



# 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. Non-metric 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

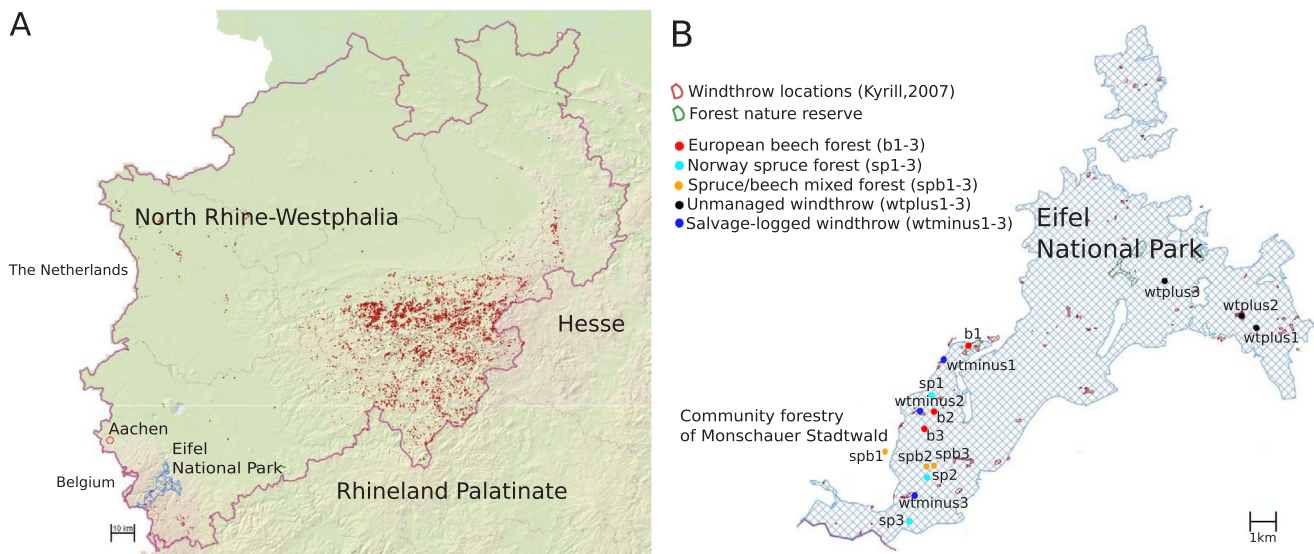
In forest ecosystems, fungi are among the most important organism groups due to their specialized functional roles in nutrient recycling, symbiotic associations and plant community dynamics. They drive fundamental ecological functions in various ecosystem processes, e.g. nitrogen transfer, phosphate 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; Dobrovlny, 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 (Schlichte, 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.

## 2. Material and methods

### 2.1. Study area

The study area is located in the Eifel National Park (50°34'12.60"N 6°21'38.50"E) and in the neighbouring community forestry Monschauer Stadtwald (50°31'51.43"N 6°18'53.93"E) in Western Germany (Fig. 1A). The Eifel National Park, established in 2004, covers a total area of 10,770 ha. Currently, several parts are dominated by single species forests with the conifer Norway spruce. Smaller areas are characterized by forests of Scots pine (*Pinus sylvestris*), Sessile oak (*Quercus petraea*) or European beech (*Fagus sylvatica*). The latter forest type can be characterized as acidophilic Luzulo-Fagetum association (Meusel, 1937) with the EU habitat code: 9110, where the broadleaf European beech is the dominant or co-dominant tree species (Krause and Mösel, 1995) and the acidophil herb layer includes white wood-rush (*Luzula luzuloides*). In some regions of the park area, beech habitats with old-growth characteristics already exist and indicate the current potential natural vegetation type. Such reference sites can be used for fungal monitoring (Avis et al., 2017). Today, the Eifel National Park is classified as a protected area of the category II type with development status by the IUCN (International Union for the Conservation of Nature) (Dudley and Phillips, 2006), implying active management with focus on climate change adaptation. Between 2004 and 2034, different forest management practices are and will be applied with focus on climate change adaptation by converting non-native coniferous forest into native broadleaved forest. Planned forest management practices include mainly selection cutting of single spruce trees combined with tree underplanting of shade-tolerant European beech (Röös and Mauerhof, 2014), which can establish uneven-aged beech forests with a few light gaps (Dobrovlný and Cháb, 2013; Brang et al., 2014). Additionally, salvage logging is applied in Norway spruce forests after windstorm events to minimize possible bark beetle attacks (Eriksson et al., 2007). The Eifel National Park is influenced by Atlantic climate with a mean annual temperature of 6.5 °C and a mean annual precipitation of 1200 mm. The altitude ranges from 490 m a.s.l. (North-East) to 630 m a.s.l. (South-West). The parent rock has been shaped during Lower Devonian (Meyer, 1994) and is mainly dominated by red sandstone and slate, which are predominantly overlain by Cambisol and Stagnosol according to World Reference Base (WRB) for Soil Resources.

### 2.2. Study design

For the initial and final vegetation types of the spruce forest conversion process in the Eifel National Park, we used even-aged Norway spruce forests, which were managed with silvicultural strategies until 2004, and unevenaged, old-growth European beech forests that are likely to have been formed naturally in the last 100 years.

In addition, we pre-classified a spruce/beech mixed stage, which was close-to-nature managed by single spruce tree selection cutting and subsequently underplanted with beech trees. In 2007, beech trees (0.8–1.2 m) were planted beneath ~70-year-old Norway spruce trees, in a single-cut spruce forest to encourage the development of beech forests in the Eifel National Park (Röös and Mauerhof, 2014).

Contrary to the study design of Küffer and Senn-Irlet (2005), we decided to include two different post-disturbance management strategies in our study design as the area is occasionally affected by windstorm events. For the first strategy, we chose unmanaged spruce-windthrow areas, which have been formed by natural wind disturbance and were characterized by a high amount of coarse woody debris (CWD). For the second strategy, we chose salvage-logged spruce windthrow areas formed by natural wind disturbance and managed by salvage logging, which leaves fine woody debris (FWD) behind (Fraver et al., 2017; Rosenvald et al., 2018). Salvage logging without further management, such as tree planting, is comparable to clear-cutting (Thorn et al., 2018) and is also included in the management plan of the

Eifel National Park (until 2034).

To disentangle the process of fungal community shifts caused by the spruce forest conversion, we used a space-for-time substitution approach (Pickett, 1989; Blois et al., 2013). Thereby, in a stratified sampling design, five different forest conversion stages were *a priori* classified into three spatially independent replicated sites each, based on similar vegetation structure, site history and management impact to guarantee the following homogeneous habitat structures (Fig. 1B):

- (I) Norway spruce sites (*sp1* – *sp3*): Single species, even-aged, ~70-year-old Norway spruce forests, used for commercial wood production until 2004. After 2004, no further management was applied, but fallen trees were taken out, while only FWD remained.
- (II) Unmanaged windthrow sites (*wtp1* – *wtp3*): Single species Norway spruce forests that experienced high levels of windthrow in 2007. Thrown spruce trees were left behind at the time of our study, this CWD ( $\geq 7$  cm) had mostly the decay class II (bark and twigs present, solid) (Stöcker, 1999). Natural forest regeneration was already recognizable due to young trees of European beech or European white birch (*Betula pendula*).
- (III) Salvage-logged windthrow sites (*wtm1* – *wtm3*): Single species Norway spruce forest, influenced by the large-scale disturbance of various devastating windstorms in the years 1990 and 2007, followed by salvage logging. Thereby, all stems were removed, while both uprooted and rooted cut stumps were left.
- (IV) Spruce/beech mixed sites (*spb1* – *spb3*): ~70-year-old Norway spruce forest, close-to-nature managed by selection cutting of single spruce trees and underplanting of European beech trees in 2007. The sampling site *spb1* was in the neighbouring community forestry Monschauer Stadtwald due to limited areas of similar historical and management conditions within the National Park area. During the selection cutting process, only FWD remained, as the coarse wood was harvested.
- (V) European beech sites (*b1* – *b3*): Uneven-aged (multi-aged), old-growth beech forests with European beech as dominant tree species and without any management in a long period ( $> 100$  years). No fallen or standing dead wood were removed and led to high amounts of CDW and FWD. With 191 years, the study site *b1* was the oldest habitat and was characterized as a forest nature reserve of North Rhine-Westphalia (State Enterprise for Forestry and Timber North Rhine-Westphalia, 2016). The other study sites *b2* and *b3* were ~120 years old.

### 2.3. Site characteristics

All 15 study sites (each 10 m × 10 m) were buffered by an appropriate distance ( $\geq 100$  m) from each other (Fig. 1B). At five sample locations in each study site (middle & each corner), topsoil (0–10 cm depth, soil core  $\varnothing$  5 cm) and aboveground litter (layer OL) were separately collected. Topsoil is supposed to have the strongest effects on tree species (Augusto et al., 2003; Cools et al., 2014) and fungal abundance (Nacke et al., 2016). One part of each air-dried sample was used to measure pH values (pH) in deionized H<sub>2</sub>O at a 1:5 (w/v) ratio (shake for 60 min and rest for 3 h) by using a glass electrode (HANNA Instruments, HI 991300 pH EC/TDS). The other part was crushed using a mortar and a pestle. The powder was dried at 105 °C (topsoil) or 80 °C (litter) for 48 h to measure the total carbon (C) and nitrogen (N) contents using dry combustion on an Elementar VarioEL v.4.01 (Hanau Germany). We performed all determinations in duplicate.

In July/August of 2010 and 2011, cover values of vascular plant abundance were recorded in each study site using the Braun-Blanquet scale (Braun-Blanquet, 1964) in a modified version of Reichelt and Wilmanns, 1973. Species taxonomy was documented according to Jäger (2011). The vegetation data were mainly recorded to pre-classify the replicated study sites to represent the 5 forest conversion stages and to calculate Ellenberg indicator values (EIV). Average EIVs for light

availability (EIVL), for soil moisture (EIVM), for temperature (EIVT), for soil reaction (EIVR) and for nutrient/soil fertility (EIVN) were computed for each study site (Ellenberg, 2001). EIVs can act as representatives for environmental habitat conditions (Schaffers and Šýkora, 2000; Bartelheimer et al., 2016) within fungal surveys (Halbwachs and Bässler, 2013) instead of a direct determination of site variables, e.g. EIVN for biomass productivity (Hill and Carey, 1997; Wagner et al., 2007). Species richness (mean number of plant species observed in three replicates per stage) of light-demanding plant species (PRL) with EIVL values from 7 to 9 can act as a disturbance level indicator according to Boch et al., 2013. We recorded the surface temperature [°C] of each study site on ground-level with one data logger (OM-EL-USB-2, 2004–12, Omega Engineering Inc.). We used hourly recordings from 28th May to 16th September in the years 2011 and 2012. Subsequently, we calculated the difference of the daily surface temperature, defined as  $\Delta T_s = T_s(\max) - T_s(\min)$ , where  $T_s(\max)$  and  $T_s(\min)$  are the daily maximum and minimum surface temperature of each study site. Due to loss or damage of some data loggers in sites *spb1*, *spb3*, *b2* and *wtminus1*, the data from both years were merged. Averages of the daily surface temperature were used in the analyses. The same data collection was performed for the relative humidity [%] at ground level ( $\Delta H_s$ ). Microclimate (especially temperature) can be affected by changes in tree species (Augusto et al., 2003) and which is supposed to be an important driver for sporocarp establishment, growth or spore production (Boddy, 1983; Heilmann-Clausen et al., 2014; Pouska et al., 2016; Castaño et al., 2018). Canopy closure was assessed by visual estimation at one point during the vegetation surveys in comparable weather conditions and expressed as the percentage of each study site. GPS coordinates and elevation [m a.s.l.] of each site were determined with a GPS navigator (Garmin eTrex Legend® HCx). The overview about all environmental variables assessed can be found in the corresponding Data in Brief paper.

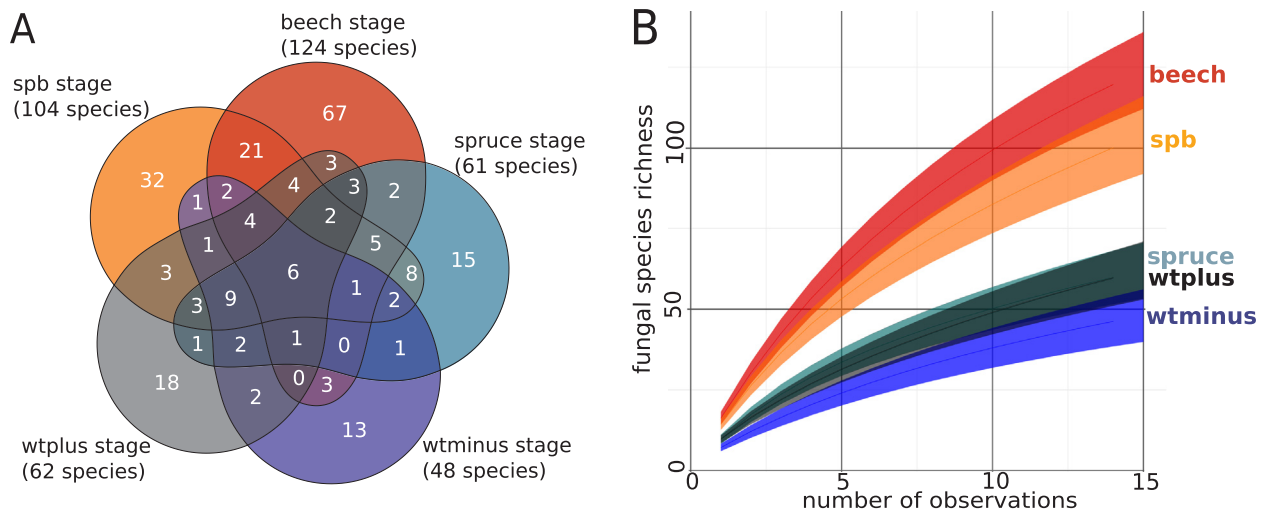
#### 2.4. Fungal data

We recorded the presence of all epigeous macrofungi (Basidiomycetes and Ascomycetes) visible to the naked-eye (Watling, 1995; Mueller et al., 2007). We examined sporocarps over 3 years (2010–2012) within the 15 study sites. Both windthrow sites were monitored only for 2 years (2011–2012). Here, we tried to compensate the time difference by similar observation frequencies for every site and stage (Data in Brief paper). Within each survey period, all study sites were sampled for ~3 h. Analyzing the fungal diversity, we did not measure the sporocarp abundance, as this parameter is species-specific. Most of these sporocarps were photographed in their natural habitat and identified *in situ*, while difficult species were collected to confirm their micro-morphological characteristics in the lab. Species identifications were performed using mainly Breitenbach and Kränzlin, 1984; Hansen et al., 1992; Gminder et al., 2000; Hansen et al., 2000; Krieglsteiner, 2000; Krieglsteiner and Gminder, 2001; Gminder and Krieglsteiner, 2003; Consiglio and Setti, 2008; Knudsen et al., 2008; Wergen, 2017b and Wergen, 2017a. Critical taxa were confirmed by experienced mycologists (see acknowledgments). The current nomenclature was validated using the Mycobank Database ([www.mycobank.org](http://www.mycobank.org); last accessed 26 March 2018). Myxomycetes inside the 10 m × 10 m study site were excluded, while taxonomically critical taxa and anamorph forms were included. Doubtfully identified species are indicated by the abbreviation ‘cf.’ or ‘aff.’ in the species names. Fungi identified to the genus only are indicated ‘sp.’. The threat status of each species was selected by red lists for fungi available for North Rhine-Westphalia (LANUV NRW, 2011) and for Germany (Matzke-Hajek et al., 2016). We estimated the mean species richness by averaging the total number of fungi of the three replicated sites per each stage. Further, the fungal frequency was defined as the number of occurrences of the fungal species across all 15 observations per stage. We distinguished the fungal species based on similar functional roles in

ecosystem processes (Blondel, 2003) according to field conditions and literature (Winterhoff, 1992; Ferris et al., 2000; O’Hanlon, 2011) into eight different functional groups: wood-decaying fungi existing on dead wood of branches, stumps, sticks, and trunks (WDF), litter-decaying fungi living on litter, needles on the ground (LDF), ectomycorrhizal fungi (EMF), pathogenic fungi (P), wood- or litter-decaying fungi (WDF/LDF), fruit-decaying fungi living on spruce cones and beechnuts (FDF), wood-decaying fungi existing on dead wood or living wood (WDF/P) and dung-decaying fungi (DDF). Any fungi with bryophyte- or pyrenomycete-macrofungus relationships were grouped with EMF, such as *Rickenella fibula* or *Tremella globiospora*.

#### 2.5. Statistical analysis

Statistical analyses were performed using R software version 3.3.1 (R Development Core Team, 2016) and PC-ORD version 6 (McCune and Mefford, 2011). We prepared sample-based rarefaction curves to show how the cumulative species richness responds by following an increased sampling effort up to the maximum of 15 observations per stage (*iNEXT* function, *iNEXT* package in R, Hsieh et al., 2016). Sample-based rarefaction curves were plotted only with interpolated measures up to the maximum observed species richness, where the significance was determined graphically by an overlap of 95% confidence intervals with 500 bootstrap replications. The proportions of unique and shared fungal species among the five forest conversion stages were calculated and visualized in a Venn diagram (*venn* function, *venn* package in R, Dusa, 2017). We fitted generalized linear models (GLM) to determine the effects of different forest stages on the mean species richness of all fungi and fungi within the dominant functional groups respectively (wood-decaying fungi, ectomycorrhizal fungi and litter-decaying fungi). The dependent variable was the mean species richness, meanwhile the independent variable represented the forest conversion stage (*glm* function, *stats* package in R, R Development Core Team, 2016). As our fungal data were not significantly over-dispersed (*dispersiontest* function, *AER* package in R, Kleiber and Zeileis, 2008), we modeled based on the Poisson distribution ( $p < 0.05$ ). That was followed by a Tukey’s honestly significantly different (TukeyHSD) post hoc test (*glht* function, *multcomp* package in R, Hothorn et al., 2008) to perform a pairwise comparison for each forest conversion stage. The visualization of the mean species richness per stage was carried out using GraphPad Prism version 6.00 (GraphPad Software, La Jolla California USA, [www.graphpad.com](http://www.graphpad.com)). We used non-transformed species community data to test the hypothesis of no difference in species composition between the five forest conversion stages using a multi-response permutation procedure (MRPP; Mielke, 1991) test on Jaccard similarities and subsequently a pairwise comparison (PC-ORD). Further, unconstrained NMDS (non-metric multidimensional scaling; Shepard, 1962; Kruskal, 1964) ordinations were employed (*metaMDS* function, *vegan* package in R, Oksanen et al., 2015) to visualize the community composition of (i) all fungi, (ii) wood-decaying fungi, (iii) ectomycorrhizal fungi and (iv) litter-decaying fungi respectively, across different forest conversion stages in a 2D-solution using Jaccard distance measure (999 permutations). Various environmental variables (topsoil pH, litter pH, topsoil C/N, litter C/N, EIVL, EIVN, EIVM, EIVR, EIVT, topsoil C, litter C, topsoil N, litter N, CC,  $\Delta T_s$ ,  $\Delta H_s$ , PRL and mean fungal species richness) were used for the additional vector analysis to fit possible variables onto the NMDS ordination (*envfit* function, *vegan* package in R, Oksanen et al., 2015). NMDS scores were calculated by multiple coefficient of determination ( $R^2$ ) and all significant explanatory environmental variables were plotted as vectors in the NMDS ordination space ( $p < 0.1$ ).



**Fig. 2.** **A:** Venn diagram with all 235 fungal species of the five forest conversion stages, displaying shared and unique fungi. Numbers represented in parentheses are the value of all observed fungi per study stage (cumulative species richness). **B:** Sample-based rarefaction curves (thin solid lines,  $n = 15$  observations per stage) with 95% confidence intervals (shaded areas, 500 replications) of all five forest conversion stages (only interpolated and observed data); Norway spruce (*spruce*, cyan), salvage-logged windthrow (*wtminus*, blue), unmanaged windthrow (*wtplus*, black), close-to-nature managed spruce/beech forest (*spb*, orange) and European beech (*beech*, red). Note that *spruce* showed a similar cumulative species richness as *wtplus*, and so is hidden by *wtplus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 3. Results

#### 3.1. Species richness

A total of 235 fungal species in 141 genera were observed within the 15 study sites, including 5 taxa identified only to genus level (Data in Brief paper). The most frequent species were *Fomitopsis pinicola*, *Calocera viscosa* and *Lycoperdon perlatum*. The most species-rich genera were *Mycena* and *Phaeosphaeria*. Half of the dataset (118 species) were found only in one study site, whereas no species occurred in all fifteen sites. Six species (*Fomitopsis pinicola*, *Lycoperdon perlatum*, *Hypholoma fasciculare*, *Hypholoma capnoides*, *Clitocybe fragrans* and *Trichaptum abietinum*) were observed in all five conversion stages, whereas unique species (found only in one stage) increased from *wtminus* < *spruce* < *wtplus* < *spb* < *beech* and consisted of 13, 15, 18, 32 and 67 fungi respectively (Fig. 2A). Nine of these unique species were found in all three replicate study sites of the representing forest conversion stage, from which eight were observed in *beech* and one (*Panellus mitis*) in *wtplus*. The beech stage shared 37 species with all other stages apart from the spruce stage. In contrast, the spruce stage shared 26 species with all other stages, apart from the beech stage, including the aggressive plant pathogen *Heterobasidion annosum*. Twenty-one species were exclusively found in the beech reference stage and the spruce stage, including ubiquitous species such *Ampulloclitocybe clavipes* or *Clitocybe nebularis*. We found 14 species in the *spruce* and both beech-inhabiting stages (*beech* and *spb*), whereas 18 species co-existed in *spruce* and both windthrow stages (Fig. 2A). Both windthrow stages shared only two species exclusively: *Antrodia serialis* and *Pseudolachnea hispidula*, while only one species (*Calocera furcata*) exclusively occurred in *spb* and both windthrow stages.

The cumulative species richness increased from *wtminus* < *spruce* < *wtplus* < *spb* < *beech* and consisted of 48, 61, 62, 104 and 124 fungi respectively (Fig. 2A and B). None of the sample-based rarefaction curves reached an asymptote but distinctly differed in curve slopes. The confidence intervals of both beech-inhabiting stages (*beech* and *spb*) did not overlap with those of the other stages (*spruce*, *wtminus*, *wtplus*), indicating a significant difference. In contrast, we observed a total curve overlap of *spruce* and *wtplus*, followed by *wtminus*, which had the lowest cumulative species richness.

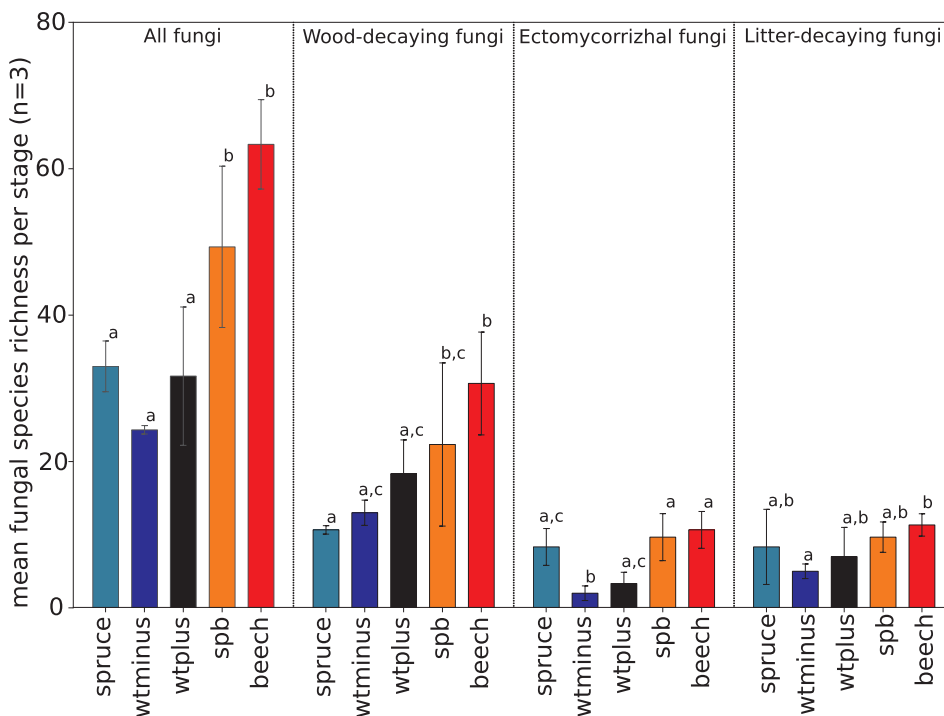
The number of red listed and threatened fungal species increased

from *wtplus* < *wtminus* < *spruce* < *spb* = *beech* and consisted of 2, 3, 5, 6 and 6 species respectively (Data in Brief paper), while the number of unique red list species increased from 1, 1, 3, 3 and 4 fungi respectively. The *spb* stage exhibited exclusively one red list species (*Fayodia bishaerigera*) and two threatened species (*Stropharia hornemannii* and *Ramaria gracilis*).

The mean species richness increased from *wtminus* < *wtplus* < *spruce* < *spb* < *beech* and consisted of 24.3, 31.7, 32.3, 49.3 and 63.3 fungi respectively (GLM,  $p < 0.05$ , Fig. 3). Overall, *wtminus* showed the lowest unique, cumulative and mean species richness, which did not differ remarkably from those of *wtplus*. Further, we found not significant difference in the mean species richness among *spruce* and both windthrow stages (Fig. 3), together with a large overlap in the cumulative species richness of *spruce* and *wtplus* (Fig. 2B). This result indicated, that despite different survey periods (2 years versus 3 years), a comparison between the windthrow stages and all other stages could be performed due to a low species variability in the windthrow stages.

#### 3.2. Functional structure

The dominant functional groups (> 15% of the total species richness) were WDF (95 species, 40.4%), LDF (62 species, 26.4%) and EMF (42 species, 17.9%). The remaining taxa (36 species, 15.3%) were almost equally divided into the other five functional groups. Due to the very low presence and limited significant responses of the other five functional groups, we focused on the three dominant groups. The most common WDF were *Calocera viscosa* and *Dacrymyces stillatus*. The most frequent EMF were *Laccaria laccata* var. *pallidifolia* and *Russula ochroleuca*. Within the LDF, *Lycoperdon perlatum* and *Clitocybe fragrans* showed the highest occurrence. The mean species richness of WDF, LDF and EMF increased from *spruce* < *spb* < *beech* (Fig. 3). Interestingly, we found a continuous increase of the WDF species richness from *spruce* < *wtminus* < *wtplus* < *spb* < *beech*, whereas the EMF richness and the LDF richness showed a decline within both windthrow stages, similar to the response pattern of the overall fungal species richness. Only the EMF richness showed a significant decrease from *spruce* to *wtminus*, whereas the only significant difference of the LDF richness was found between *wtminus* and *beech* (GLM,  $p < 0.05$ , Fig. 3). The WDF richness of *spruce* and both windthrow stages were similar, while the beech-containing forests (*beech* and *spb*) had higher species richness



**Fig. 3.** Mean species richness with standard deviation in bar plots ( $n = 3$  study sites) of all 235 fungal species in general and within the dominant functional groups; wood-decaying fungi, ectomycorrhizal fungi and litter-decaying fungi at all five forest conversion stages; Norway spruce (*spruce*), salvage-logged windthrow (*wtminus*), unmanaged windthrow (*wtplus*), close-to-nature managed spruce/beech forest (*spb*) and European beech (*beech*). Bars that share the same letter are not significantly different from each other (GLM,  $p < 0.05$ , TukeyHSD).

(GLM,  $p < 0.05$ , Fig. 3).

### 3.3. Community composition

MRPP indicated distinct community compositions of all fungi ( $A = 0.14$ ,  $p < 0.001$ ), WDF ( $A = 0.12$ ,  $p < 0.001$ ), EMF ( $A = 0.17$ ,  $p < 0.001$ ) and LDF ( $A = 0.1$ ,  $p < 0.001$ ) among each forest conversion stage. Further pairwise comparisons showed that the fungal community composition of both windthrow stages could not be distinguished from each other. This result is supported by site-based NMDS ordination plots (Fig. 4A–D).

The fungal community composition of the beech sites showed the largest distance to all other conversion stages (Fig. 4A). The community composition of *spb* was positioned between both single species forest stages (*beech* and *spruce*). This separation remained when the three dominant functional groups were considered separately (Fig. 4B–D). Further, NMDS clustered both windthrow stages together, in contrast to the forested stages (*spb*, *beech* and *spruce*), while the LDF community did not separate in this pattern (Fig. 4D).

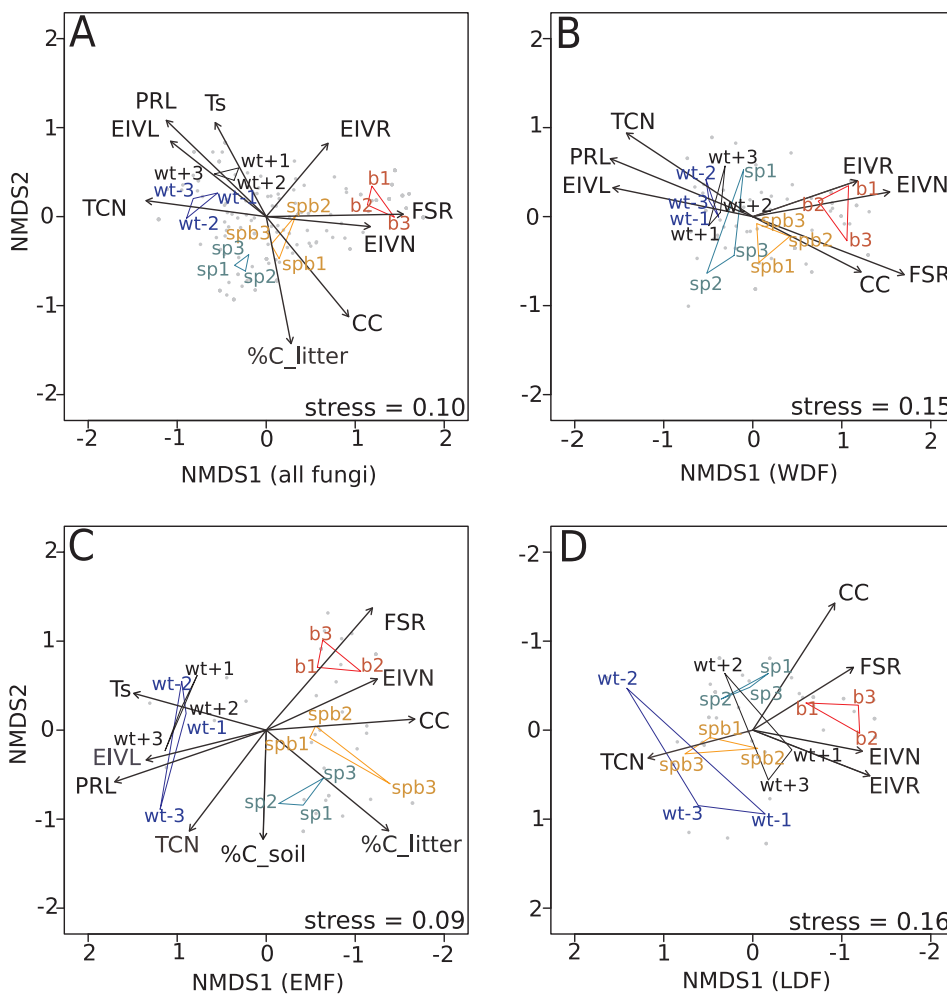
Beside the tree species composition change from spruce to beech and forest management, the fungal community was strongly affected by two other drivers. The nutrient availability changed according to correlations with topsoil C/N ( $R^2 = 66\%$ ), EIVN ( $R^2 = 49\%$ ) and litter C ( $R^2 = 75\%$ ), demonstrating higher soil fertility and better litter quality within the beech-inhabiting stages (*beech* and *spb*) compared to the spruce stage and windthrow stages (Fig. 4A). Further, the overall fungal species composition was affected by a light regime change according to correlations with canopy closure (CC,  $R^2 = 76\%$ ), delta Ts ( $R^2 = 52\%$ ), PRL ( $R^2 = 87\%$ ) and EIVL ( $R^2 = 67\%$ ), indicating higher temperature fluctuation and light transmission within both open windthrow stages compared to the three more dense forested stages (*beech*, *spb*, *spruce*). Both windthrow stages showed high surface temperature fluctuations (in average up to  $29.1 \pm 12.0$  in *wtplus2*) compared to the low temperature fluctuations within the forested stages, where the beech forest sites showed the lowest mean surface temperature fluctuations with  $2.7 \pm 1.6$  in *b2* (Data in Brief paper). The mean fungal species richness (FSR,  $R^2 = 85\%$ ) was highly related to the community distribution and showed the highest FSR within the beech-inhabiting stages (*beech* and

*spb*). The latter pattern remained when the three dominant functional groups were considered separately (Fig. 4B–D). Excluding both windthrow stages from the community composition analysis, CC and Ts were not influencing factors, while PRL and EIVL still indicated a closer canopy cover of the beech forests. Neither litter C/N, delta Hs nor EIVM or pH in litter or topsoil were significantly correlated ( $p < 0.1$ ) (Fig. 4A–D). Our study showed, that the three dominant functional groups responded differently to different explanatory variables. Thus, the WDF community (Fig. 4B) was not significantly influenced by the investigated microclimate (represented by delta Ts), in contrast to the EMF community distribution (Fig. 4C). Further, the EMF community was affected by carbon sources from topsoil and litter layer as indicated by the correlations with total litter C ( $R^2 = 72\%$ ) and topsoil C ( $R^2 = 34\%$ ), whereas the LDF community was more affected by CC ( $R^2 = 63\%$ ) and EIVR ( $R^2 = 43\%$ ) than by microclimate, PRL, EIVL or litter and topsoil variables.

## 4. Discussion

### 4.1. Effect of tree host species on macrofungal communities

We found distinct fungal community compositions, each with a different species richness, among habitats with different tree species compositions, consistent with findings from previous studies (Buée et al., 2011; Goldmann et al., 2015). Thereby, the fungal community composition of the old-growth beech forests showed the largest distance to those of all other forest conversion stages (Fig. 4). We showed that the unique, the cumulative and the mean fungal species richness in single species forest stage with European beech (*beech*) was twice as high as in single species forest stage with Norway spruce (*spruce*). We found many host-specific fungi within *beech*, such as *Xylaria carpophila*, *Kretzschmaria deusta*, *Mycena crocata*, *Mycena rosea* or *Bisporella citrina* (Breitenbach and Kränzlin, 1984; Krieglsteiner and Gminder, 2001). Further, the spruce/beech mixed forest stage (*spb*), which was managed by single tree species selection cutting and beech underplanting, showed an intermediate position between *beech* and *spruce* in terms of species composition and species richness, while *spb* shared 21 species exclusively with *beech* and only 8 species with *spruce*. Thus, one striking



**Fig. 4.** Two-dimensional NMDS biplots of all fungi (A), wood-decaying fungi (B), ectomycorrhizal fungi (C) and litter-decaying fungi (D) in relation to five different forest conversion stages respectively; Norway spruce (*sp1-sp3*, cyan), salvage-logged windthrow (*wtminus1-wtminus3*, blue), unmanaged windthrow (*wtplus1-wtplus3*, black), close-to-nature managed spruce/beech forest (*spb1-spb3*, orange) and European beech (*b1-b3*, red). The final stress values are listed in the graphs. Grey points represent fungal species and the envelopes mark the three replicated study sites of each *a priori* classified forest conversion stages. The ordinations are based on Jaccard distance, including the significantly correlated environmental variables as fitted vectors ( $p < 0.1$ ): topsoil C/N (TCN), delta Ts (Ts), total carbon in topsoil (%C<sub>soil</sub>) and in litter (%C<sub>litter</sub>), EIV for nutrient (EIVN), EIV for light availability (EIVL), EIV for soil reaction (EIVR), plant richness of light-demanding species (PRL), mean fungal species richness (FSR) and canopy closure (CC) (999 permutations). All other environmental variables were not correlated and were excluded. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pattern in terms of the fungal species richness and community structure, in general as well as within EMF and WDF, was the contrast between beech-inhabiting stages (*beech* and *spb*) and *spruce*. Our results showed that the fungal community structure is highly related to the tree species, which is similar to the findings from Kutzegi et al. (2015), Rosinger et al. (2018) and Dvořák et al. (2017).

The mean species richness of WDF, the most dominant functional group, increased fourfold from *spruce* < *spb* < *beech* and consisted of 8.3, 21.3, 29.0 species respectively. Hereby, the beech forest was characterized by highly substrate-specific WDF such as *Panellus stipticus*, *Phlebia radiata*, *Mycena haematopus*, *Jackrogersella multiformis*, or *Xylaria hypoxylon* (Tyler, 1992; Winterhoff, 1992). In contrast, the spruce forest displayed more WDF generalists, such as *Hypholoma fasciculare* or *Gymnopilus penetrans*, which were partially observed in *beech* as well, and are known to grow commonly with other tree species (Winterhoff, 1992; Buée et al., 2011). Further, the beech forest harbored WDF species such as *Ganoderma applanatum*, *Meripilus giganteus* and *Fomes fomentarius*, which are typical of old growth deciduous forests in central Europe (Müller et al., 2007) but also known as weak parasites together with *Kretzschmaria deusta*, whereas the spruce forest community consisted of more phytopathogens such as *Stereum sanguinolentum*, *Armillaria ostoyae* and *Heterobasidion annosum* (Honold et al., 1997). The latter can lead to annosum root rot, which is widely regarded as the most important economically and ecologically destructive forest disease in forests of the northern hemisphere (Asiegbu et al., 2005). This result is coherent to previous studies, showing that *spruce* harbor a lower number of WDF compared to *beech* (Küffer and Senn-Irlet, 2005; Dvořák et al., 2017), probably due to the absence of old-growth characteristics

such as spruce-CWD (Paillet et al., 2010). WDF richness and community structure are most likely dependent on the tree species identity of the dead wood (Baber et al., 2016; Purahong et al., 2017), on the available amount, quality and decomposition degree of CWD or FWD, as well as on forest management (Høiland and Bendiksen, 1996; Heilmann-Clausen, 2001; Heilmann-Clausen and Christensen, 2004; Küffer and Senn-Irlet, 2005; Ódor et al., 2006; Blaser et al., 2013). Different forest managements or a low time frame since management abandonment can cause fungal species reductions (Winterhoff, 1992; Blaser et al., 2013). After 2004, no further management was applied in the investigated spruce forests, but fallen trees were taken out, while only FWD remained. The *spb* was close-to-nature managed, while only FWD remained, which was in contrast to the < 100 years unmanaged beech forests, where the CWD remained. As our results showed a significant increase in the WDF species richness of *spb*, over corresponding single spruce forests, we assumed that the applied forest thinning produced appropriate amounts of spruce-FWD. Further, no negative response of WDF richness was observed when comparing the mixed and the single species spruce tree forests, similar to the finding of Purahong et al. (2014), indicating a moderate thinning process.

The work of Utschik and Helfer (2003) showed that the fungal species richness is increased even when only a few beech trees are mixed within spruce forests. The introduction of beech as another valuable tree host was substantiated by beech-related EMF species such as *Lactarius subdulcis*, *Lactarius blennius*, *Xerocomellus chrysenteron* and *Russula nigricans* (Winterhoff, 1992; Buée et al., 2011; Kutzegi et al., 2015), which were found exclusively in both beech-inhabiting stages. We observed an increase of the EMF richness from *spruce* to *spb* to *beech*

by 8.6, 10.3 and 12 species respectively. This is coherent to the results of Buée et al. (2011). Other EMF discovered exclusively in *spb* were, e.g. *Caloboletus calopus*, which is known to grow in montane spruce and beech habitats on acid soil (Gminder et al., 2000) and *Cortinarius albobolaceus*, which is beech- and spruce-associated.

Theoretically, similar amounts of species richness among the spruce forests and beech forests are possible, as many EMF in temperate forests are associated with the tree families *Fagaceae* and *Pinaceae* (Ishida et al., 2007; Courty et al., 2010). Focusing on the total amount, under European beech we found 24 EMF with deciduous- or even beech-associated tree preferences, such as *Byssocorticium atrovirens* (Buée et al., 2005), whereas under Norway spruce we observed 15 EMF with a range of high to low host preferences such as *Hygrophorus olivaceoalbus* (high preference) or *Russula ochroleuca* and *Laccaria amethystina* (lower preferences) (Gminder et al., 2000; Krieglsteiner and Gminder, 2001). Previous studies indicated that non-native tree species have difficulties forming mycorrhizal associations with native EMF and thus may fail to establish themselves (Dickie et al., 2010). Another factor could be the different root biomass, structure and density between Norway spruce and European beech, which can lead to differences in the EMF community composition (Peay et al., 2011; Goldmann et al., 2015; Nacke et al., 2016). Although all stages exhibited EMF, the six shared fungal species in all forest conversion stages were saprotrophic fungi on wood or litter with lower host, substrate or management preferences (Fig. 2A). Eleven EMF found in *spruce* coexisted in *beech*, as well as within the other forest conversion stages. The ability to accept native EMF is essential to ensure a successful introduction of non-native ectomycorrhizal tree species (Pringle et al., 2009).

Another reason for the species richness increase in the *spb* stage could be the introduction of beech trees after forest thinning as a valuable substrate source due to their easy-to-decompose leaves, compared to highly recalcitrant spruce needles (Ludley et al., 2008; Nacke et al., 2016). This is enforced by the occurrence of the LDF *Rhizomarasmius setosus*, found in all three replicates of the *spb* stage (and one beech site), which is highly related to beech litter and a red list species for North Rhine-Westphalia (LANUV NRW, 2011). We observed four red list species in the spruce stage, including two red list species found exclusively in this stage; *Mycena aurantiomarginata* and *Psilocybe crobula*. In general, species richness and the amount of red list fungi increase with higher forest age and dead wood availability (Nordén et al., 2013). However, both species were LDF with lower substrate and soil preferences. *Mycena aurantiomarginata* can be found in coniferous forest such as spruce or fir, while *Psilocybe crobula* can inhabit either deciduous or coniferous woody sticks or branches (Krieglsteiner and Gminder, 2001; Gminder and Krieglsteiner, 2003). LDF is a substrate associated functional group (Boddy, 2008), where the type of tree debris, such as needles or leaves, strongly influences the presence or absence of specialized saprotrophic fungi (Zhou and Hyde, 2001). Our results indicated a slight increase of the LDF richness and composition change from *spruce* to *spb* to *beech*, probably due to adverse environmental conditions under Norway spruce through a thicker litter layer and a lower decomposition rate of spruce needles (Kazda and Pichler, 1998; Augusto et al., 2002; Berger and Berger, 2014).

The introduction of beech as another valuable tree host is coupled with different litter and soil conditions (Jones et al., 2003; Kutszegi et al., 2015; Urbanová et al., 2015). Indeed, we found that the forest conversion from Norway spruce forests to European beech forests benefits from a nutrient increase together with a decrease in temperature fluctuations. The contribution of environmental variables showed that nutrient availability in topsoil was one of the most important factors for the fungal community distribution. This is not surprising, as the tree species is a major factor explaining C/N ratios in European forest soils (Cools et al., 2014), also in terms of fungal communities (Goldmann et al., 2015; Dvořák et al., 2017). Although other studies indicated a high relation between pH and macrofungal communities (e.g. Wubet et al., 2012), our study did not indicate that. This result was

confirmed by pH-intolerant fungal species, such as *Ricknella fibula*, *Trichaptum abietinum* and *Russula ochroleuca*, existing randomly in all study stages. Our functional group analysis showed that species with a high substrate or host specificity were also more sensitive about environmental variables than those with a lower substrate or host specificity (Fig. 4A–D) and can reveal group-specific environmental variables as previously indicated by other studies (O'Hanlon, 2011; Kutszegi et al., 2015). Compared to beech, differences in the light regime due to lower light transmittance in Norway spruce are known (Augusto et al., 2002; Dobrovolský and Cháb, 2013). However, our results suggested the opposite, as we saw a lower light regime together with a more stable and humid microclimate of the *beech* compared to *spruce*, probably due to the more protective canopy closure. As sporocarp growth of WDF and EMF is reduced at higher temperatures (Straatsma et al., 2001), the lower temperature fluctuations in *beech*, compared to *spruce*, were probably a driver for the fungal species richness.

Comparing the total species richness of 235 taxa, we found 6.4% unique spruce-related fungi, in contrast to 28.5% fungi, which were only associated with the studied beech forests. Comparable observations showed similar proportions studying beech-related macrofungal diversity (Tyler, 1985; Brunet, 2007; Brunet et al., 2010). Differences in species richness between spruce and beech habitats can also be found within other important soil organism groups such as oribatids or nematodes (Scheu et al., 2003; Elmer et al., 2004; Chauvat et al., 2011; Zaitsev et al., 2014). We observed only two fungal taxa occurring exclusively in the spruce forest and the beech forest; *Ampulloclitocybe clavipes* and *Clitocybe nebularis*, which had low host preferences, as we found them either in beech or spruce habitats.

#### 4.2. Effects of windstorm events and management in Norway spruce forests on fungal communities

We assumed that unmanaged and salvage-logged Norway spruce windthrow stages would vary in fungal species richness and community composition, especially due to different dead wood amounts and structures (CWD vs. FWD). Our results did not support this hypothesis, as we could not find a significant difference of the fungal species richness or community composition, may be due to a short sampling period. However, we found a slight increase of the WDF richness, when comparing the salvage-logged windthrow stage (*wtminus*) with the unmanaged windthrow stage (*wtplus*). The occurrence of *Pycnoporellus fulgens* only in *wtplus* indicated a high spruce dead wood availability. Consistent with previous findings of Runnel and Löhmus (2017), our study suggested, that this polypore has no indicator quality for old-growth forests, which was previously suggested by Piatek (2003), but rather indicates large dead wood amounts. Despite huge differences in dead wood amounts and structure, we recognized a dominance of similar fungal generalists in both windthrow stages. In general, changes in species richness are related to changes in rare species that are more sensitive to unfavorable environmental conditions or changes in soil attributes. However, both windthrow stages showed the typical fungal community of spruce windthrow stages in a temperate zone with the occurrence of e.g. *Gloeophyllum sepiarium* and *Stereum sanguinolentum* (Schlechte, 2002). As different structures and amounts of dead wood can influence the fungal diversity, and the fact that especially FWD can encourage higher fungal diversity compared to CWD (Heilmann-Clausen and Christensen, 2004; Küffer and Senn-Irlet, 2005), we assumed that after salvage logging in *wtminus*, probably enough FWD was available and led to these indistinguishable results between *wtminus* and *wtplus*. This is supported by the fact that we observed 18 unique species in the *wtplus* consisting of 50% WDF (including two red list species, *Mycena amicta* and *Mycena purpureofusca*), while *wtminus* harbored 13 unique species of which 50% were LDF such as the ascomycetous fungus *Leptosphaeria maculans*. Previous studies showed that the presence of FWD can be important for many fungi, especially for ascomycetes (Nordén et al., 2004) and some rare or red list species



(Schlechtle, 2002; Heilmann-Clausen and Christensen, 2004).

We observed a reduction of EMF richness and a fungal community shift to fast-growing species with ruderal-like characteristics within both windthrow stages, compared to intact and single species Norway spruce forests, most likely due to the tree mortality (Durall et al., 2006). The reduction of EMF richness will probably have effects on the nutrient availability and the ecological succession of these disturbed windthrows. Molecular methods have shown that some EMF, such as *Thelephora terrestris* (found in both windthrow stages), can still be found 10 years after a windstorm event in the soil layer of cleared windthrow areas without an adequate tree host (Egli et al., 2002; Jones et al., 2003). Such disturbance-adapted EMF can grow from resistant propagules in soil or from wind dispersed spores of the surrounding environment (Egli et al., 2002; Kranabetter, 2004; Simard, 2009). Nevertheless, we found e.g. the EMF *Leccinum scabrum* in the unmanaged windthrow stage, which is known to grow closely associated to birch (*Betula pendula*) (den Bakker et al., 2004). Young birch trees, present in the unmanaged windthrow stage, indicate that we would group *wtplus* as an early successional habitat after natural wind disturbance. Indeed, the fungal community composition analysis confirmed this, as the EMF *Paxillus involutus* (found in the unmanaged windthrow) together with the EMF *Laccaria laccata* (observed in both windthrow stages) are known to form associations with several tree species and are also primary-stage fungi according to Buée et al. (2011).

## 5. Conclusion

Introducing native European beech trees in single Norway spruce tree selection cutting forests on acidophilic soil significantly increased the macrofungal species richness over corresponding single Norway spruce forests. Our findings indicated that Norway spruce can act as a suitable host tree for some native macrofungi, even outside its natural growth area. However, in terms of a climate-adaptive tree species change, we reinforced the assumption that European beech, on suitable sites, can harbor a more unique, specialized and diverse fungal community, especially for the dominant functional groups EMF and WDF, compared to plantations of Norway spruce, where this tree host is not native. Further, we showed that windstorm events in Norway spruce forests will have a negative impact on richness and structure of the fungal community composition, especially after further salvage logging. We indicated that old-growth European beech forests (> 120 years old) showed highly distinct macrofungal communities together with a two times higher fungal species richness compared to ~70 years old Norway spruce forests. This reflects the importance of reestablishing European beech ecosystems and their related environmental conditions for fungal communities. A follow-up survey of periodic fungal monitoring in relation to dead wood amounts may elucidate further insights.

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