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Separating forest continuity from tree age effects on plant diversity in the ground and epiphyte vegetation of a Central European mountain spruce forest

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ABSTRACT

Forest continuity has been identified as an important factor influencing the structure and diversity of forest vegetation. Primary forests with centuries of continuity are usually more diverse than young secondary forests as forest are colonized only slowly and because the former are richer in old tree individuals. In the present study, performed in unmanaged high-elevation spruce forests of the Harz Mountains, Germany, we had the unique opportunity to separate the effects of forest continuity and tree age on plant diversity. We compared an old-growth spruce forest with century-long habitat continuity with an adjacent secondary spruce forest, which had naturally established on a former bog after 1796 when peat exploitation halted. Comparative analysis of the ground and epiphyte vegetation showed that the plant diversity of the old-growth forest was not higher than that of the secondary forest with a similar tree age of >200 years. Our results suggest that a period of >200 years was sufficient for the secondary forest to be colonized by the whole regional species pool of herbaceous and cryptogam forest plants and epiphytes. Therefore, it is likely that habitat structure, including the presence of old and decaying trees, was more important for determining plant diversity than the independent effect of forest continuity. Our results are probably not transferrable to spruce forests younger than 200 years and highly fragmented woodlands with long distances between new stands and old-growth forests that serve as diaspore sources. In addition, our results might be not transferable to remote areas without notable air pollution, as the epiphyte vegetation of the study area was influenced by SO_2 pollution in the second half of the 20th century.

Introduction

The distribution and abundance of forest plants is strongly influenced by forest age and stand history (Peterken and Game, 1984). Many forest species of vascular plants, lichens and bryophytes are assumed to be restricted to forests with a habitat continuity of at least several centuries (Brunet, 1993; Edwards, 1986; Peterken and Game, 1981; Rose, 1976). The same is true for invertebrates, fungi and other organism groups (Alexander, 1998; Bredesen et al., 1997; Nilsson et al., 1995). The main cause of these restrictions is the limited dispersal ability of many forest species (Hilmo and Såstad, 2001; Sillett et al., 2000; Verheyen et al., 2003). Therefore, such species are bound to (primary) old-growth forests or at least ancient secondary forests with long habitat continuity. Managed forests with repeatedly interrupted habitat continuity lack many species of old-growth forests (Gustaffson and Hallingbäck, 1988; Kuusinen and Siitonen, 1998). Young, small forest patches in fragmented landscapes can even be largely devoid of typical forest species (Dzwonko and Loster, 1988).

In Central Europe, where humans began to interrupt the continuity of forest cover with the import of agriculture from the Middle East as early as in the Neolithic (Haak et al., 2010; Pichler et al., 2011), completely undisturbed forests are lacking. However, a few primeval forest patches still exist where stand history can be traced back for many centuries and at the same time, stand structure suggests that these forests have likely never experienced stand-level disturbance by humans (Ellenberg and Leuschner, 2010). Such primeval forests are today often located in conservation areas, whereas most forest stands with interrupted habitat continuity are managed and, thus, lack over-mature and decaying trees. Therefore, it is often difficult to separate the effect of forest continuity on species diversity from the effect of tree age.

Though many species have been classified as to be characteristic of ancient forests in the sense of long habitat continuity in expert assessments (e.g. Rose, 1976; Wulff, 1997), such studies do not distinguish between species whose reproduction biology restricts them to forests with uninterrupted or, at least, long-term continuity (Grashof-Bokdam and Geertsema, 1998; Hilmo et al., 2011) and species with a preference for site conditions which are mainly

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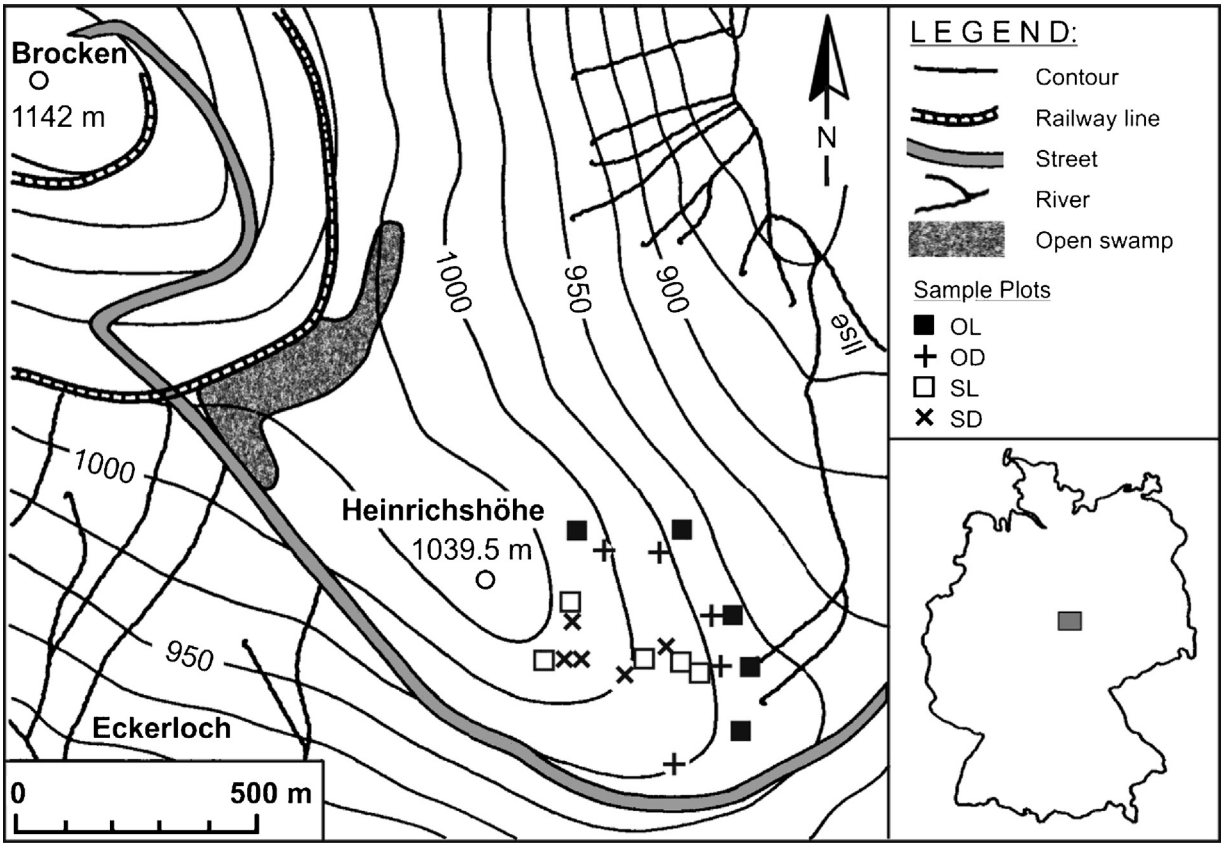

Fig. 1. Location of the study area within Germany and location of the sample plots (old growth forest, live [OL] and dead trees [OD]; secondary forest, live [SL] and dead trees [SD]) on Mt. Brocken.

found in forests with old tree individuals (Hauck, 2011; McGee and Kimmerer, 2002; Moning et al., 2009). The greater importance of substrate specificity and habitat persistence over continuity in forest cover and dispersal limitations has been discussed for species in boreal forests (Gibb et al., 2006; Lõhmus and Lõhmus, 2011; Nordén and Appelqvist, 2001). In Central Europe, options for the comparative study of forests with old trees with or without interrupted continuity are naturally limited because of the scarcity of unmanaged forest stands with different continuity. Comparative approaches partly include forests with contrasting site conditions and different tree species composition, which limits conclusions (Kühn, 2000).

In the present study, we had the unique opportunity to directly compare two montane stands of Norway spruce (*Picea abies* (L.) H. Karst.) with contrasting history. Both stands were comprised of more than 200-year old trees, but strongly differed in the duration of forest cover. One stand is an old-growth forest, which had been banned for logging since the early Middle Ages. The other stand developed through natural succession on an exploited and drained bog at the end of the 18th century and was, like the old-growth forest, never logged afterwards and, thus, has a cohort structure. Both the old-growth forest and the secondary forest share old trees with an age far beyond the rotation age in managed forests. However, these stands strongly differ in the continuity of their existence. We used this setting for an attempt to separate the effect of forest age (or continuity) on plant diversity from that of tree age. Our study covered the ground vegetation as well as epiphytic lichens and bryophytes on live and dead trees. The aim of the study was to test the hypothesis that both ground vegetation and epiphyte vegetation are more diverse in the old-growth (primary) forest than in the secondary forest despite similar tree age.

Materials and methods

Study sites

The study was conducted in a forest of Norway spruce (*Picea abies* (L.) H. Karst.) in the Harz National Park on Mt. Brocken in Germany (51°47′ N, 10°38′ E, Fig. 1). Our investigations were carried out on the eastern and south-eastern slopes of Mt. Brocken between 950 and 1025 m a.s.l. The regional climate is characterized by high annual precipitation of 1600 mm (including annual snowfall of 1.9 m) and a mean annual temperature of 2.9 °C (Glässer, 1994). The local bed rock is iron-rich granite, creating strongly acidic soils. Dominant soil types (FAO, 2006) include cambisol and stagnogley, depending on the groundwater level. The predominant humus form is more-like mold.

The old-growth (putatively primary) spruce forest ('Brockenurwald', 300 ha) had been banned for logging and forest pasture, as it was part of a hunting ground for nobility and clergy since the time of Charles the Great (ca. 800 AD; Jacobs, 1870; Schade, 1926). This way of protection lasted until the High Middle Ages; from the plague pandemic in the mid 14th century until the early 16th century the Harz Mountains had a very low population density. Documents and charcoal remnants give evidence of logging activities at lower elevation of Mt. Brocken, but not in the upper elevations of our study sites because of bad accessibility (Greger, 1992; Kortzfleisch, 2008). Since the introduction of systematic forest management in the late 17th century, the forest was never subjected to timber harvest (Bei der Wieden and Böckmann, 2010). Therefore, this forest is considered a forest with uninterrupted habitat continuity and is probably a primary forest. The co-occurrence of different forest age stages in a small-scale pattern of irregularly distributed patches is characteristic of this old-growth forest (Kathke and Bruelheide, 2010;