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Do diverse overstoreys induce diverse understoreys? Lessons learnt from an experimental–observational platform in Finland

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ABSTRACT

The understorey fulfils many important ecosystem services, such as mediation of carbon dynamics, provision of habitats, and it contains most of the plant diversity in forest ecosystems. Changes in the overstorey diversity may affect understorey diversity as trees have a species-specific impact on resource availability and soil conditions that influence the understorey. In an attempt to disentangle the overstorey–understorey diversity relations, we combined the strengths of an experimental and observational approach in the boreal vegetation zone in Finland.

The Satakunta tree diversity experiment was planted in 1999 using a pool of five tree species and four species richness levels (1, 2, 3, 5 species per plot) (only the first three levels were analysed in this study). Each level was replicated with different species composition to avoid complete dilution, which allows the separation of identity and diversity effects. Understorey surveys were performed in three subplots per plot in 2003 (*young phase*) and 2011 (*established phase*). In the *full-grown forest* surrounding Joensuu, a similar design was used in an observational plot-based study with three tree species richness levels (1, 2, 3 species per plot), containing trees from a pool of three species. The understorey was surveyed in 2012, also in three subplots per plot. We unravelled the relations between (1) tree species richness and (2) understorey composition, diversity, compositional dissimilarity within and between plots and temporal turnover, and searched for tree species identity effects.

Tree species richness had a significant influence on the understorey composition in the established phase of the experiment. In contrast with the expectations, plot-level understorey diversity showed no significant differences between the tree species richness levels, neither at the experiment nor at the full-grown forest. At the established phase of the experiment, interplot compositional dissimilarity was significantly higher for monocultures than for mixtures. Monocultures have distinct influences on resources and soil conditions, leading to larger differences with other plots, while mixtures often share the same tree species or species with similar environmental impact. Tree species identity effects were present in monocultures but were predominantly tempered in mixed stands due to stronger dilution.

Neither research approach found a clear relation between tree species richness and understorey diversity. The presence of tree species identity effects may partially have skewed the diversity relations. However, results on interplot compositional dissimilarity indicated that creating mixtures using a chessboard pattern of monocultures may positively influence understorey diversity at the forest level.

1. Introduction

Despite its small contribution to the overall forest biomass, the understorey fulfils many important ecosystem services. Among others, it mediates carbon dynamics and energy flow, influences nutrient fluxes (Wedraogo et al., 1993), serves as a habitat for insects, mammals, etc., produces a variety of non-timber forest products and houses most of the plant diversity in forest ecosystems (Gilliam, 2007), especially in boreal ones (De Grandpré et al., 2003). In order to maintain or enhance the provision of services such as habitat or forest biodiversity, the preservation or increase of understorey diversity may be beneficial.

In many present-day forest landscapes, semi-natural mixed forests have been converted into monocultures of fast-growing tree

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species or species producing high-quality wood (Lenière and Houle, 2006). Such decrease in tree species richness may affect the understorey via modifications of resource availability at the forest floor. Trees influence the availability and quality of understorey light (Messier et al., 1998), soil water (Barbier et al., 2009) and nutrient availability (Prescott, 2002). In addition to resources, soil conditions for plant growth are also changed by the overstorey (Barbier et al., 2008): soil acidity is affected (Hagen-Thorn et al., 2004) and a thick litter layer and the presence of phytotoxic compounds may hamper understorey performance and exclude several understorey species that cannot endure these conditions (Rodríguez-Calcerrada et al., 2011). Nature and strength of the impact on resources and soil conditions differ considerably between tree species (Augusto et al., 2003). Compositional changes in the overstorey may thus induce shifts in the understorey composition. The local-scale tree species diversity influences the heterogeneity of resource availability and soil conditions at the forest floor. Namely, comparatively homogeneous environmental conditions in monocultures contrast with the heterogeneous pattern of patches with distinct resource availability and soil conditions within mixed stands (Morin et al., 2011; Yankelevich et al., 2006). At the same time, resource availability and soil conditions in monocultures can reasonably be assumed to be quite divergent from monocultures or mixtures with other tree species or species that are not closely related. As mixed stands within a certain region often share tree species, or species with a similar impact on resources and soil conditions, with monocultures and other mixed stands, the dissimilarity in resources and soil conditions with other stands is expected to be lower compared to monocultures.

The spatio-temporal variation in resource availability and soil conditions plays a key role in the structuring of plant communities. Each understorey species has its own optimal requirements concerning resources and soil conditions. According to the universal niche theory, species differences stabilize coexistence (Levine and HilleRisLambers, 2009). Moreover, the resource (and condition) heterogeneity hypothesis suggests that the understorey diversity partly depends on environmental heterogeneity (Ricklefs, 1977; Huston, 1979). The relatively higher environmental heterogeneity within a mixed stand might thus be reflected in an elevated compositional dissimilarity between patches (Golodets et al., 2011), leading to a higher stand-level understorey diversity (Reich et al., 2012). The more homogeneous distribution of resources and soil conditions in monocultures are mirrored in a uniform understorey composition (Beatty, 2003).

Several observational studies examined the relation between overstorey and understorey diversity. Vockenhuber et al. (2011) showed that temperate deciduous forests with high tree species diversity feature a more diverse understorey. The study of Aubert et al. (2004) in temperate forest revealed a homogenizing effect of a pure beech stand on the understorey composition in contrast with a mixed beech-hornbeam stand. However, Both et al. (2011) could not prove the positive overstorey–understorey diversity relation in a subtropical forest in China. In the study of Thomsen et al. (2005) the overstorey had only a weak control of the understorey composition in near-natural temperate deciduous forest. Moreover, in their review on overstorey–understorey diversity relations in temperate and boreal forests, Barbier et al. (2008) found indications that monospecific stands can be more favorable to understorey diversity than two-species stands.

Factors such as soil and altitude may confound the relation between overstorey and understorey diversity, in case their variability within the examined site is related to tree species identities or diversity levels. In order to reduce covariation, Both et al. (2011) recommended decoupling tree species diversity effects from covarying environmental variables using experimental approaches. However, experiments with planted tree stands take a long time to reach maturity and therefore may lack some of the complexity of environmental conditions and processes occurring in mature natural forests (Leuschner et al., 2009). Moreover, diversity effects grow stronger as trees become older (Cardinale et al., 2012). An integrated approach using experimental and observational data is therefore promising for forest biodiversity and ecosystem functioning research (Leuschner et al., 2009). In this study, we focussed on the young Satakunta tree species diversity experiment (http://www.treedivnet.ugent.be; last accessed on 27 September 2013) as well as on full-grown forests in Finland. We are not aware of any other study that has used this combined approach before. Although the impact of the planted tree species was probably limited during the first years of the experiment, measurements in this phase may give insights in early identity and diversity effects of the planted trees. Moreover, the use of a true temporal comparison approach (vegetation surveys at the Satakunta experiment at four and twelve years of age) as well as a space-for-time approach (experiment versus full-grown forest) enable us to evaluate the diversity effects through time. We formulated the following hypotheses:

(1) A higher number of tree species in the overstorey is accompanied by a different composition of the understorey and positively influences understorey diversity.
(2) The compositional dissimilarity between patches within a stand increases with increasing number of tree species in the overstorey, while the compositional dissimilarity between different stands decreases with higher tree species richness (TreeSR[1]).
(3) The overstorey–understorey diversity relations grow stronger through time, with a lower temporal turnover in understorey composition for stands with a species-rich overstorey, compared to monocultures.
(4) In addition to a species diversity effect, individual species also exert an influence on understorey diversity, compositional dissimilarities between and within stands and temporal turnover (i.e. tree species identity effects).

2. Materials and methods

2.1. General information

The study was performed in experimental forest plantations and full-grown forests in Finland, in the boreal vegetation zone with potential natural vegetation of the *myrtillus* type (Cajander, 1926). Located at the border between humid continental and subarctic climate types, mean annual precipitation was 650 mm and mean annual temperature was 4.5 °C (experiment) and 3.0 °C (full-grown forest) for the period 1981–2010 (Finnish Meteorological Institute, en.ilmatieteenlaitos.fi; last accessed on 27 September 2013). We studied plots along a gradient of TreeSR. Complete dilution, i.e., species richness gradients in which a certain species was present in every tree species combination, was avoided to enable separating the effect of tree species diversity from that of tree species identities (Nadrowski et al., 2010).

2.2. Tree diversity experiment (experimental data)

Established in 1999, the Satakunta experiment is among the oldest tree biodiversity experiments worldwide, aiming at quantifying the influence of tree species diversity on forest ecosystem functioning. The three experimental areas of ca. 1.5–2 ha each lie 20–30 km apart near Noormarkku (area 1: 61°43′N, 21°59′E, eleva-

[1] TreeSR: Tree Species Richness.