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Multi-taxon alpha diversity following bark beetle disturbance: Evaluating multi-decade persistence of a diverse early-seral phase

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ABSTRACT

Early-successional forest ecosystems developing after natural disturbances, such as fire, windthrow or insect outbreaks, can support high diversity of habitat structures, species and processes. However, the specific structural and multi-taxon responses that best define a distinct early-seral pre-forest phase, and the longevity of that phase, remain important research questions. To address these questions, we assessed stand structural heterogeneity and species density of various taxa across three biological kingdoms in the initial early-seral period (~3 years after severe bark beetle outbreak), advanced early-seral period (~17–25 years after severe bark beetle outbreak) and mature spruce forests in unmanaged montane/high-montane ecosystems in Southeastern Germany. We evaluated the hypothesis that changes in structural heterogeneity and increases in diversity would peak in the initial stage and attenuate toward mature forest conditions by 17–25 years as the tree canopy closed.

We found a clear change in forest structural heterogeneity following the outbreak – most prominently in reduced cover and more clustered patterning of live trees, increased light availability, increased cover of shrubs and herbs, and high volume of dead wood. Most of these structural changes were not ephemeral after outbreaks, but remained high or even increased after multiple decades, suggesting persistence of early-seral heterogeneity well into succession.

Biodiversity as measured by species density and rarefaction curves showed variable responses to early-seral conditions depending on taxon and functional group. While some groups either showed no significant change with disturbance (e.g., most epigeics associated with the ground surface), or initially peaked after disturbance before declining quickly (e.g., saproxylic beetles specializing on fresh dead wood), several key groups showed maximum diversity in the advanced early-seral stage (e.g., herbs, herbivores, pollinators) – indicating that the timeframe over which increases occurred tended to be on the order of decades rather than years.

Our findings suggest that in unmanaged forests after bark beetle attack, a structurally complex phase prior to tree canopy closure can last several decades, and that many aspects of early-seral biodiversity and ecosystem function only fully develop given this extended time period. Where management of montane forests includes objectives for sustaining biodiversity, accommodating the protracted early-seral stage is important to supporting the full range of organisms and functions associated with canopy-opening disturbances.

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1. Introduction

Early-successional forest ecosystems have previously been considered as a short phase of stand initiation that plays only a minor role in ecosystem functioning and biodiversity (Bormann and Likens, 1979; Franklin et al., 2002). However, young forest

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stands developing after natural disturbances, such as fire, windthrow or insect outbreaks, can support high diversity of habitat structures, species and processes – as such, this "forgotten stage of forest succession" has recently received much greater attention (Swanson et al., 2011). According to the habitat heterogeneity hypothesis, species diversity is positively correlated with habitat complexity (e.g., Tews et al., 2004; McElhinny et al., 2005). Indeed, in a recent extensive meta-analysis, Stein et al. (2014) showed a positive relationship between environmental heterogeneity and species richness across taxa, biomes and spatial scales. Thus, the high structural complexity characteristic of some early-seral post-disturbance forests (Donato et al., 2012) should also host high species diversity, as has been shown for insect communities after windthrow (Bouget and Duelli, 2004).

The structural diversity of early-seral stands after disturbances is composed of legacies including dead wood derived from the pre-disturbance stand, the spatial and temporal variability of tree regeneration, and the co-dominance of diverse vegetation components including shrubs, herbs, and trees (Zenner, 2005; Swanson et al., 2011, 2014). Structural variations in the initial successional stages may influence both biodiversity and forest development pathways over the longer term. According to the hypotheses posed by Donato et al. (2012), the rate and pattern of tree canopy closure following stand-replacing disturbances is a key factor: dense and synchronous tree establishment truncates the diverse early-seral phase quickly ('conventional pathway'), while sparse or protracted tree establishment allows structurally diverse conditions to develop ('analogous precocity pathway' due to certain structural similarities to old forests) and, if tree canopy closure never occurs, this diversity may persist throughout succession to the old-growth stage ('homologous precocity pathway'). These alternative pathways relate to the crucial question of longevity of the early-seral phase, which has conservation implications for species dependent on these ephemeral patches within larger landscapes (Swanson et al., 2014). Thus far, there have been few direct empirical tests of how various types of biodiversity develop and persist for multiple decades in early-seral forest communities – particularly the degree to which such biodiversity may indicate the persistence of structural complexity farther into succession than suggested by traditional models, which tend to focus solely on the conventional pathway of rapid uniform stand development (Donato et al., 2012).

Along with wildfire and windthrow, bark beetles (Curculionidae, Scolytinae) are one of the most important drivers of natural disturbances in forest ecosystems of the Northern Hemisphere. Between 1950 and 2000, bark beetles, mainly *Ips typographus* and *Pityogenes chalcographus,* caused mortality in about 2.9 million m^3 of timber per year in European forests (Schelhaas et al., 2003). With changing climatic conditions, bark beetle activity is likely to increase when, under mild spring and dry summer conditions, species such as *I. typographus* and *P. chalcographus* are able to build up large populations even in high-elevation mountain forests (Krehan and Steyrer, 2006; Jönsson and Bärring, 2011). Following large-scale bark beetle disturbances, tree canopy closure and live phytomass are diminished significantly due to the dieback of mature trees, leading to higher solar radiation to the ground, more extreme temperatures, increased cover and height of the understory and often accelerated nutrient fluxes in the soil (Sousa, 1984; Roberts, 2004; Swanson et al., 2011). At the same time, large amounts of dead wood are created (Donato et al., 2013). If no forest management such as salvage logging or planting is applied, this early-seral stage is likely to support light-, nutrient-, dead-wood- and flower-demanding species of arthropods and fungi, as well as disturbance-indicating autotrophs (Müller et al., 2008, 2010).

Biodiversity response can be measured in terms of alpha or beta diversity, reflecting, respectively, the number of species within a site or the differences in species composition among sites (Whittaker et al., 2001). In this study we focused on the alpha diversity response of several functional groups to canopy-opening by bark beetle outbreaks in the Alpine Berchtesgaden National Park, Germany. We assessed stand structure and species density of various taxa in mature spruce forests (no or only endemic beetle activity), initial early-seral vegetation (~3 years after severe bark beetle outbreak) and advanced early-seral vegetation (~17–25 years after severe bark beetle outbreak) in unmanaged montane and high montane forests. We tested the following hypothesis: relative to mature forests, changes in structural heterogeneity and increases in compositional diversity following disturbance are strongest in the initial early-seral stage, and attenuate to intermediate levels by ~ two decades (i.e., return toward pre-disturbance condition, consistent with a closed-canopy pathway) (Fig. 1). An alternative hypothesis states that structural heterogeneity and compositional diversity could remain elevated for several decades if an open-canopy pathway is followed for an extended period (Fig. 1). Our findings are then discussed in the context of management implications following severe beetle outbreaks in mountain forests.

2. Methods

2.1. Study area

The Berchtesgaden National Park, founded in 1978, is located in the south-eastern corner of Germany in the Northern Limestone Alps and covers an area of 20800 ha (Fig. 2). With an altitudinal gradient from 603 m a.s.l. in the *Königssee* valley to 2713 m a.s.l. at the top of the *Watzmann* massif, the mean annual temperature ranges from +7 °C to −2 °C. Annual precipitation values vary between 1500 and 2600 mm. The mean duration of snow cover increases from approximately 110 days in the valleys to 200 days at 1500 m a.s.l. and 270 days at 2000 m a.s.l. (Spandau, 1988). The main soil types are rendzic leptosols of intermediate and shallow soil depth, eutric leptosols (humus layer > 15 cm – 35 cm) on steep slopes and chromic cambisols on less steep slopes and in the valleys.

The natural zonation of forest types in the region are mixed-montane European beech (*Fagus sylvatica*) forests with Norway spruce (*Picea abies*) and silver fir (*Abies alba*) at middle elevations, followed by Norway spruce – European larch (*Larix decidua*) – Swiss stone pine (*Pinus cembra*) forests in the subalpine zone (Köstler and Mayer, 1974). As a result of a high demand for wood for salt mining in the past, the natural composition of these forests was heavily altered by humans over centuries at accessible sites, favoring pure Norway spruce stands (Knott et al., 1988; Konnert and Siegrist, 2000).

In contrast to managed forests characterized by active control, salvage logging and, when necessary, regeneration measures after bark beetle outbreaks, no manipulation of natural forest dynamics has been taking place on approximately 6000 ha of forest in the core zone of the National Park since 1978. Following the winter storms *Vivian* and *Wiebke* in 1990, around 100 ha of spruce stands were affected by spruce bark beetles (primarily *I. typographus*) between 1990 and 1997, consisting of nearly 100% mortality in patches of up to 1 ha in size. Dead trees were removed only within the bark beetle control zone of 1900 ha at the border of the National Park in order to protect neighboring private forests from bark beetle infestation (Fig. 2). The outbreak ceased naturally at the end of the 1990s (Nationalpark Berchtesgaden, 2001). Contrary to the preceding events, the winter storms *Kyrill* in 2007 and *Emma* in 2008 caused the most disturbance in the core zone, where no management takes place. Since then, approximately 400 ha of spruce stands have been infested by bark beetles.

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