and hydrogeological conditions [11–13]. These habitats, like other types of wetland ecosystems under natural conditions, support organisms adapted to poorly aerated or water-saturated soils and represent high value at the three levels of ecological hierarchy: population, ecosystem and biosphere, in terms of biodiversity and ecosystem service protection and conservation [14]. In the highly heterogeneous mountain landscape, with steep topography and pronounced elevation gradients, mountain wetlands are areas with perennially saturated soils, but without obvious surface flooding. As in other type of wetlands, the hydrologic regime is the main environmental driving force [15] and represents a good proxy for the complex hydrologic-edaphic gradients associated with the decline of groundwater level [16]. Fluctuations in water table levels and, consequently, in saturation of soils can affect soil biota as much as flooding; however, this pattern has not been well documented and understood.

The mountain alder swamp forests of the *Caltho-Alnetum* association of the Outer Flysch Carpathians are interflow-fed forest areas where groundwater including solutes from the whole catchment seeps out and consists of aquatic and terrestrial subsystems. They develop on slope horizons where alluvial groundwater supports peat formation and in places where underground waters come to the surface. In the Polish Flysch Carpathians, they are classified among the peat-forming wetlands [17] as soligenous fens [11] or they can be classified as slope fens [18]. Although they are never large in area and often isolated, their importance for biodiversity and ecological function is high, including the storage of soil carbon, regulation of local and regional hydrologic regimes and water quality improvement [11,19]. The main threat of these forested montane wetlands, as in other peatlands in Europe, is groundwater alteration by drainage for forestry [20]. Ditching or diversion of water is a common hydrologic disturbance in peatlands and ditches have a substantial impact on the hydrology of a fen site. Drainage lowers the groundwater table and improves the aeration of the peat, which intensifies the growth of trees, and changes the processes of soil organic matter accumulation in the mineralization phase [21], which in turn affects such ecological processes as succession and decomposition [22]. Such changes in the eco-hydrologic properties of peatlands and peat soils induced by drainage might be regarded as a threat, by analogy with climate changes [23].

There is little research on soil fauna in forested wetlands in mountain regions, even though soil biota are important in many soil processes [24] and soil invertebrates are useful bioindicators of human disturbances and can be used to define soil conditions and soil quality [25,26]. Soil arthropods are often sensitive to hydrologic disturbances, including flooding [7,27,10] or climate manipulation and, in consequence, soil drying [28], but the response of soil animal communities to hydrologic regime changes in mountain wetlands has not been examined. We assumed that ground-dwelling soil invertebrates such as millipedes (Diplopoda) and terrestrial isopods (Oniscidea) are suitable as surrogate taxa for predicting environmental change induced by drainage on wetland soil biodiversity. These two taxa, although taxonomically distant, belong to the same functional guild of primary decomposers in soil ecosystems and are very convergent behaviourally, physiologically and morphologically [29,30], which allowed to assume that their response to environmental changes could also be consistent [31]. Millipedes and terrestrial isopods contribute substantially to soil invertebrate diversity and are relevant in terms of their responses to environmental change, such as climate warming and land use change [30,26,32,33]. Prolonged drought conditions affect the development rate, growth and reproduction of these two taxa sensitive to moisture changes [30,32], and could lead to shifts in community composition, among others due to filtering of species with higher desiccation resistance. However, the role of moisture, which can strongly influence habitat selection in terrestrial isopods, is relatively subtle in millipedes [34]; also, terrestrial isopods are less resistant to desiccation then, for example, insects [35], therefore, artificial regulation of groundwater resources could in different way affect their community composition. Thus it was considered worthwhile to investigate the effect of drainage-related changes in hydrologic conditions in mountain wetlands on the responsiveness of these two groups of soil fauna that are functionally similar but differ in their sensitivity to soil moisture changes and susceptibility to desiccation.

The main goal of the study was to measure the response of millipedes (Diplopoda) and terrestrial isopods (Oniscidea) communities to different degrees of alteration of natural hydrologic conditions in forested mountain wetlands, and to evaluate their sensitivity to hydrologic changes. We hypothesized that dryness of mountain fen peat soils triggered by artificial drainage will (1) affect the distribution of millipedes and terrestrial isopods and will increase the overall density and species richness of these two macro-decomposer taxa, and (2) will have a differential effect on the community composition of both taxa, with more sensitive responses to the hydrologic changes to groundwater withdrawal in terrestrial isopods than in millipedes.

2. Material and methods

2.1. Study area

The study was carried out in fens of the lower submontane and montane zones of the Babia Góra Massif in the Outer Flysch Carpathians, in the Central European Highlands biogeographic province, in a biome with mixed mountain and highland ecosystems with complex zonation. The Babia Góra is the second highest mountain range in Poland (highest peak 1725 m a.s.l.) situated in the Beskids Mountains and forms a watershed between the Baltic Sea and the Black Sea basins. The Babia Góra is a Polish-Slovak transborder mountain range, the highest in the flysch part of the Western Carpathians. Since 1954, this area has been protected as Babiogórski National Park and in 1977 it was listed as a World Biosphere Reserve by UNESCO. Babiogórski National Park (49°28′ to 49°38′N; 19°27′ to 19°38′E) covers the summits and northern slopes of the Babia Góra Massif, which belongs to the catchment area of the Baltic Sea. The climate of the area is rough. The average annual temperature is 5 °C and the total annual precipitation is 1200 mm, with maximum precipitation in June and July. A snow cover is present on average for 110–120 days a year [36].

The fens of Babia Góra Massif have formed on north-facing slopes with hardly permeable mineral layers. They represent a soligenous type of hydrological feeding [11] and are often occupied by *Caltho-Alnetum* associations [37] which are a priority biotope listed in the annex to the 1st Habitats Directive of the European Union. A characteristic feature of such non-degraded mountain fens is high accumulation of organic matter and water saturation in the soil profile. One cubic metre of fen organic soil retains between 300 and 900 mm of water [11].The majority of forest fens within the Babiogórski National Park, prior to coming under legal protection, were drained in the 1970's in order to increase timber production. Drainage works triggered significant changes in the hydro-ecological conditions of the mountain fens and led to the degradation stage, at which muck-forming process take place [38,21].