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Divergence of soil microarthropod (Hexapoda: Collembola) recovery patterns during natural regeneration and regeneration by planting of windthrown pine forests

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ABSTRACT

Windthrows are natural disturbances that influence the functioning and structure of forest ecosystems and the belowground components of an ecosystem. Soil processes such as the recycling of organic matter, energy and nutrients are controlled by soil fauna. However, little is still known about the post-disturbance recovery of soil microarthropod communities in forest stands exposed to windthrow of various severity and post-windthrow forest management over time. This study assessed soil Collembola community recovery in pine forest stands over the long-term (between 9 and 14 years after the disturbance event). We predicted that (1) different severity of windthrow disturbance in a pine forest has different effects on the recovery of Collembola community composition and functional structure, even after 10 years; (2) The recovery of Collembola communities is similar during regeneration of a forest disturbed by windthrow and in a pine plantation planted after clearing of a windthrown forest and subsequent soil preparation; (3) The changes in the Collembola community during forest regeneration after windthrow disturbance can be explained by selected environmental variables, especially the leaf area index LAI. As expected, regeneration processes within forest stands shifted the species composition of collembolan communities and changed their functional structure. The surface dwelling collembolan species (epigeic and atmobiotic life form) responded to regeneration processes mainly in pine stands, especially in a pine plantation established after a clearing of broken pines and subsequent soil preparation. Our results suggest different sensitivity of collembolan communities to environmental changes induced by various degrees of opening of the tree canopy by windthrow and to those caused by the post disturbance treatment. These findings confirm that collembolan community composition recovery is slow and divergent during natural regeneration of pine stands and regeneration by planting but does not differ between moderately and severely successional trajectories. Our results also confirm the importance of canopy closure for the possibility of Collembola community regeneration. If canopies were more closed (higher leaf area index, LAI index), the possibility of regeneration increased, especially in the young pine plantations, as seen in the final years of our study.

1. Introduction

Windthrow is a natural physical forest disturbance affecting the natural dynamics of the forest ecosystem (Fischer et al., 2013; Mitchell, 2013; Thom and Seidl, 2016). Incidence of windthrow events has increased at the turn of the century (Nilsson et al., 2004); therefore it can be assumed that strong wind storms will often disturb forest ecosystems. Windthrow generates disturbance of various intensity in forests and leads to uneven age structure and patchy occurrence of stands affected by different severity disturbance. One important consequence of windthrow is the formation of a large or even massive amount of dead wood within forest stands (Fidej et al., 2016). The formation of various quantities of dead wood in a short time has profound and long-term effects on stand fertility and soil properties, such as soil carbon and nutrient dynamic and, in association with the pit-mound complex remains, micro-topographic and microclimatic heterogeneity (Mitchell, 2013) which leads to a temporally uneven distribution of decay phases and can also influence, in particular, diversity and patterning of soil biota.

The soil-litter system is inhabited by soil invertebrate communities that vary in size and in the kind of food resources they utilize (Lavelle et al., 1995, 2006; Briones, 2014). Among them, soil microarthropod

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communities contribute significantly to the decomposition of soil organic matter, and nutrient recycling, and through feeding directly on decaying material and soil microbial communities, have an influence on soil health, ecosystem function and ecosystem services (Coleman et al., 2004; Lavelle et al., 2006; Barrios, 2007). Soil microarthropods are very sensitive to degradation and recovery of forest ecosystems, e.g. after fire (Malmström, 2012) or flood disturbances over time (Sterzyńska et al., 2014). The response of soil microarthropods to environmental changes induced by windthrow in European forest stands had attracted relatively scarce attention (Čuchta et al., 2013; Urbanovičová et al., 2014). That study was conducted in a clear-cut, burnt and non-extracted mountain windthrown spruce forest; however, it did not take into account soil fauna recovery over time following canopy disturbance of various severity and in a forest plantation established after clearing a windthrown forest. The effect of natural spontaneous regeneration after windthrow on soil invertebrates, despite their importance to soil fertility and productivity processes (Lavelle, 1997; Bardgett, 2005; Barrios, 2007) is still little known, although in the course of successional processes they can have a severe effect on the spontaneous recovery of forest stands after a disturbance by aboveground-belowground multitrophic interaction (Wardle et al., 2004; De Deyn and Van der Putten, 2005; Bardgett and Wardle, 2010).

Collembola are among the most important groups of soil microarthropods that participate directly in the formation of soil microstructure and in the redistribution of dead organic matter within the soil profile (Rusek, 1998). Due to their high sensitivity to changes occurring in the soil habitat and known susceptibility to disturbances (e.g. Sterzyńska et al., 2014), it is a convenient model to demonstrate post disturbance recovery of the soil-litter system in the forest stand. Čuchta et al. (2012, 2013) documented that post-windthrow management of a mountain spruce forest significantly changed Collembola distribution and structure; nonetheless, differences in the recovery pattern of Collembola over time following various severity of windthrow and post-windthrow management were not analyzed.

The severity of disturbance is one of the main characteristics responsible for the extent to which the disturbance modifies the soil biota community composition and associated pool of species traits (Berg et al., 2012). Functional attributes, have a highly predictive value and the potential to provide evidence on the mechanisms of how the communities respond to natural and anthropogenic disturbances (Mouillot et al., 2007, 2013; Vandewalle et al., 2010) and can determine community response to environmental change better than the taxonomic approach (Diaz et. al., 2013). Despite this, the functional approach to regeneration of forests after windthrow has been studied only for saproxylic assemblages (Thorn et al., 2014) and ground beetle assemblages (Debnári, et al. 2016; Skłodowski, 2017a, b; Skłodowski and Garbalińska, 2011). Analysis of the functional traits of Collembola species allows for understanding their response to the disturbances through defining the contribution of combinations of some environmental variables to the occurrence of life-form traits which are proxies of the vertical structure in soil (Salmon and Ponge, 2012; Salmon et al., 2014). Functional traits have been shown to be a good tool in predicting recovery patterns in Collembola species after a fire (Malmström et al., 2009; Malmström, 2012), or explaining their responses to climate manipulation (Makkonen et al., 2011).

Nonetheless, little is still known about Collembola community responses to various regeneration processes within a naturally disturbed forest ecosystem. Thus, we can ask if Collembola responses to regeneration processes within a forest ecosystem naturally disturbed by wind and left for spontaneous regeneration of trees and in an intensively managed part with a pine plantation planted after the removal of broken trees and plowing the soil are similar, and whether the later stages of succession and the most dynamic – and neglected – first few years after disturbance, follow the same recovery trends, assuming that the examined forest patches had the same species pool of soil microarthropods before the disturbance. In particular there is lack of research data showing how differences in the severity of wind disturbance, impact the recovery of Collembola community diversity and functional structure. The experimental design used in this study allowed us to ignore the primary reaction of Collembola communities to the disturbance event and focus on recovery trajectories induced by various severity of wind disturbance. It is known that the severity of windthrow can provoke differences in environmental changes and regeneration processes of post-windthrow pine forest and invertebrate communities inhabiting in (Skłodowski, 2017a). According to Skłodowski et al. (2014), indices such as: leaf area index (LAI), soil respiration, decomposition of organic material, and soil nutrient content can be used as a proxy of post-windthrow environmental changes that in consequence can have an impact on Collembola community recovery. The following hypotheses were set forth:

1) Different severity of windthrow disturbance in a pine forest has different effects on the recovery of Collembola community composition and functional structure, even after 10 years.
2) The recovery of Collembola communities follows similar successional trajectories during natural regeneration of a forest disturbed by windthrow and in a pine plantation planted after clearing of a windthrown forest and subsequent soil preparation.
3) The changes in the Collembola community during forest regeneration after windthrow disturbance can be explained by selected environmental variables, especially the leaf area index.

2. Material and methods

2.1. Study site

The study was performed in the Pisz forest district, an integral component of Puszcza Piska forests located on the Mazurska Plain in northeastern Poland (21 48E; 53 38 N), with clean air and without pollution by industry. In July 2002, over 30,000 ha of pine forest stands in Puszcza Piska forests were disturbed by windthrow, of which 475.59 ha were left without cleaning to undergo spontaneous regeneration of forest ecosystems. The remaining part was with subject to management activities such as clearing of all broken trees, salvage logging, subsequent plowing of the soil and planting. The disturbed forest stands grow on a rusty podsolic soil, Podzols, after the WRB classification (2015). The Scotch pine *Pinus sylvestris* L. predominates in the stand. *Betula pendula* Roth is another numerous tree species. *Calluna vulgaris* (L.) Hull, *Melampyrum pratense* L. and *Vaccinium myrtillus* L., predominate in the herbaceous layer of the least disturbed stands; *Vaccinium vitis-idaea* L. and *Deschampsia flexuosa* (L.) Tvim occurring as isolated, single plants predominate in the most disturbed stands. The moss layer consists of *Pleurozium schreberi* (Willd. Ex Brid.) Mitt., *Dicranum polysetum* Sw. Ex Anon., *Hylocomium splendens* (Hedw.) Schimp. and *Diphasiastrum complanatum* (L.).

2.2. Experimental design

Study sites were set up in two compartments of unmanaged and managed windthrown forest stands. Three classes of disturbed, unmanaged forest stands aged 40–80 y were distinguished on the basis of the severity of canopy cover disturbance in the part left for spontaneous regeneration. The first class comprised severely disturbed stands (“Se”, canopy cover of 10–30%); the second class involved moderately disturbed stands (“Mo”, canopy cover of 40–60%), and the third class had the least disturbed stands (“Le”), consisting of practically undisturbed stands in which all or nearly all trees had survived (canopy cover of 70–90%). This last treatment was used as a reference as it had been nearly left intact by the windthrow. Each class was replicated 6 times, for a total of 18 research plots (Fig. 1). Study sites in the managed part were set-up in young pine plantation (“P”), established four years after wind disturbance in 2006, and the soil prepared one year earlier.