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Comparing the plant diversity of paired beech primeval and production forests: Management reduces cryptogam, but not vascular plant species richness

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ABSTRACT

Conflicting evidence of the impact of forest management on biodiversity exists, either decreasing or increasing species richness. Variable diversity responses may result from the adoption of different unmanaged reference systems, ranging from stands with management abandonment in the recent past to true primeval forests. We compared the species richness of epiphytic bryophytes and lichens and vascular forest floor plants in three primeval forest/production forest pairs of *Fagus sylvatica* in Slovakia, adopting a replicated design and a reference system without any management legacy. Mean number of bryophyte and lichen species per 500 m^2-plot tended to be higher in the primeval forests, while the mean α-diversity of vascular plants was higher in the production forests. In contrast, the β-diversity of the three plant groups as expressed by the Sørensen Dissimilarity Index was generally higher in the primeval forest plot sample, reflecting a higher heterogeneity of plant community composition and habitat diversity. Plotting cumulative species numbers against plot numbers suggests that the curves for bryophyte and lichen species richness may saturate at ca. 250 plots or ~12.5 ha in the primeval forests, but already at 30–60 plots (<3 ha) in the more homogeneous production forests. Total bryophyte and lichen species numbers are estimated to be 30–100% larger in the primeval forests than the production forests. Contrary to general belief, vascular plant species richness was similarly high, or even higher, in the primeval forests when >50 plots (total area: 2.5 ha) were investigated, evidencing the importance of natural disturbance regimes for maintaining high forest biodiversity. Our results show that *Fagus sylvatica* primeval forests are inhabited by a species-rich epiphyte flora despite the species poverty of the tree layer. This evidences the outstanding value of primeval forest reserves for the conservation of temperate forest biodiversity.

1. Introduction

European beech (*Fagus sylvatica* L.) is the dominant tree species in large parts of Europe's natural temperate woodlands. Centuries of more or less intensive forest use and transformation have reduced the beech-dominated old-growth forest area to tiny fragments, while production forests, often with altered tree species composition, dominate in most areas. While windthrow, insect calamities and forest fires were once the prevailing disturbance factors, logging and other forest management activities are the dominant disturbance events in Europe's forests in our times (Kaplan et al., 2009). For forest biodiversity conservation, it is important to better understand how natural and anthropogenic disturbances modify the physical environment and thereby impact on biodiversity (Chen et al., 1999).

Since the formulation of the intermediate disturbance hypothesis (IDH) by Connell in 1978, it is generally accepted that the effect of disturbance on species diversity is not necessarily negative, but depends on disturbance intensity. Moderate levels of disturbance can create habitats for additional species immigrating from outside the ecosystem, while the original species diversity remains unaffected. Thus, disturbance can rise overall species richness. Since management actions always cause disturbances, both biodiversity and ecosystem functioning differ between primeval and production forests (Bengtsson et al., 2000). Logging in primeval forests without alteration of tree species composition can be viewed as an intermediate level of anthropogenic disturbance, whereas the establishment of production forests with modified tree species composition represents a severe disturbance. Yet, even in managed

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forests, where the tree species composition is not altered, the intensity of logging and thus disturbance can vary considerably.

Main determinants of the species composition and diversity of the understory vegetation in temperate forest ecosystems are microclimatic factors such as light, air humidity and soil temperature, and soil moisture and soil chemistry (Friedel et al., 2006; Gilliam, 2014; Ellenberg and Leuschner, 2010; Leuschner and Lendzion, 2009). Temperate broad-leaved primeval forests often consist of several canopy layers and have a small-scale patchy structure of tree groups differing in age (Korpel, 1995). A consequence is a spatially more heterogeneous microclimate than found in production forests with cohort-like structure. Natural disturbances, like stand break-up after storm events, insect calamities or age-related tree mortality (Brunet et al., 2010), contribute on different scales to the high structural heterogeneity of primeval forests. Characteristic features of primeval forests, which usually are lacking in production forests, are the presence of tall overmature trees and large amounts of deadwood in different stages of decay (Bunnell and Houde, 2010; Jonsson et al., 2005; Ódor and van Hees, 2004). Deadwood represents an indispensable habitat for many bryophytes and lichen species, but in late stages of decay also represents a substrate for the establishment of vascular plants, including tree offspring, which profit from reduced competition (Bače et al., 2012; Dittrich et al., 2013). The deadwood legacy from the previous tree generation also bridges the lack of microsites for many epiphytic bryophytes and lichens in regrowing primeval forests, while absence of deadwood hampers the colonisation of production forests after intense timber harvest (Dittrich et al., 2013).

Many authors have studied the effect of forestry on the species richness of wood-inhabiting cryptogams (Király et al., 2013; Lonsdale et al., 2008; Nascimbene et al., 2013) and vascular plants (Bremer and Farley, 2010; Decocq et al., 2004; Wagner et al., 2011) in the temperate forests of Europe and other regions. Various studies suggest that bryophytes and lichens respond more sensitively to forest management-related changes in forest structure than vascular plants, but these studies typically addressed only one systematic group, either the vascular forest floor vegetation (e.g. Aude and Poulsen, 2000) or cryptogamic epiphytes (Bardat and Aubert, 2007; Nascimbene et al., 2007). Systematic comparisons between temperate primeval and production forests with respect to vascular plant, bryophyte, and lichen diversity have been conducted in the temperate and boreal regions of North America (Lesica et al., 1991; Halpern and Spies, 2008), but are lacking for Europe.

We investigated the vascular plant, bryophyte and lichen flora in three *Fagus sylvatica* primeval/production forest pairs in eastern Central Europe and tested the hypotheses that (i) the α-diversity of vascular plants is higher in production forests in agreement with the intermediate disturbance hypothesis, while bryophyte and lichen α-diversity do not meet the predictions of IDH, and (ii) the β-diversity of all three systematic groups is higher in primeval forests reflecting the high spatial heterogeneity of these forests. If correct, this would suggest to focus on β-diversity and the regional species pool rather than on α-diversity in assessments of the conservation value of natural and managed forests.

2. Material and methods

2.1. Study areas

The study was conducted in the western Carpathian Mountains in eastern Slovakia where some remnant beech primeval forests have survived (Fig. 1). This region belongs to the eastern part of the distribution range of *F. sylvatica*. These forests were added in 2007 to the World Heritage List of UNESCO (Primeval Beech Forests in the Carpathians), including several forests in Slovakia and Ukraine. Three primeval forest areas were selected for study, Havešová, Stužica (in Poloniny National Park) and Kyjov (in the Vihorlat Protected Landscape Area; detailed information on these conservation areas is found in Vološčuk (2014)). The beech primeval forest area extends over 659 ha in Stužica, 171 ha in Havešová, and 53 ha in Kyjov. These stands have not been subjected to any forest management activity for several hundred years.

In close vicinity to the primeval stands, three beech production forests were selected in Havešová (3.8 ha), Kyjov (8.3 ha) and Stužica (6.9 ha). The age of these stands varied between 90–100 (Havešová and Kyjov) and 70–100 years (Stužica). These beech forests are managed in a shelterwood cutting system with two cuts conducted within 10 years at the end of the production cycle, while no or only scarce management activities are conducted in the first 80–90 years. This type of forest management is the most widespread in Slovakian beech production forests and practiced in strips parallel to the slope, structuring the production forests in longitudinal sections of beech cohorts of similar age and high stem density (Green Report, 2009; Marušák, 2007). The rotation period is often relatively short (typically 80–100 years) with the consequence that more than 90% of the Slovakian beech production forests are younger than 100 years (National Forest Centre, 2009).

All studied forests are located at sub-montane to montane elevation. The three sites differ slightly in elevation; these differences are related to some differences in mean annual precipitation and temperature. Due to different geologies (andesite vs. flysh), the soils in Kyjov (dystric Cambisols) are nutrient-poorer than those in Havešová and Stužica (eutric Cambisols, Table 1) (Vološčuk, 2014). While south-facing slopes dominate in Havešová and Stužica, the forests in Kyjov grow predominantly on north-facing slopes.

Based on our relevés of the vascular forest floor vegetation, it is not possible to assign the local communities to any of the acidophilous beech forest associations (alliances *Luzulo-Fagion sylvaticae* and *Fagion sylvaticae*) listed for Slovakia by Slezák et al. (2016). Most relevés can best be assigned to the *Dentario-glandulosae Fagetum*, a western Carpathian association (Neuhäusl et al., 1982) characterized by *Dentaria glandulosa*, a Carpathian endemic and other eastern European species, like *Symphytum cordatum*. *Fagus sylvatica* dominates the tree layer in all study areas. In the primeval forests of Havešová and Kyjov, a few individuals of other tree species like *Acer platanoides* and *Fraxinus excelsior* were admixed. In Stužica, beech was locally associated with major proportions of *Abies alba*, which was sporadically even dominant in the shrub layer. The production forests had higher shares of tree species other than beech as compared to the primeval forests, though beech was always dominant.

2.2. Study design

Forty circular plots of 500 m^2 size were established in each primeval forest in systematic grids that had a mesh size of 140 m (Havešová), 100 m (Stužica) or 64 m (Kyjov) as minimum distance between neighbouring plot centres. In Stužica, we selected all plots at elevations <1.000 m due to a tree species change toward higher elevations. For that reason, the study area of 659 ha was reduced resulting in shorter distances between the plot centres. In Kyjov, the smallest study site, 64 m was the maximum distance between the plot centres to guarantee the establishment of 40 plots. A 100 m-wide buffer zone was excluded from the margins of each primeval forest to avoid influences from the adjacent production stands.

Due to the typical management regime applied to beech production forests in eastern Slovakia that starts with the clear-cut of forest strips and is followed by the subsequent regrowth of tree