



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.

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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

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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

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 co-varying 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 (TreeSR¹).
- (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 sub-arctic 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.

tion 47 m; area 2: 61°39'N, 22°9'E, elevation 59 m; area 3: 61°41'N, 21°42'E, elevation 20 m). Soils are podzols (IUSS Working Group WRB, 2006) composed of granodiorite bedrock beneath a 10–30 cm thick clay-textured mineral horizon (area 1) or organic layer (areas 2 and 3). Slopes are absent (area 2) or very gentle (areas 1 and 3). Area 2 showed severe moose damage, which might have affected understorey development. Therefore, this area was not included in this study.

After a clearcut of forest dominated by *Picea abies* (L.) Karsten, 38 adjacent plots of 20 m × 20 m were marked on each area and in spring 1999, one-year old seedlings were planted without fertilization (planting distance 1.5 m). The species pool consisted of *Pinus sylvestris* L., *P. abies* (L.) Karsten, *Betula pendula* Roth, *Alnus glutinosa* (L.) Gaertner (natives) and *Larix sibirica* Ledeb. (non-native). Four TreeSR levels were created: five monocultures, seven two-species mixtures, six three-species mixtures and one five-species mixture (each replicated two times per area and randomly assigned to the plots). The two- and three-species mixtures were not chosen randomly from the pool of possible combinations between the five tree species. A gradient was created from evergreen coniferous stands via mixed (coniferous and deciduous) to purely deciduous stands (see Appendix A: Table A.1). Every species was included in at least two different two-species and three-species mixtures and none of the species was present in every mixture. The same monocultures and mixtures were used for areas 1 and 3. In order to realize the mixtures, a random within-plot planting design was used. Dead trees were replaced the first two years after planting and spontaneously established trees were removed in 2010. In 2010, mean tree height was 5–6 m and canopy closure was reached in most plots, except for some monocultures of *A. glutinosa*.

The understorey (here defined as vascular species smaller than 1.3 m) was surveyed in July 2003 (*young phase of the experiment*; 4 years old) and 2011 (*established phase of the experiment*; 12 years old). In each plot, the percentage cover of each species was estimated in three random subplots of 1 m × 1 m, that were located at least 2 m from the plot edge. Compared to guidelines on vegetation surveys that encourage survey plot sizes of 100–400 m², our subplots were rather small. However, by using small subplots we were able to study within-plot differences in understorey composition at the level of the individual tree (species). Steps of 1% and 5% were used for covers below respectively above 20%, and a cover value of 0.01% was given to rare species. As subplots were not permanent, their location differed between the two surveys.

In 2001 and 2011, the upper mineral soil layer (0–10 cm) was sampled at six random locations per plot (independent of location of understorey subplots). The samples were pooled per plot, dried and analysed for total C, total N (CHN analyser) and total P (flame atomic absorption spectroscopy) in 2001 and for exchangeable K, Ca, Mg, Al (extraction with BaCl₂), total C, total N (Elementar analyser, type Vario Macro Cube in configuration CNS, with Argon as carrier gas), total P (extraction with HNO₃, HClO₄ and H₂SO₄), Olsen P (extraction with NaHCO₃) and pH(KCl) in 2011 (see Appendix A: Table A.2). We calculated C/N and N/P ratios and Cation-Exchange Capacity (CEC, based on K, Ca, Mg and Al). A *t*-test was performed using R 2.15.1 (R Development Core Team, 2010) to detect significant differences between area 1 and 3.

2.3. Full-grown forest (observational data)

In contrast with the Satakunta experiment, the forest in the neighborhood of Joensuu (62°24'N, 29°24'E) is characterized by complex environmental conditions and processes, typical for full-grown forests. It represents one out of six study regions in the Exploratory Platform of the European FunDivEUROPE project. This research platform was designed to study the relation between

overstorey diversity and ecosystem functioning, while controlling for covariation with other environmental variables and forest stand characteristics (Baeten et al., 2013). Soils are podzols, glacial tills, and histosols on peatlands (IUSS Working Group WRB, 2006), with a bedrock of mica schists, granites and granodiorites or quartzites. In 2011, 28 plots of 30 m × 30 m were selected in this managed forest (elevation 80–200 m, area size 150 km × 150 km). The species pool consisted of *P. sylvestris*, *P. abies* and *B. pendula*/*Betula pubescens* Ehrh. A limited portion of other tree species was tolerated in the plots (<5% of the total basal area for each non-target tree species, with a maximum of 10% for the sum of all non-target species). Four plots were selected for each of the three monocultures, for each of the three possible two-species mixtures and the three-species mixture (so 28 plots in total). Within the mixed stands, tree species were randomly located. In 2011, a number of characteristics were collected for each plot concerning the site where the plot is located (e.g. elevation, slope), the soil (e.g. sand content, rock cover) and the stand (e.g. age canopy trees, canopy closure) (see Appendix A: Table A.3). All trees were between 32 and 49 years old in 2011 (the original stand was clearcut), with tree ages approximately evenly distributed among all species mixtures. The selected plots were single layered and had received low intensity thinning. Each plot was divided into nine squares of 10 m × 10 m of which the southwest, central and northeast quadrant were used for the understorey surveys in 2012 (*full-grown forest*) (Baeten et al., 2013). In each of these three squares, the cover of each species was estimated in a subplot of 5 m × 5 m.

2.4. Data analyses

All analyses were performed in R 2.15.1. Data from the five-species mixtures at the Satakunta experiment were not used due to a lack of independent replications and an unbalanced number of plots. First, we checked for covariation between the TreeSR levels and the environmental characteristics. Using available plot-level soil data of the experiment (data of 2001) and site, soil and stand characteristics of the full-grown forest (data of 2011) (see Appendix A: Table A.3), we calculated a dissimilarity matrix on normalized data using the Euclidean distance, i.e., expressing the environmental dissimilarity between plots. Differences between TreeSR levels in the multivariate environmental space were tested using a permutational multivariate analysis of variance (PERMANOVA). PERMANOVA results (*p* > 0.05) indicated no covariation with TreeSR for the experiment and full-grown forest. Moreover, for each area in the experiment, TreeSR levels were randomly assigned to the plots, in this way controlling for other potential, hidden within-area gradients.

In order to examine Hypothesis 1 and 2, we averaged the cover data of the three subplots per plot (thus 3 × 1 m² for the experiment and 3 × 25 m² for the full-grown forest) to obtain plot-level cover (and presence/absence) data. In a first step, we calculated a dissimilarity matrix based on plot-level presence/absence data of the established phase of the experiment (separately for area 1 and 3) and the full-grown forest. We used the Lennon distance, which expresses community differentiation derived from true species turnover. Nonmetric Multidimensional Scaling (NMDS) was used to visualize the compositional variation between plots, followed by PERMANOVA to test the significance of the difference between the levels of TreeSR (999 permutations). Next, we calculated understorey diversity in the young and established phase of the experiment and the full-grown forest at different spatial scales (plot-level, interplot and intraplot). Plot-level diversity (i.e. alpha diversity) was quantified as species richness, Shannon–Wiener index and Pielou's evenness index. In order to calculate the *interplot* compositional dissimilarity, a dissimilarity matrix was calculated for each area using the Lennon distance (based on plot-level pres-

ence/absence data). The mean of the pairwise dissimilarities of a plot against all other plots (within the same area) determines its interplot dissimilarity, expressing the plot's compositional differentiation from the other plots. The *intraplot* (i.e. within-plot) compositional dissimilarity was determined analogously, deriving the mean pairwise dissimilarity of a subplot against the two other subplots within the same plot (Lennon distance, based on subplot-level presence/absence data). The impact of TreeSR, Area and their interaction on understorey species richness, Shannon–Wiener and evenness indices and intra- and interplot dissimilarities were analysed using a mixed model structure. The model took into account a random effect due to differences in tree species combination [R-syntax using *lme* and restricted maximum likelihoods: $y \sim \text{TreeSR} * \text{Area} + (1 | \text{TreeCombination})$; *nlme* package, Pinheiro et al., 2013]. Although the same tree species combinations were used for area 1 and 3, codes for *TreeCombination* were different for Area 1 and 3 in order to test the combination of tree species combination and Area in a nested way. Area was deleted from the model for analyses based on full-grown forest data [R-syntax: $y \sim \text{TreeSR} + (1 | \text{TreeCombination})$].

Hypothesis 3 was tested by comparing the patterns in the young experimental phase with the patterns in the established phase of the experiment (true temporal comparison) and the full-grown forest (space-for-time), and by looking at the turnover in understorey composition between the young and the established phase in relation to the TreeSR. In order to evaluate this compositional turnover, the datasets of the young and established phase were used together to calculate a dissimilarity matrix based on plot-level presence/absence data (Lennon distance; indicates compositional changes due to turnover) and cover data (Euclidean distance; indicates abundance shifts). NMDS was used to visualize the compositional variation between plots based on these dissimilarity metrics, followed by PERMANOVA to test the significance of the difference between the young and the established phase of the experiment (999 permutations, constrained within plots to account for the paired nature of the design). Subsequently, the compositional turnover between the young and the established phase was calculated for each plot separately. Lennon (plot-level presence/absence) and Euclidean (plot-level cover) distances were used to quantify the changes in the understorey community between the two time steps. Data could not be used on subplot-level as the three subplots per plot were randomly located during the surveys in the young and established experimental phases. Hence, the turnover quantifies both a temporal and a spatial effect. Relative differences in turnover between TreeSR should thus be evaluated rather than absolute values. The effect of TreeSR, Area and their interaction on compositional turnover was evaluated using the mixed model structure as mentioned in the previous paragraph [R-syntax: $y \sim \text{TreeSR} * \text{Area} + (1 | \text{TreeCombination})$]. We also calculated mean Ellenberg values for each plot in the young and established experimental phases and the full-grown forest, based on the cover of the understorey species. Ellenberg values are widely used indicator values expressing species' preferences for some environmental variables on an ordinal scale (Ellenberg and Leuschner, 2010). In our study, they are used as an indication for differences in environmental conditions between the young and established phase of the experiment. The effect of TreeSR on mean Ellenberg values in the experiment (areas and experimental phases analysed separately) and the full-grown forest was checked using a mixed model structure with R-syntax: $y \sim \text{TreeSR} + (1 | \text{TreeCombination})$. A second mixed model was used to check the significance of the shift in Ellenberg values between the young and established experimental phases (areas analysed separately), controlling for the fact that measures were repeated on the plot-level [R-syntax using *lme* and restricted maximum likelihoods: $y \sim \text{Phase} + (1 | \text{Plot})$].

In order to detect potential tree species identity effects (**Hypothesis 4**), we looked at the effect of tree species dilution on understorey diversity and temporal turnover. Increases in TreeSR on the plot-scale are accompanied by a greater dilution and thus decreasing proportion of the individual tree species in substitutive designs. To examine the species identity effects, we calculated the residuals of the mixed models that tested for the effect of TreeSR, Area and their interaction on species richness, interplot and intraplot dissimilarity in the established phase of the experiment and at the full-grown forest and on compositional turnover (based on presence/absence data) between the young and established experimental phases. Subsequently, for each tree species, residuals were averaged for each of its possible shares in the overstorey (100% for monocultures, 50% for two-species mixtures, 33.33% for three-species mixtures). Horizontal lines close to zero indicate the absence of a clear identity effect in all TreeSR levels, while more remote horizontal lines show a strong impact of the tree species on the examined measure independent of its dilution degree. Rising or descending lines mean that the strength of the identity effect depends on the dilution degree of the tree species. Dilution series of area 1 and 3 were presented separately to illustrate potential differences between both areas.

3. Results

A total number of 63 (area 1) and 54 (area 3) species were recorded in the young phase of the experiment while the total species number was 54 (area 1) and 55 (area 3) in the established phase. PERMANOVA results on the effect of TreeSR on plot-level understorey composition indicated a significant difference between TreeSR levels at area 1 in the established phase of the experiment (Fig. 1; $p < 0.05$). The young phase nor the established phase of the experiment showed a significant interaction between TreeSR and Area (Fig. 2; $p_{\text{TreeSR:Area}} > 0.05$) for alpha diversity, indicating that the effect of TreeSR was similar for both areas. Understorey species richness, Shannon–Wiener and evenness indices were not significantly affected by TreeSR ($p_{\text{TreeSR}} > 0.05$). The results for the evenness index in the young experimental phase and the Shannon–Wiener index in the established phase seemed to differ significantly between the two areas ($p_{\text{Area}} < 0.05$). At the full-grown forest, 56 species were found in total. Here, three-species mixtures had the lowest species richness, Shannon–Wiener and evenness indices, but differences with monocultures and two-species mixtures were insignificant ($p_{\text{TreeSR}} > 0.05$).

For intraplot dissimilarity, the interaction between TreeSR and Area was again insignificant in both experimental phases (Fig. 3; $p_{\text{TreeSR:Area}} > 0.05$). At area 1 in the young phase of the experiment and at both areas in the established phase, the highest intraplot compositional dissimilarities were found for three-species mixtures, but the influence of TreeSR seemed to be insignificant ($p_{\text{TreeSR}} > 0.05$). At the full-grown forest, there was neither a significant increase towards higher TreeSR. The interplot compositional dissimilarity in understorey composition was highest for monocultures at both areas in the young and established phase of the experiment and at the full-grown forest. But only at area 1 in the established phase of the experiment, differences between levels of TreeSR were significant, inducing a significant interaction between TreeSR and Area ($p_{\text{TreeSR:Area}} = 0.038$) for the established phase of the experiment.

The NMDS showed a clear distinction in understorey composition between the young and the established phases at both areas of the experiment, based on presence/absence data as well as cover data (see Appendix B: Fig. B.1). PERMANOVA indicated this compositional turnover to be significant (presence/absence: $p = 0.001$ for both areas; cover: $p = 0.026$ for area 1, $p = 0.001$ for area 3). Plot-le-

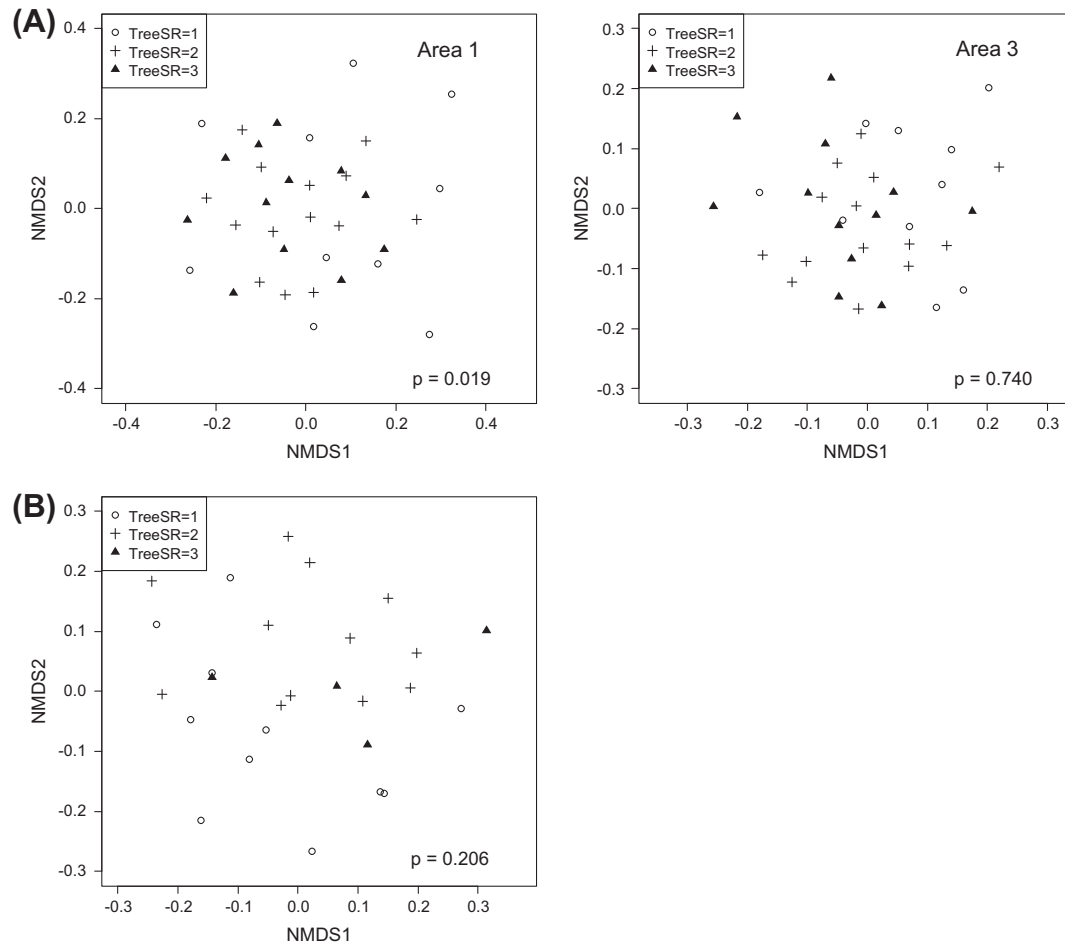


Fig. 1. Variation in understorey vegetation composition in function of TreeSR. Nonmetric multidimensional scaling visualizing the variation in understorey community composition between plots in function of tree species richness (TreeSR) in (A) the established phase of the experiment (Satakunta, 12 years old, areas 1 and 3) and (B) the full-grown forest (based on plot-level presence/absence data; Lennon distance) (p -values indicate the significance of the difference between the levels of TreeSR, based on PERMANOVA).

vel mean Ellenberg values also indicated a clear shift over time with lower values in the established versus the young experimental phase (see Appendix C: Fig. C.1, p -values predominantly smaller than 0.001) but Ellenberg values were not significantly influenced by TreeSR ($p_{\text{TreeSR, young or established}} > 0.05$). There was no clear relation between TreeSR and compositional turnover based on presence/absence data (Fig. 4; $p_{\text{TreeSR}} > 0.05$), so the (dis)appearance of understorey species between the young and established phase of the experiment was similar for all three levels of TreeSR. Compositional turnover based on cover data (i.e. abundance shifts between the young and established phase) seemed to be higher for monocultures than for the mixtures, but the difference remained insignificant.

The dilution series (Fig. 5) consisted predominantly of ascending and descending lines (identity effects dependent of dilution degree or thus the tree species richness level) and a few horizontal lines close to zero (identity effects absent), while more remote horizontal lines were absent. Monocultures (i.e. 100% share in the overstorey) often showed a wider range in mean residuals for the examined variables, compared to two-species (i.e. 50% share in the overstorey) and three-species mixtures (i.e. 33% share in the overstorey). This indicates a divergent understorey impact between tree species in monocultures. At the full-grown forest, monocultures of *Betula* spp. seemed to be accompanied by higher species richness in the understorey, which was, to a smaller extent, also found in the experiment (area 1 and 3). The opposite was true for *P. abies* at

the full-grown forest, and *L. sibirica* at area 1 of the experiment. Monocultures of *A. glutinosa* seemed to induce relatively low intraplot compositional dissimilarity and relatively high interplot compositional dissimilarity and compositional turnover between the two surveys compared to the other monocultures at area 1. Conversely, at area 3, monocultures of this tree species induced rather high intraplot compositional dissimilarity and relatively low interplot compositional dissimilarity and compositional turnover. Contrasting results for the two experimental areas were also found for monocultures of *P. sylvestris* that showed relatively low interplot dissimilarity and compositional turnover at area 1, in contrast with area 3. The above-mentioned effects predominantly disappeared when the tree species were diluted in two-species, although large variation in mean residuals was still visible for understorey species richness (lower values for *L. sibirica*) and intraplot dissimilarity (lower values for *L. sibirica* and *P. sylvestris*) at area 1. The spread in mean residuals for three-species mixtures was even smaller than or equal to the spread for the monocultures and two-species mixtures, except for compositional turnover.

4. Discussion

Hypothesis 1. A higher number of tree species in the overstorey is accompanied by a different composition of the understorey and positively influences understorey diversity.

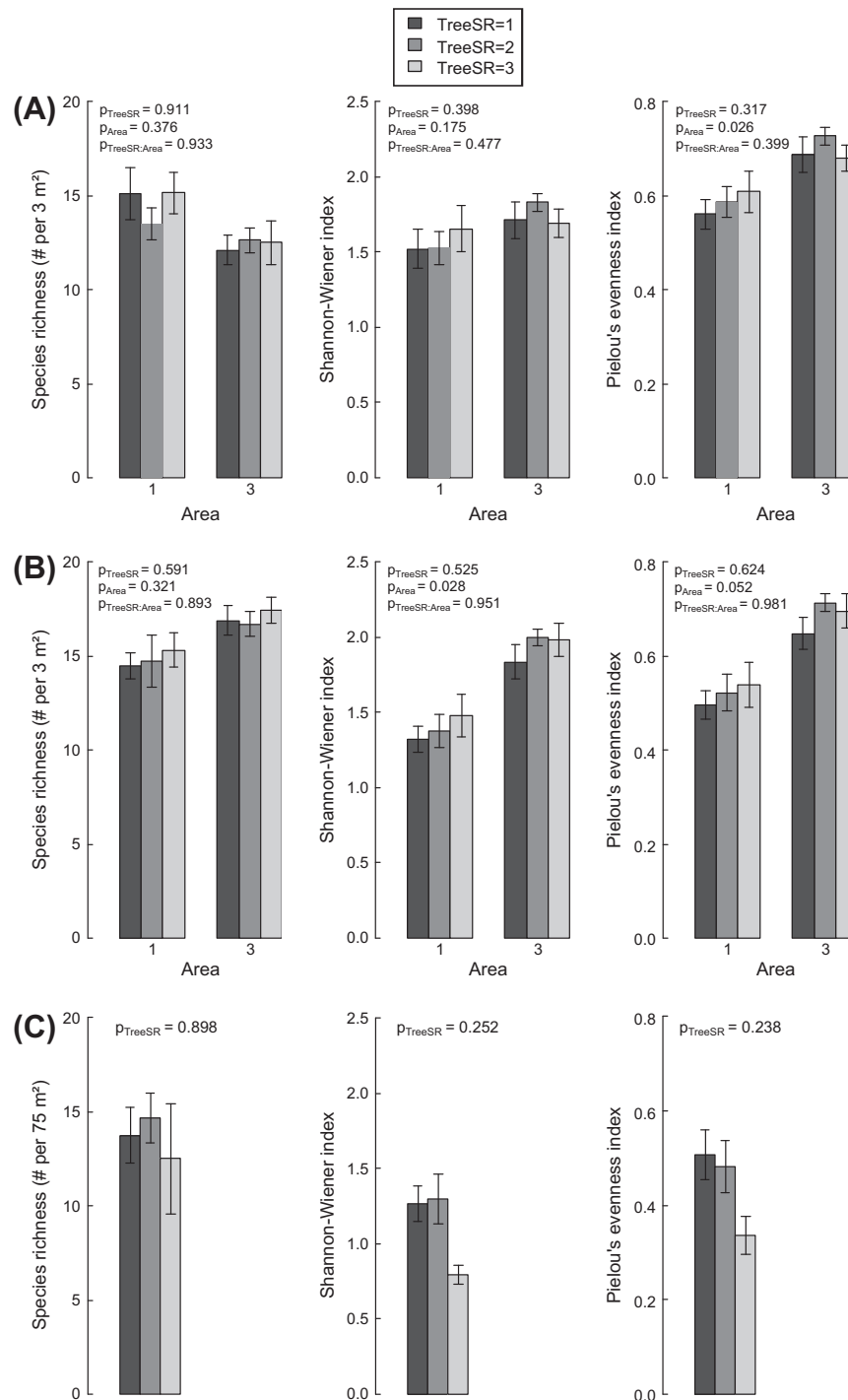


Fig. 2. Plot-level understorey diversity in function of tree species richness. Mean plot-level species richness, Shannon–Wiener index and Pielou's evenness index (based on cover data averaged over the three subplots per plot, i.e. $3 \times 1 \text{ m}^2$ at the experiment and $3 \times 25 \text{ m}^2$ at the full-grown forest) at each level of tree species richness (TreeSR) in (A) the young (4 years old) and (B) established phase (12 years old) of the experiment (Satakunta, areas 1 and 3), and at (C) the full-grown forest (Joensuu, 2012) (bars represent mean \pm standard error; p -values indicate the significance of the effect of TreeSR (p_{TreeSR}), Area (p_{Area}) and their interaction ($p_{\text{TreeSR:Area}}$), based on mixed models that also took into account the nested random effects of tree species combination and area).

The hypothesized positive relation between TreeSR and understorey diversity was not validated by our results. In contrast, at the full-grown forest three-species mixtures showed lower alpha-diversity compared to monocultures and two-species mixtures (although differences were not significant). However, we did find differences in understorey composition in function of the level of TreeSR at area 1 of the experiment.

Mixing tree species in two- and three-species mixtures normally induces higher environmental heterogeneity (Yankelovich

et al., 2006). According to the resource heterogeneity hypothesis and niche theory this would lead to a higher number of coexisting understorey species. Chávez and MacDonald (2010) found that this mosaic of patches in mixed boreal forest stands allows for understorey plant communities that include both shade-intolerant and shade-tolerant species. Higher understorey diversity with increasing overstorey species richness was also found by Vockenhuber et al. (2011). Neither the experiment nor the full-grown forest offered clear evidence that a multiple-species overstorey in boreal

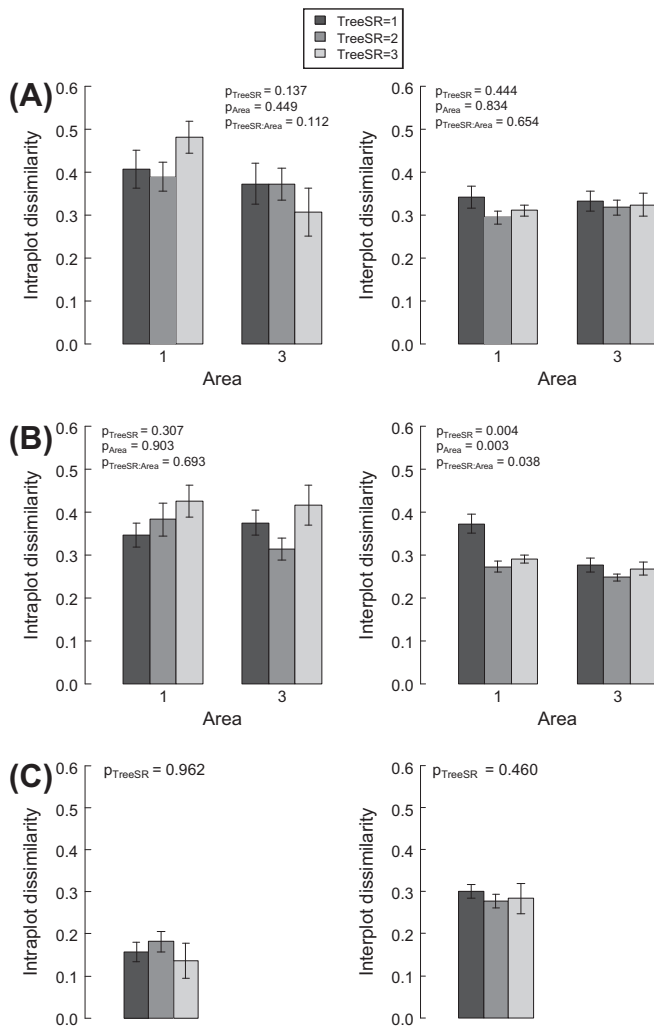


Fig. 3. Intraplot and interplot compositional dissimilarity in function of tree species richness. Mean intraplot (between subplots within a plot) and interplot compositional dissimilarity (between plots within the same area) (based on presence/absence data; Lennon distance) at each level of tree species richness (TreeSR) in (A) the young (4 years old) and (B) established phase (12 years old) of the experiment (Satakunta, areas 1 and 3), and at (C) the full-grown forest (Joensuu, 2012) (bars represent mean \pm standard error; p -values indicate the significance of the effect of TreeSR (p_{TreeSR}), Area (p_{Area}) and their interaction ($p_{Area:TreeSR}$), based on mixed models that also took into account the nested random effects of tree species combination and area).

forest would lead to a more diverse understorey on the stand level compared to monocultures. As the Satakunta experiment was relatively young, the impact of the trees on the understorey was probably limited up to now. Moreover, the restricted TreeSR gradient at the full-grown forest (one, two and three-species mixtures), which is typical for overall species-poor boreal forests, might not have been large enough to detect strong diversity relationships between understorey and overstorey. In addition, the functional diversity of the tree species mixtures may have been rather limited as well. For example, *P. sylvestris* and *P. abies* are coniferous species with an acidifying impact on the soil, while *P. sylvestris* and *B. pendula/pubescens* are both light-demanding species with crowns that transmit high amounts of incident light to the forest floor. Their similar impacts on resource availability and soil conditions may explain the lack of influence of TreeSR on the understorey vegetation at the full-grown forest. Potential tree species identity effects may also have skewed the overstorey–understorey diversity relation (see further). Despite the lack of effects on understorey diver-

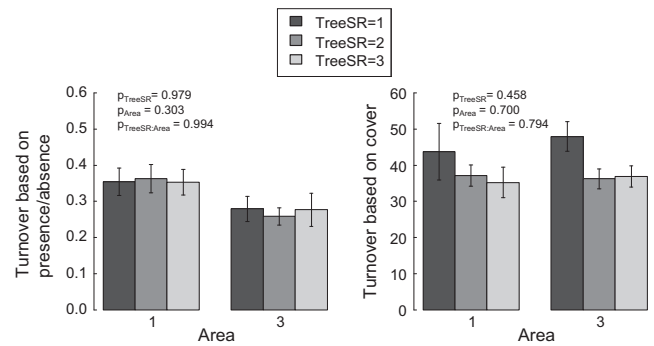


Fig. 4. Compositional turnover in function of tree species richness. Mean compositional turnover based on plot-level presence/absence (Lennon distance) and cover data (Euclidean distance) between the young (4 years old) and established phase (12 years old) of the experiment (Satakunta, areas 1 and 3) at each level of tree species richness (TreeSR) (bars represent mean \pm standard error; p -values indicate the significance of the effect of TreeSR (p_{TreeSR}), Area (p_{Area}) and their interaction ($p_{Area:TreeSR}$), based on mixed models that also took into account the nested random effects of tree species combination and area).

sity, the understorey composition was influenced by the level of tree species richness. The combination of tree species in the two- and three-species mixtures may have created new environmental conditions, favouring understorey species that are not present in plots of other treeSR levels.

Hypothesis 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 treeSR.

We found no significant increase of intraplot dissimilarity in function of TreeSR at the experiment nor at the full-grown forest. This led to the rejection of the first part of this hypothesis. At the experiment (especially area 1 in the established phase) and the full-grown forest, interplot compositional dissimilarity was higher for monocultures compared to two-species and three-species mixtures, leading to the acceptance of the second part of the second hypothesis.

Based on (presumed) increased environmental heterogeneity in the mixtures we were expecting stronger differences in understorey composition between different patches within a plot, compared to monocultures (Golodets et al., 2011). The young age of the experiment might again explain the absence of clear overstorey–understorey relations. Apart from the limited TreeSR range with low functional diversity and potential tree species identity effects (see further), the lack of significant differences at the full-grown forest may be due to the fact that each of the three relatively large subplots ($5 \times 5 \text{ m}^2$) in mixed stands was influenced by all the tree species composing the mixed stands, as tree species were mixed tree by tree. This may have limited the variation in environmental conditions between subplots and therefore the intraplot compositional dissimilarity as well. The use of smaller subplots (that are influenced by a smaller number of trees) might have resulted in higher values of intraplot compositional dissimilarity.

The understorey in the monocultures tended to be compositionally more differentiated from other plots compared to the two-species and three-species mixtures. Mixtures generally share tree species (and the environmental conditions they induce) with other mixed and monoculture stands, and the overlap increases along the richness gradient in case of a fixed species pool. The presence of similar environmental conditions leads to relatively low environmental variation between plots and, so, the understorey composition might appear less differentiated. In contrast, in monocultures, one tree species determines the resource availabil-

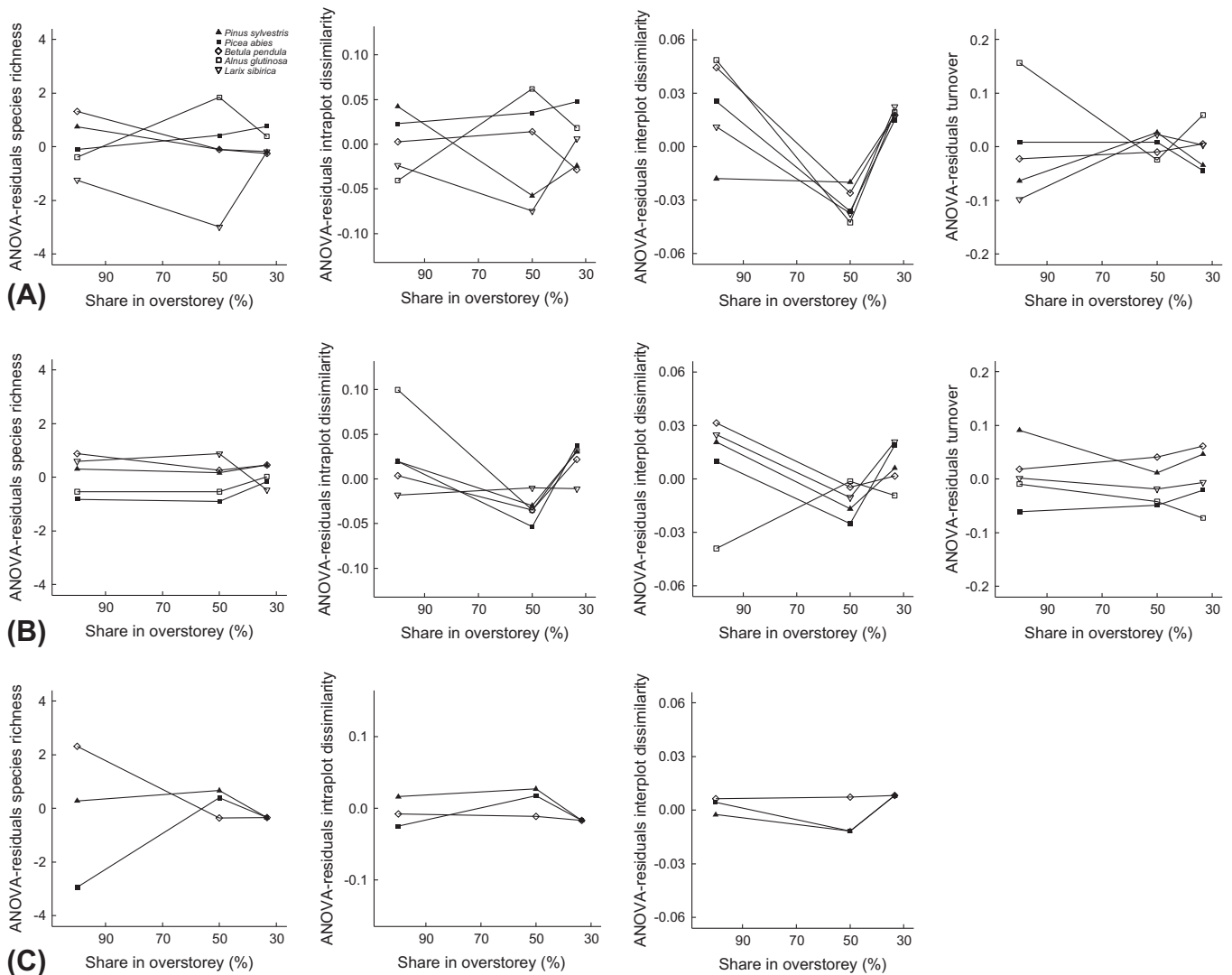


Fig. 5. Tree species identity effects on understorey diversity and turnover. Dilution series based on residuals of mixed models that tested for the effect of tree species richness (TreeSR), Area and their interaction (taking into account the nested random effects of tree species combination and area) on species richness, intraplot (between subplots within a plot) and interplot (between plots within the same area) dissimilarity (based on presence/absence data; Lennon distance) in the established phase of the experiment (12 years old, Satakunta) and compositional turnover (based on presence/absence data; Lennon distance) between the young (4 years old) and established (12 years old) phase of the experiment at (A) area 1 and (B) area 3, and species richness, interplot and intraplot dissimilarity at (C) the full-grown forest (Joensuu, 2012). Values represent the mean of the residuals for each species as a function of its proportion in the mixture. Symbols indicate the tree species (*Betula* spp.: *Betula pendula* at the experiment, *Betula pendula/pubescens* at the full-grown forest).

ity and soil conditions (Augusto et al., 2003), which can be quite distinct and therefore only optimal for a limited set of understorey species. The understorey composition in a monoculture is likely to show some resemblance with the understorey in mixtures containing the same tree species, but is differentiated from the understorey in all other mixtures and monocultures, leading to higher interplot compositional dissimilarity compared to mixtures.

Hypothesis 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.

Results indicated that the negligible differences in understorey diversity between levels of TreeSR in the young phase of the experiment were also predominantly insignificant in the established phase and the full-grown forest, in contrast with the hypothesis. Monocultures seemed to induce higher compositional turnover in

the understorey (when based on cover data), but compositional turnover based on presence/absence nor cover data showed a significant influence of TreeSR.

In the young phase of the experiment, trees were too small to significantly influence resources and soil conditions. Soil nutrient conditions were probably still dominated by legacies of the preceding *P. abies* stand. In the established phase, canopy closure was reached (leading to more shade) and tree height and litter fall (influencing soil conditions, e.g. soil nutrient status, acidity) were starting to become substantial, leading to the clear shift in understorey composition between the young and established phase of the experiment (as was shown by the NMDS, based on presence/absence data as well as cover data). Ellenberg values of the understorey species also indicated a shift towards more shade, higher soil acidity and lower soil nutrient status. Cardinale et al. (2012) indicated that diversity effects would grow stronger as experiments run longer due to the increasing magnitude of complementarity (e.g. resource partitioning, positive species interactions) allowing

for competing understorey species to stabilize their interactions and coexist (Cardinale et al., 2007). Therefore, we expected the effects of the tree species on the understorey diversity to become more clear after a longer duration of the experiment, but that was not stated by our results. Cardinale et al. (2011) also concluded that effects will be stronger when studies are performed in natural systems at larger scales, as this may incorporate more heterogeneity and more niche and complementarity opportunities for species to exploit resources than are available in experiments. One would thus expect the relation between overstorey and understorey diversity to be clearer at the large-scale, full-grown forest. However, results indicated similar insignificant differences as in the established experimental phase. The impact of TreeSR on mean Ellenberg values was also insignificant in both the young and established phase of the experiment and at the full-grown forest. Apart from the reasons that were previously mentioned (young age of the experiment, restricted TreeSR gradient, limited functional diversity, potential tree species identity effects), this might also indicate that the influence of overstorey species richness on understorey diversity is actually not that strong as expected in these boreal forests.

Compositional turnover between the two surveys based on presence/absence data was neither influenced by TreeSR. The (dis)appearance of understorey species between the young and established phase of the experiment was thus not influenced by the level of TreeSR. The impact of the tree species on the environmental conditions in this young experiment was probably not yet strong enough to induce the disappearance or appearance of species. TreeSR neither had a significant impact on turnover based on cover data although we did find somewhat higher values for monocultures compared to mixtures, indicating a stronger abundance shift of understorey species for monocultures. In the longer term, when the impact of the trees becomes more prevalent, this might lead to the disappearance or appearance of understorey species. Before the original forest was cut in order to install the experiment, *P. abies* was the only tree species influencing the resources and soil conditions of all plots. After the experiment was installed, the other tree species that were planted (apart from *P. abies*) affected the environmental conditions differently, leading to a shift in the cover of the understorey species. In contrast with the monocultures (2 out of 10 plots per area planted with *P. abies*), most mixtures still contained *P. abies* (16 out of 28 plots per area) and its environmental impact was thus still apparent in mixed plots. As a result, the difference in soil conditions between 2001 (experiment 2 years old) and 2011 (experiment 12 years old) was lower for the mixtures (but $p > 0.05$, data not shown). This was reflected in stronger compositional turnover for monocultures when based on cover data (i.e. understorey abundance shifts). Moreover, the compositional turnover (based on cover data) was lower in plots holding *P. abies* compared to plots without this species ($p > 0.05$ at both areas, data not shown).

Hypothesis 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).

Distinct tree species identity effects present in all levels of treeSR would skew the relation between overstorey and understorey diversity and make conclusions dependent on the overstorey composition. Results indeed indicated clear tree species identity effects, but predominantly in monocultures. Monocultures of *Betula* spp. had higher understorey species richness compared to the other tree species. *Betula* spp. is known to have relatively fast-decomposing litter (Hobbie et al., 2006), inducing good soil conditions for a species-rich understorey. *P. abies* and *L. sibirica* on the other hand negatively affected species richness, as both

species produce acidifying litter with a negative effect on the understorey (Augusto et al., 2003; Liu et al., 1998). The other tree species identity effects present in monocultures, namely for *A. glutinosa* (intraplot and interplot dissimilarity and compositional turnover) and *P. sylvestris* (interplot dissimilarity and compositional turnover), were contrasting for the two experimental areas. Results on altitude and soil analyses indicated a clear difference between the two areas. This may have interfered with the tree species identity effect on resource availability and soil conditions, leading to different patterns for the two areas. In two- and especially three-species mixtures, most of these extreme conditions seemed to be tempered. This is due to dilution of the tree species and the environmental conditions they induced, decreasing the impact of individual tree species on the understorey vegetation. However, even in two-species mixtures, some identity effects could still be discerned. These effects may have blurred the effects of TreeSR and may therefore be one of the reasons why the overstorey–understorey diversity relation is less clear than expected. We expect the identity effects in the mixtures to disappear when trees grow older as a result of more intense interactions between tree species and therefore stronger diversity effects that overrule the effect of tree species identities.

Results of both the experiment and the full-grown forest showed that the effect of TreeSR on understorey diversity was negligible in general. This was probably due to the young age of the experiment, the limited TreeSR range typical for boreal forests, possibly combined with limited functional differences between the present tree species. Moreover, tree species identity effects visible in mixtures, may also have skewed the effects of tree species diversity on the understorey vegetation. However, results on interplot dissimilarity indicated that, at the forest level, a higher understorey diversity might be obtained by creating a chessboard pattern of small monoculture stands. Trees exert a species-specific influence on the environment in these small monocultures, leading to a patch-scale heterogeneous pattern of resources and soil conditions. Chávez and MacDonald (2012) point to the importance of creating an intermix of small patches of varying overstorey composition to conserve and restore understorey plant species richness and diversity. As some understorey species are related to a specific overstorey composition, the loss of an overstorey composition type might be associated with decreasing understorey diversity (Légaré et al., 2001). We must remark that in this chessboard structure neighborhood effects between tree species are lower compared to tree-by-tree mixed forests, as interactions only occur at the borders between two stands. Some ecosystem components and processes are intensified when tree species are in close contact. For example, competition with other nearby tree species alters growth rates of trees (Cavard et al., 2011) and mixing litter of different qualities induces additive and non-additive effects on decomposition (Ball et al., 2008). When deciding which tree mixing structure to use, one must therefore keep in mind how this decision might affect the various ecosystem components, processes and services.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.01.030>.

References

- Aubert, M., Bureau, F., Alard, D., Bardat, J., 2004. Effect of tree mixture on the humic epipedon and vegetation diversity in managed beech forests (Normandy, France). *Can. J. For. Res.* 34, 233–248.
- Augusto, L., Dupouey, J.L., Ranger, J., 2003. Effects of tree species on understory vegetation and environmental conditions in temperate forests. *Ann. For. Sci.* 8, 823–831.
- Baeten, L. et al., 2013. A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspect. Plant Ecol. Evol. Syst.* 15, 281–291.
- Ball, B.A., Hunter, M.D., Kominoski, J.S., Swan, C.M., Bradford, M.A., 2008. Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. *J. Ecol.* 96, 303–313.
- Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. *For. Ecol. Manage.* 254, 1–15.
- Barbier, S., Balandier, P., Gosselin, F., 2009. Influence of several tree traits on rainfall partitioning in temperate and boreal forests: a review. *Ann. For. Sci.* 66, 602.
- Beatty, S.W., 2003. Habitat heterogeneity and maintenance of species in understory communities. In: Gilliam, F.S., Roberts, M.R. (Eds.), *The Herbaceous Layer in Forests of Eastern North America*. Oxford University Press, New York, pp. 177–198.
- Both, S., Fang, T., Böhne, M., Bruehlheide, H., Geißler, C., Kühn, P., Scholten, T., Trogisch, S., Erfmeier, A., 2011. Lack of tree layer control on herb layer characteristics in a subtropical forest, China. *J. Veg. Sci.* 22, 1120–1131.
- Cajander, A.K., 1926. The theory of forest types. *Acta For. Fenn.* 29.
- Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *PNAS* 104, 18123–18128.
- Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M.I., Gonzalez, A., 2011. The functional role of producer diversity in ecosystems. *Am. J. Bot.* 98, 572–592.
- Cardinale, B.J., Duffy, E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 60, 59–67.
- Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., Laganière, J., Brassard, B., 2011. Competition and facilitation between tree species change with stand development. *Oikos* 120, 1683–1695.
- Chávez, V., Macdonald, S.E., 2010. The influence of canopy patch mosaics on understory plant community composition in boreal mixedwood forests. *For. Ecol. Manage.* 259, 1067–1075.
- Chávez, V., MacDonald, S.E., 2012. Partitioning vascular understory diversity in mixedwood boreal forests: the importance of mixed canopies for diversity conservation. *For. Ecol. Manage.* 271, 19–26.
- De Grandpré, L., Bergeron, Y., Nguyen, T., Boudreault, C., Grondin, P., 2003. Composition and dynamics of the understory vegetation in the boreal forests of Canada. In: Gilliam, F.S., Roberts, M.R. (Eds.), *The Herbaceous Layer in Forests of Eastern North America*. Oxford University Press, New York, pp. 238–261.
- Ellenberg, H., Leuschner, C., 2010. Zeigerwerte der Pflanzen Mitteleuropas. In: Ellenberg, H., Leuschner, C. (Eds.), *Vegetation Mitteleuropas mit den Alpen*, 6. Auflage. Ulmer, Stuttgart, Germany.
- Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57, 845–858.
- Golodets, C., Kigel, J., Sternberg, M., 2011. Plant diversity partitioning in grazed Mediterranean grassland at multiple spatial and temporal scales. *J. Appl. Ecol.* 48, 1260–1268.
- Hagen-Thorn, A., Callesen, I., Armolaitis, K., Nihlgard, B., 2004. The impact of six European tree species on the chemistry of mineral topsoil in forest plantations on former agricultural land. *For. Ecol. Manage.* 195, 373–384.
- Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytowskiak, R., Hale, C., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology* 87, 2288–2297.
- Huston, M., 1979. A general hypothesis of species diversity. *Am. Nat.* 113, 81–100.
- IUSS Working Group WRB 2006. World reference base for soil resources 2006. *World Soil Resources Reports*, No. 103. Rome, FAO.
- Légaré, S., Bergeron, Y., Leduc, A., Paré, D., 2001. Comparison of the understory vegetation in boreal forest types of southwest Quebec. *Can. J. Bot.* 79, 1019–1027.
- Lenière, A., Houle, G., 2006. Response of herbaceous plant diversity to reduced structural diversity in maple-dominated (*Acer saccharum* Marsh.) forests managed for sap extraction. *For. Ecol. Manage.* 231, 94–104.
- Leuschner, C., Jungkunst, H.F., Fleck, S., 2009. Functional role of forest diversity: pros and cons of synthetic stands and across-site comparisons in established forests. *Basic Appl. Ecol.* 10, 1–9.
- Levine, J.M., HilleRisLambers, J., 2009. The importance of niches for the maintenance of species diversity. *Nature* 461, 254–258.
- Liu, S.R., Li, X.M., Niu, L.M., 1998. The degradation of soil fertility in pure larch plantations in the northeastern part of China. *Ecol. Eng.* 10, 75–86.
- Messier, C., Parent, S., Bergeron, Y., 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *J. Veg. Sci.* 9, 511–520.
- Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H., 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecol. Lett.* 14, 1211–1219.
- Nadrowski, K., Wirth, C., Scherer-Lorenzen, M., 2010. Is forest diversity driving ecosystem function and service? *Curr. Opin. Environ. Sustain.* 2, 75–79.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2013. nlme: linear and nonlinear mixed effects models. R package version 3.1-111.
- Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. *Tree Physiol.* 22, 1193–1200.
- R Development Core Team 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. (URL <<http://www.R-project.org>>).
- Reich, P.B., Frelich, L.E., Voldseth, R.A., Bakken, P., Adair, E.C., 2012. Understorey diversity in southern boreal forests is regulated by productivity and its direct impacts on resource availability and heterogeneity. *J. Ecol.* 100, 539–545.
- Ricklefs, R.E., 1977. Environmental heterogeneity and plant species diversity: a hypothesis. *Am. Nat.* 111, 376–381.
- Rodríguez-Valcarrada, J., Nanos, N., del Rey, M.C., López de Heredia, U., Escribano, R., Gil, L., 2011. Small-scale variation of vegetation in a mixed forest understory is partly controlled by the effect of overstorey composition on litter accumulation. *J. For. Res.* 16, 473–483.
- Thomsen, R.P., Svenning, J.-C., Balslev, H., 2005. Overstorey control of understory species composition in a near-natural temperate broadleaved forest in Denmark. *Plant Ecol.* 181, 113–126.
- Vockenhuber, E.A., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D., Tschamntke, T., 2011. Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. *Perspect. Plant Ecol. Evol. Syst.* 13, 111–119.
- Wedraogo, F.X., Belgé, G., Berthelin, J., 1993. Seasonal nitrification measurements with different species of forest litter applied to granite-sand-filled lysimeters in the field. *Biol. Fertil. Soils* 15, 28–34.
- Yankelevich, S.N., Fragoso, C., Newton, A.C., Russell, G., Heal, O.W., 2006. Spatial patchiness of litter, nutrients and macroinvertebrates during secondary succession in a tropical montane cloud forest in Mexico. *Plant Soil* 286, 123–139.