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Forest conversion from Norway spruce to European beech increases species richness and functional structure of aboveground macrofungal communities

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ABSTRACT

This study investigated the response patterns of aboveground macrofungal communities to different management stages representing a forest conversion from Norway spruce (*Picea abies*) to European beech (*Fagus sylvatica*) in the Eifel National Park, Germany. We used a space-for-time substitution approach with three replicate study sites for each forest conversion stage: (I) even-aged single species Norway spruce, (II) unmanaged Norway spruce windthrow, (III) salvage-logged Norway spruce windthrow, (IV) single Norway spruce tree selection cutting (close-to-nature managed) with European beech underplanting and (V) old-growth, uneven-aged European beech (as reference). We assessed environmental variables and macrofungal sporocarps, while the latter were categorized into functional groups to link taxonomic information to potential ecosystem functions.

Overall, we observed 235 macrofungal species. The highest species richness was found in the European beech reference stage, followed by the close-to-nature managed spruce/beech stage, while the Norway spruce stage showed approximately half the species richness, similar to the species level of both windthrow stages. Nonmetric multidimensional scaling (NMDS) ordination separated each forest conversion stage into distinct fungal communities, while both windthrow stages could not be distinguished from each other. Beside tree species composition change and forest management, nutrient availability and microclimate were the main drivers of fungal community changes among the five differently-managed stages. Further, different functional groups responded in different patterns to forest management and to explanatory environmental variables.

We reinforced the assumption, that old-growth, uneven-aged European beech forests (> 120 years) can act as a refugium for unique forest type specific fungal communities with a higher functional structure, especially contrary to non-native, even-aged Norway spruce forests (~70 years). Single Norway spruce tree selection cutting with further introduction of European beech trees can be an adequate strategy to allow a spruce forest conversion without necessarily reducing the macrofungal species richness and its functional structure. We displayed that ecological consequences of windthrow events can be a depression of fungal species richness and a collapse for the functional structure of fungi, especially after salvage logging. Our study underlines the need of including fungal conservation in forest conversion plans to optimize forest ecosystem integrity and resilience against biotic and abiotic agents, such as windstorm events.

1. Introduction

In forest ecosystems, fungi are among the most important organism groups due to their specialized functional roles in nutrient recycling, symbiotic associations and plant community dynamics. They drive fundamental ecological functions in various ecosystem processes, e.g. nitrogen transfer, phosphate uptake, carbon storage, dead wood decomposition, litter degradation and humus formation (Winterhoff, 1992; Govindarajulu et al., 2005; Smith et al., 2009; Smith and Read, 2009; Clemmensen et al., 2013; Talbot et al., 2013). All these functions indicate their highly relevant contribution to energy flows and nutrient cycles in forest ecosystems.

Changes in forest ecosystems, induced by the replacement of dominant tree species, cause strong shifts in understory vegetation as well as soil and litter characteristics (Klimo et al., 2000; Augusto et al., 2003; Durall et al., 2006; Berger and Berger, 2012; Konôpka et al., 2013; Verstraeten et al., 2013; Dobrovolny, 2016). Previous forest studies indicated that changes in environmental conditions, such as topsoil acidity, nutrient availability or amount of coarse woody debris (CWD) influence fungal communities and their ecosystem functioning (Kranabetter et al., 2005; Buée et al., 2011; O'Hanlon and Harrington, 2012; Walker et al., 2012; Urbanová et al., 2015). Such sensitivity

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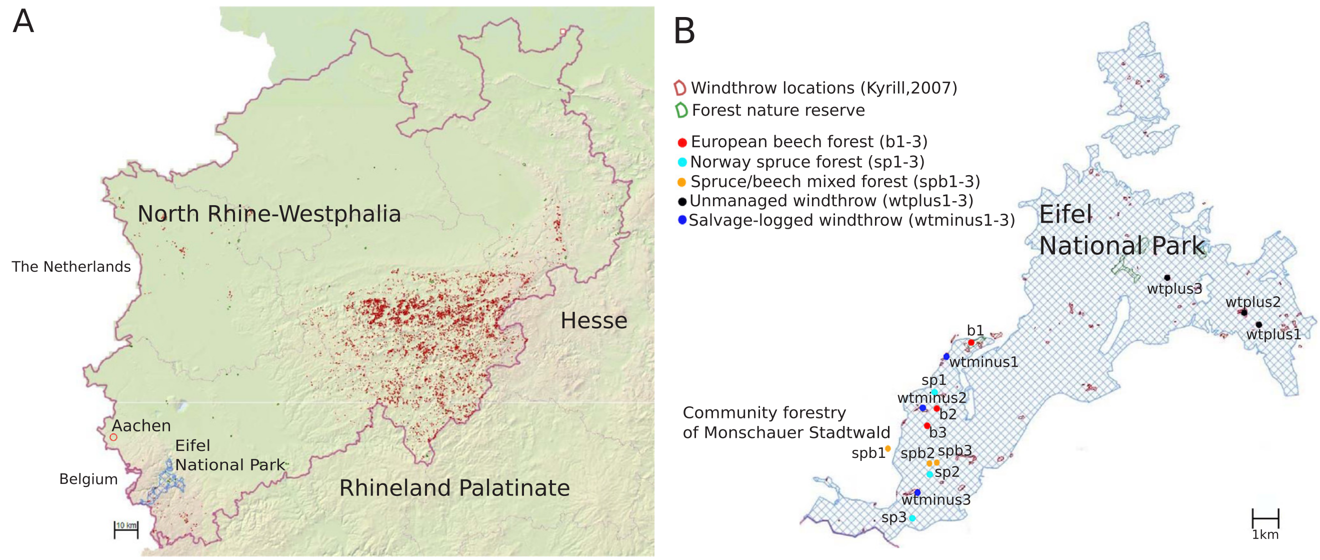

Fig. 1. **A**: The geographical location of the Eifel National Park (blue) in the federal state North Rhine-Westphalia in the west part of Germany. **B**: All study sites were located in the Eifel National Park, only *spb1* was located in the neighbouring community forestry of Monschauer Stadtwald. The study site *b1* was situated in a forest nature reserve of North Rhine-Westphalia (State Enterprise for Forestry and Timber North Rhine-Westphalia, 2016). Both maps are from the German biotope land registry office (Kadaster) and modified by the authors. The red marked areas in both maps represent windthrow locations caused by windstorm Kyrill in 2007. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

suggests fungi to be promising bioindicators in environmental studies of forest ecosystems (Tóth and Barta, 2010; Heilmann-Clausen et al., 2015; Halme et al., 2017).

Since the 19th century, intensive forest management has been applied in many parts of Europe, for example in Germany or the Netherlands, while native European beech (*Fagus sylvatica*) has been replaced with fast-growing coniferous tree species, such as Norway spruce (*Picea abies*) (Ellenberg, 1986; Spiecker, 2004; Verstraeten, 2013). Replacing native deciduous forests by non-native coniferous forests induced condition changes of, e.g. understory vegetation, canopy closure, soil acidification and litter structure, which can lower the value for nature conservation (Ulrich et al., 1977; Kazda and Pichler, 1998; Augusto et al., 2003; Verstraeten et al., 2013) and shift the fungal community composition (Goldmann et al., 2015; Kutszegi et al., 2015). In contrast, old-growth beech forests can harbor a highly diverse fungal community of rare and specialized species which are related to old-growth forest characteristics such as large dead wood amounts and undisturbed forest soils (Winterhoff, 1992; Müller et al., 2007; Holec et al., 2015). Other studies indicated that coniferous tree species (particularly mature > 100 years) can harbor similar level of fungal species richness inside and outside their native distribution range (Ferris et al., 2000; Humphrey, 2005; Küffer and Senn-Irlet, 2005; O'Hanlon et al., 2013). Today, the economically most important forests in Western Europe consist to a large extent of managed, even-aged Norway spruce forests with an age of 20–80 years (Johann, 2006; Forest Europe, 2015).

Changing climate conditions are predicted to facilitate native European beech dominance over Norway spruce, since the latter is highly vulnerable to abiotic and biotic impacts, e.g. windstorms or bark beetle attacks, while beech is relatively resilient against these factors (Harz and Topp, 1999; Bradshaw et al., 2000; Schroeder and Lindelow, 2002; Bolte et al., 2010). Consequently, forest conversion of Norway spruce plantations to native broadleaves has become an important topic (Spiecker, 2004; Fritz et al., 2006) to enhance biodiversity and create ecologically stable ecosystems by reestablishing European beech forests (Kazda and Pichler, 1998; Spiecker, 2009). Forest conversion is done primarily with the help of different close-to-nature management practices (Klimo et al., 2000; O'Hara, 2016), such as single or group tree selection cutting and admixture of beech trees in spruce stands (Dobrovolný and Cháb, 2013).

The ecological impact of Norway spruce forest conversion processes on important soil organisms is still not fully understood. To our knowledge, there were only evaluation studies of Norway spruce forest conversion on the oribatid mite community (Zaitsev et al., 2014), invertebrate decomposers (Elmer et al., 2004) or macrofauna (Salamon et al., 2008; Salamon and Wolters, 2009), while studies with fungal communities are missing. Due to their fundamental role in ecosystem functioning and their high sensitivity to environmental changes, it is crucial to understand the impact of different spruce forest conversion strategies on fungal communities and to research the ecological consequences, in order to design a sustainable management.

Our study was conducted along a forest conversion process from Norway spruce (*Picea abies*) to European beech (*Fagus sylvatica*) in the Eifel National Park (Germany), which has been occasionally impacted by catastrophic windstorms in 1990 and 2007. As more devastating windstorm events may occur in the next decades (Seidl et al., 2009, 2014), post-disturbance management practices can result in a high reduction of fungal species richness and changes in the fungal community composition (Schlechte, 2002), thus we included two differently-managed windthrow stages in our evaluation study design. Our main objectives were to determine to what extent the species richness, functional structure and species composition of macrofungal communities respond to different management stages along a Norway spruce forest conversion. The different spruce forest conversion stages were: (I) even-aged single species spruce, (II) unmanaged spruce windthrow, (III) salvage-logged spruce windthrow, (IV) single spruce tree selection cutting with beech underplanting, and (V) old-growth, uneven-aged European beech (reference).

We hypothesized that fungal species richness in different managed forest conversion stages would increase sequentially from the even-aged spruce forests to spruce/beech mixed ecosystems (close-to-nature managed) to uneven-aged beech forests. Further, we hypothesized that the forest conversion process from spruce to beech would result in compositional and functional shifts in macrofungal communities in response to changes in soil and litter conditions. In contrast to the forested conversion stages, we also expected that both windthrow stages will induce a strong variation in species richness, functional structure and fungal community composition, especially of ectomycorrhizal fungi due to tree mortality.

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