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Overstorey dynamics controls plant diversity in age-class temperate forests

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ABSTRACT

Forest management is widely considered to have an impact on the understorey plant diversity, which is essential for sustainable forestry and nature conservation. However, contradictions among previous large-scale studies and meta-analyses raised the need for better-designed research. Such research should identify drivers controlling diversity and species composition, quantify the overstorey-understorey relationships and their dynamics in the temperate forests.

Two spatial scales (2.25 m^2; 314 m^2) and stratified random sampling design were used to record understorey vegetation and overstorey and environmental properties along the whole lifecycle of managed Norway spruce (108 years) and European beech (140 years) stands, the most wide-spread mountain forest types in European temperate zone. The dataset also includes primeval fir-beech forests located in the same area.

Forest management significantly altered understorey diversity and species composition in both beech and spruce stands. Diversity measures changed considerably over the development of managed stands, exhibiting the rapid decline from species-rich forest clearings to poor stands of 30–40 years, later slowly recovering and reaching the average level of old-growth forests at the age of over 100 years. The impact of management was stronger at the smaller scale. It is caused by the fine-scale character of overstorey-understorey interactions, and it is weakened due to stand structure heterogeneity in larger scales.

Competition of overstorey trees was identified as the most important driver of understorey diversity and its temporal dynamics. It was also reflected in the litter amount, which negatively affected diversity especially in the beech forests. In contrast, the light amount was a more important factor in the spruce stands.

We conclude that comparisons between datasets that are heterogeneous regarding overstorey age and proportion of development stages, as well as meta-analyses based on such inconsistent studies, can lead to confusing conclusions and improper applications. As a practical implementation, we recommend using overstorey tree density as the most efficient measure for assessment, prediction and managing understorey plant diversity.

1. Introduction

Forest management affects biodiversity of forest ecosystems and ecosystem services. Maintaining forest biodiversity is a complex issue related to various management approaches within different habitats. While abandonment of traditional land-use in temperate lowland forests leads to the species richness decline and community assemblage shifts (e.g. Hermy and Verheyen, 2007; Kopecký et al., 2013), different, less intense and close-to-nature forestry can retain biodiversity of mountain forests. Latest studies showed that developing of sustainable management strategies for biodiversity conservation and provisioning of ecosystem services in temperate mountain forests should be regionally adapted and requires more scientific effort (Kräuchi et al., 2000; Mina et al., 2016; Paillet et al., 2010).

The biodiversity of temperate forests is largely a function of the herb-layer assemblages (Gilliam, 2007), whose richness and

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overall diversity is affected by structure and composition of tree overstorey (e.g. Barbier et al., 2008). Overstorey modifies the environment of understorey plants, such as light, microclimate or soil properties (De Frenne et al., 2013; Rothe et al., 2002; Tinya and Ódor, 2016). Therefore, periodical tree cutting accompanied by changes in resource availability is a key factor affecting plant diversity in managed forests (Decocq et al., 2004). The dynamics of understorey is thus a function of silvicultural technique (Durak, 2012). Close-to-nature techniques producing a more complex stand structure are expected to have a positive effect on the understorey diversity (Chaudhary et al., 2016; Fedrowitz et al., 2014). On the other hand, clear-cutting and shelterwood systems result into even-aged stands with homogenous structure and uniform temporal development. According to conceptual model of Roberts and Gilliam (1995), high stand density in the young stages induces diversity loss. However, recent meta-analyses of Duguid and Ashton (2013) and Paillet et al. (2010) do not fully support the diversity decline and show a vague response of understorey diversity to forest management. Confusing results most likely arise from differences in stand ages, plot sizes, local site conditions, management practices and missing comparisons with old-growth forests in the case studies involved. Some of them revealed that the stands with natural tree species composition had lower species richness, whereas another studies recorded no effect or even indicated a higher species diversity in the managed forests with changed tree species composition (e.g. Ewald, 2000; Máliš et al., 2012; Martinák et al., 2014; Verstraeten et al., 2013).

Considering the above mentioned weaknesses of the previous research, we performed a complex investigation of the influence of overstorey structure on the understorey environmental conditions, plant diversity and species composition in the sites of mesotrophic fir-beech forests. Unlike the previous studies, we covered the entire life-cycle of managed forests and the development cycle of adjacent primeval forests. Using a sampling design which eliminates the impact of site conditions, we explored (i) whether and how the age-class forestry affects vascular plant diversity and species composition compared to primeval forests. Further, (ii) we investigated whether the understorey diversity in managed forests is a function of overstorey age, and (iii) we evaluated the influence of environmental and overstorey properties on the understorey diversity and species composition and identified the most significant drivers of the overstorey-understorey interactions. Within the managed forests, we compared naturally regenerated beech forests and spruce monocultures, which actually represent the most widespread stand types in the Central-European mountains.

2. Methods

2.1. Study site

The model study area situated within the Pol'ana Mts range (Western Carpathians, Central Slovakia, Fig. 1) was restricted to the montane zone with mesotrophic fir-beech forest sites, which ranges from 950 to 1250 m a.s.l. Soils developed on Tertiary lava-flows of andesites are fertile deep Eutric Cambisols with transitions to Andosols at the highest altitudes. Mean annual temperature varies between 2 and 4 °C and mean annual precipitation between 900 and 1200 mm (Šťastný et al., 2002). The site and vegetation type represents the most typical and broadly distributed example of temperate forest ecosystems in European mountains. The study area also includes the largest primeval forest in Western Carpathians protected as natural reserve since 1972, what enables comparison of natural old-growth stands with secondary managed forests within the same site type. The old-growth uneven-aged stands are characteristic by complex spatial structure and mixed tree-species composition. They are dominated by European beech (*Fagus sylvatica* L.), with regularly admixed silver fir (*Abies alba* Mill.) and sycamore (*Acer pseudoplatanus* L.) and less frequently with common ash (*Fraxinus excelsior* L.), Norway spruce (*Picea abies* (L.) H. Karst.) and wych elm (*Ulmus glabra* Huds.). Gap dynamics prevails in the area, larger patches (exceeding 1000 m^2) originated after windstorms are rare.

Adjacent managed stands belong mostly to the first or second (younger stands) forest generation developed after clear-cutting of primeval forests, forming a pattern of single layered even-aged stands characteristic for the age-class forestry approach. Secondary

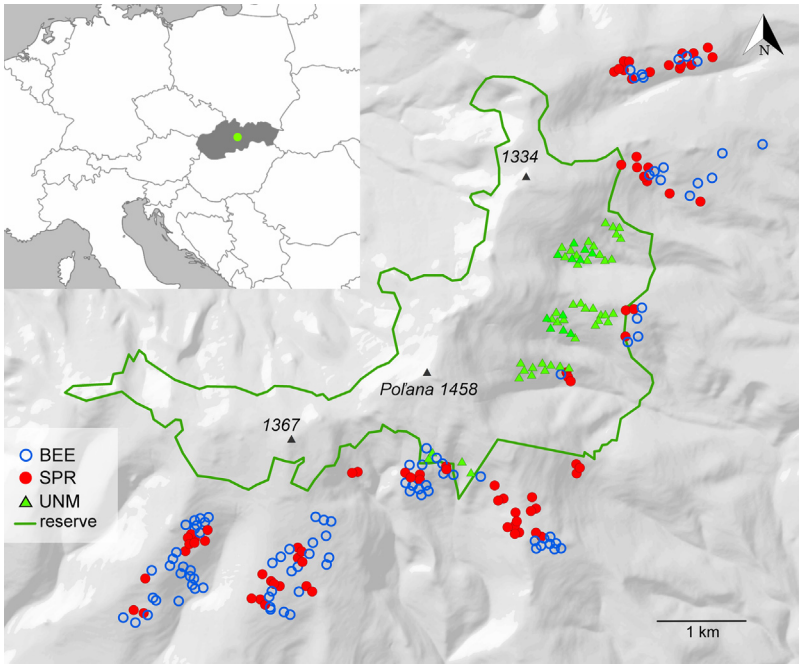

Fig. 1. Location of the study site and distribution of plots within the area (abbreviations are explained in Methods).