



Functional response of lignicolous fungal guilds to bark beetle deforestation



Claus Bässler^{a,*}, Jörg Müller^{a,b}, Marc W. Cadotte^c, Christoph Heibl^d, Johannes H. Bradtka^e, Simon Thorn^a, Hans Halbwachs^f

^a Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

^b Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center for Food and Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising-Weihenstephan, Germany

^c University of Toronto – Scarborough, Department of Biological Sciences, 1265 Military Trail, Toronto, ON, Canada M1C 1A4

^d Technical University Munich, Plant Biodiversity Research, Emil-Ramann Strasse 2, 85354 Freising, Germany

^e AELF Tirschenreuth, Bereich Forsten, Wunsiedler Str. 15, 95478 Kemnath, Germany

^f German Mycological Society, Danzigerstr. 20, 63916 Amorbach, Germany

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ABSTRACT

Conifer-dominated forests in the northern hemisphere are prone to large-scale natural disturbances, yet our understanding of their effects beyond changes in species diversity is limited. Bark beetle disturbances provide dead wood for lignicolous fungal guilds and increase insolation but also desiccation. We investigated whether species richness of these guilds increases and functional diversity decreases after bark beetle disturbance, which would promote through habitat filtering the coexistence of species adapted to harsh conditions, i.e. light stress for lichens and substrate desiccation for wood-inhabiting fungi.

We sampled epixylic and epiphytic lichens (primary producers) and wood-inhabiting fungi (mainly wood decomposers, some form ectomycorrhizas) in the Bohemian Forest (Long Term Ecological Research – LTER – Site Bavarian Forest National Park), an area in Central Europe most heavily affected by the bark beetle *Ips typographus*, on undisturbed plots and disturbed plots with spruce (*Picea abies*) dieback 8 years ago. We analysed species diversity, functional diversity (optimized by phylogeny), and functional compositions.

Species richness of lichens but not that of wood-inhabiting fungi was higher on disturbed plots than on undisturbed plots. Community compositions of both guilds differed considerably on disturbed and undisturbed plots. On both types of plots, lichen communities were clustered according to functional diversity, which indicated habitat filtering, and fungal communities were overdispersed, which indicated competition. Disturbance increased the strength of these two patterns only slightly and was significant only for fungi. Single-trait analysis revealed changes in the functional composition; on disturbed plots, lichenous species with larger and more complex growth forms and fungi with large, perennial fruit bodies were favoured. Although the forest canopy changed tremendously because of the bark beetle disturbance, the most important driver of lichen and fungal diversity and mean trait assemblages seemed to be the enrichment of dead wood. The changes in insolation and moisture did not act as habitat filters for either guild. This indicated that the assembly patterns of lichen and fungal communities in coniferous forests are not affected by stand-replacing disturbances in contrast to the predictions for other disturbance regimes.

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1. Introduction

In Europe alone, coniferous forests cover about 88 million hectares, compared to 65 million ha of deciduous forests (Pope, 2014). Most coniferous forests are prone to stand-replacing natural disturbance, such as windthrow, fire or insect outbreaks (Seidl et al., 2011). Such disturbances in Europe damaged 1.75 billion m³ of timber during the second half of the 20th century (Schelhaas

* Corresponding author. Tel.: +49 85529600157.

E-mail addresses: baessler.forst@gmx.de (C. Bässler),

joerg.mueller@npv-bw.bayern.de (J. Müller), mcadotte@utsc.utoronto.ca

(M.W. Cadotte), christoph.heibl@gmx.net (C. Heibl), johannes.bradtka@t-online.de

(J.H. Bradtka), simon@thornonline.de (S. Thorn), halb.wax@onlinehome.de

(H. Halbwachs).

et al., 2003). It is predicted that the frequency and severity of disturbances will increase within the next century. One reason is the change in tree species composition during the first half of the 20th century towards even-aged conifers (Spiecker, 2000). Another contributing factor will probably be climate change (Schelhaas et al., 2003; Seidl et al., 2011, 2014).

After severe disturbances, forest sites are characterized by open environments with a high level of structural complexity (e.g. snags, downed boles) and spatial heterogeneity at multiple spatial scales (Swanson et al., 2011). The complexity arises because disturbances normally do not damage forests uniformly. Moreover, legacies are retained, e.g. undisturbed understorey and few still-living trees (e.g. Swanson et al., 2011). It is therefore not surprising that disturbance overall increases species diversity, as has been documented across different disturbance regimes (reviewed in Swanson et al., 2011) and also explicitly in areas heavily affected by the spruce bark beetle (*Ips typographus*) in Central Europe (Beudert et al., 2015).

Apart from vascular plants (e.g. Halpern, 1989; Huston and Smith, 1987; Jonsson and Esseen, 1998), the mechanisms and underlying patterns of why and how species of most taxa assemble following disturbance is poorly understood (Mouillot et al., 2013). One way to deepen our understanding of the underlying mechanisms is to consider the phylogenetic and phenotypic (functional) similarity among species. On one hand, such information provides clues on possible shifts of the dominant assembly pattern along disturbance, from neutral or limiting similarity towards habitat filtering (e.g. Gravel et al., 2006; Hubbell, 2001; Mouillot et al., 2013; Pausas and Verdú, 2010). On the other hand, studying the functional diversity (calculated from the trait dissimilarity among species within assemblages) along disturbance gradients provides information on ecosystem processes, as functional diversity is defined as “the value and range of those species and organismal traits that influence ecosystem functioning” (Tilman, 2001).

Post-outbreak habitats are often characterized by higher insolation and heat, huge temperature variations, higher wind speeds, lower humidity and increased desiccation compared to the conditions before (Boddy, 1983; Peterson and Leach, 2008; Swanson et al., 2011). Hence, following a deterministic model (sensu Mouillot et al., 2013), the total trait space should decrease non-randomly with disturbance, as species with specific functional traits may be favoured under the altered conditions (Mouillot et al., 2013).

Fungi are major players in the functioning of forest ecosystems. Those having a mutualistic relationship with trees (e.g. ectomycorrhizal fungi) or with algae (lichens) contribute substantially to the primary production of forests (Ellis, 2012; van der Heijden and Sanders, 2002). Others are most effective in the breakdown of organic matter (lignocellulose) and therefore contribute to nutrient cycling (Boddy et al., 2008; Ekblad et al., 2013). A large number of studies have shown that variables characterizing the forest stand (e.g. age, dead-wood amount, habitat continuity, microclimate) are important drivers of species diversity of epixylic and epiphytic lichens (e.g. Jüriado et al., 2009a, 2009b; Meier et al., 2005; Moning et al., 2009; Peterson and McCune, 2001; Werth et al., 2005) and of wood-inhabiting fungi (e.g. Bässler et al., 2010b; Heilmann-Clausen and Christensen, 2004; Junninen et al., 2006). However, studies on the response of diversity of these two fungal guilds (hereafter referred to as “lichens” and “fungi” including the ectomycorrhizal guild) to “natural” disturbance caused by, e.g. bark beetle or fire, are scarce (but see Junninen et al., 2006 for wood-inhabiting fungi; Treu et al., 2014 for terricolous fungi). To our knowledge, there are no studies attempting to understand the underlying mechanisms of the response of fungal diversity to such disturbance regimes that consider functional properties.

Three habitat features significantly change after bark beetle infestation that affect lichens and fungi: (i) increased dead-wood

amount, which provides habitats or resources for both guilds; (ii) increased insolation through opening of the canopy, which might stress lichens as a high photon flux density could lead to photooxidation damage (e.g. Gasulla et al., 2012); and (iii) desiccation of dead wood through reduced canopy cover, which should stress primarily fungi (Bässler et al., 2010b). Hence, the changes in insolation and moisture after deforestation might make the environment more extreme and stressful for both guilds. We specifically tested the following hypotheses: (1) disturbance increases species diversity of both guilds owing to dead-wood enrichment, and (2) disturbance decreases the functional diversity of both guilds, which should shift the assembly mechanisms towards habitat filtering.

2. Methods

2.1. Study area and study design

We sampled epixylic and epiphytic lichens and wood-inhabiting fungi within the Bavarian Forest National Park at the Long Term Ecological Research (LTER) Site, which covers approximately 24,000 ha in south-eastern Germany, at elevations between 650 and 1450 m a.s.l. Along this elevation, the mean annual temperature ranges from 3.5 to 7.0 °C, and the total annual precipitation ranges from 1300 to 1900 mm (based on the climate time series 1972–2001). The dominating tree species along the entire altitudinal gradient is Norway Spruce (*Picea abies*). Below 1100–1200 m a.s.l., spruce stands are more often mixed with European Beech (*Fagus sylvatica*) and Silver Fir (*Abies alba*) (Walentowski et al., 2004). In the beginning of the 20th century, forestry slightly changed the natural tree species composition towards spruce, and logging regularly took place during the 20th century (Müller et al., 2008).

In the 1990s, a massive outbreak of *I. typographus* killed around 5500 ha of spruce stands, which remained unsalvaged owing to a benign-neglect management strategy in the national park (Lehnert et al., 2013). We set up 30 plots in disturbed stands, i.e. mature spruce stands completely killed by bark beetles within a very short time span (1998–2000), and 30 plots in undisturbed stands. The plots in disturbed stands were surrounded by an area of at least 1 ha in which all spruce had been killed. The minimum distance between the sample plots was 100 m (see Bässler et al., 2008 for more details).

2.2. Environmental data

As variables that reflect the change in environmental conditions due to deforestation by bark beetles, we chose insolation, moisture and dead-wood amount, all known to be important drivers for the investigated taxa (see references in Section 1 and also Figs. 1 and 2a).

To estimate gradients of insolation and moisture, we used data from a vegetation survey. The mean Ellenberg indicator values (Ellenberg, 1991), calculated from vegetation surveys, are a reliable measure for the effective environmental conditions on a plot. They reflect even small-scale variation but at the same time are robust against short-term environmental oscillations, such as weather conditions (e.g. Bässler et al., 2010b for the study area; Dupré and Diekmann, 1998). Hence, we mapped vascular plants via relevés that report species and percent cover in four strata (herb layer, <1 m height; shrub layer, 1–5 m; tree layer 2, >5–15 m; tree layer 1, >15 m). We calculated the canopy cover (%) by summing up the total coverage across the shrub and tree layers. For each plot, we also calculated mean light and moisture Ellenberg values based on presence data in the herb layer (not abundance weighted, according to Diekmann, 2003). Finally, we applied these variables to a PCA

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