

Driving mechanisms of overstorey–understorey diversity relationships in European forests



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ABSTRACT

Forest ecosystem multifunctionality and the provision of ecosystem services benefit from high biodiversity, including from the understorey. Hence, it is crucial to get insight into the mechanisms that influence the composition and diversity in this forest layer. Understorey species have specific environmental requirements which are influenced by the overstorey in a species-specific way. Mixing tree species may create a heterogeneous pattern of environmental conditions similar to the component species' monocultures, or induce new environmental conditions. We quantified overstorey–understorey taxonomic and functional diversity relationships at different spatial scales in an innovative large-scaled European diversity-oriented research platform that allows the separation of tree species identity and diversity effects. We considered our results in relation to the divergent patterns expected, depending on whether environmental heterogeneity or novel environment creation is the mechanism driving overstorey–understorey diversity relationships.

We examined the understorey in mature forests in six European regions. Per region, three to five tree species were selected and 28–43 plots of 30 m × 30 m were established (209 in total), covering a tree species richness gradient from monocultures to three- to five-species mixed plots. Within each plot, we performed vegetation surveys in three vegetation quadrats. We examined the understorey compositional variation among and within regions and the influence of overstorey taxonomic and functional diversity on understorey diversity at different spatial scales.

The understorey composition showed clear interregional differences. We found lower compositional differentiation among quadrats with a higher tree species richness level (Finland, Germany and Italy). These quadrats share more tree species and probably have more similar environmental conditions. Neither overstorey taxonomic nor functional diversity affected the stand-level understorey species richness. At the forest-level, adding two-species mixtures to component monocultures clearly increased the understorey species richness, while adding mixtures with a higher tree species richness level to component monocultures had a negligible or negative impact.

Overstorey–understorey diversity relationships depend on the spatial scale. At the stand-level, our results lacked support for the environmental heterogeneity hypothesis and revealed the possibility of novel environment creation in tree-by-tree mixed stands. At the forest-level, favouring the mixture of two-species mixed stands and their component monoculture stands offers the best prospects for a higher understorey species richness.

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1. Introduction

In the last two decades, numerous studies have focussed on the relationship between biodiversity and ecosystem functioning (BEF; e.g. Cardinale et al., 2006; Pasari et al., 2013). Although some species appear functionally redundant at any given time, high biodiversity is needed to maintain ecosystem multifunctionality (Hector and Bagchi, 2007) and the provision of ecosystem services (Morin et al., 2011; Zhang et al., 2012) now and in the future. Forests have been underrepresented in the BEF-research area (Nadrowski et al., 2010; Verheyen et al., 2015), but recent studies confirm that the beneficial effects of diversity on functioning are also present in forest ecosystems (e.g. Gamfeldt et al., 2013; Hulvey et al., 2013; Jucker et al., 2014). Despite its very small contribution to the total aboveground forest biomass (Welch et al., 2007), the forest understorey accounts for most of the total vascular plant species diversity in deciduous forests, leading to an average understorey–overstorey species richness ratio of 5 (Gilliam, 2014). In coniferous stands, this ratio may even be higher, due to lower overstorey richness in general (Gilliam, 2007). Moreover, the understorey contributes to numerous ecosystem functions and services, such as carbon dynamics, nutrient fluxes and habitat provision (e.g. Muller, 2014). As the preservation of the understorey community is important for forest ecosystem functioning, it is crucial to get insight into the factors that influence its composition and diversity.

Understorey species have specific environmental requirements (Ellenberg and Leuschner, 2010), and some of these conditions are heavily influenced by the composition of the overstorey (e.g. Augusto et al., 2003; Canham et al., 1994). Tree species affect understorey light availability and quality differently (Messier et al., 1998; Reich et al., 2012). Their effect on rainfall interception, transpiration and water uptake by roots is also species-dependent, meaning soil water availability can significantly vary among tree species (e.g. Barbier et al., 2008, 2009). Furthermore, the composition of the overstorey influences soil nutrient availability and soil acidity, as a result of differences among tree species in litter quality and quantity, nitrogen fixation, nutrient uptake and atmospheric deposition on leaves and needles (e.g. Augusto et al., 2003; Finzi et al., 1998a, b; Hagen-Thorn et al., 2004). In addition, phytotoxic litter compounds and the thickness of the litter layer, which is related to the degradability of the leaf litter, may affect the germination and performance of certain understorey species (e.g. Holderegger, 1996; Rodríguez-Calcerrada et al., 2011). Because of these tree species identity effects on the environmental conditions and the species-specific niches of the understorey species, changes in the diversity and hence composition of the overstorey may affect the diversity and composition of the understorey (Martin et al., 2011; Meers et al., 2010; Wulf and Naaf, 2009). Nevertheless, these effects also depend on the functional effect traits of the tree species that are mixed, indicating their effect on the environmental conditions, e.g. specific leaf area, foliar C content (Suding et al., 2008). Consequently, functional diversity effects may be different from taxonomic diversity effects (Cadotte et al., 2011; Díaz and Cabido, 2001).

Monoculture stands are characterized by relatively homogenous environmental conditions and thus rather small

compositional differences in the understorey among different patches in a stand are expected. This implies a low intrastand compositional turnover (i.e. the replacement of species by others when comparing species communities among patches in the stand) and a high intrastand compositional nestedness (i.e. the species community at a certain patch in the stand is a subset of the species community at another patch; Baselga, 2010). As these monoculture stands share only one or even no tree species with other monoculture and mixed stands, strong understorey compositional differences with other stands are expected (high interstand compositional turnover and low interstand compositional nestedness).

Increasing the tree species diversity within a stand may affect the understorey in two different ways (Table 1). On the one hand, the presence of multiple tree species in the stand may induce *environmental heterogeneity* that results in a patchy matrix of environmental conditions, determined by the tree species covering the patch. The patch-level environmental conditions then reflect the tree species identity effects (Yankelevich et al., 2006). The resulting higher number of niches in the mixed stand is expected to promote the coexistence of more understorey species (Huston, 1979; Levine and Hille Ris Lambers, 2009; Silvertown, 2004) and this may lead to strong compositional differences among patches within the mixed stand (i.e. high intrastand compositional turnover and low intrastand compositional nestedness). Consequently, the stand-level understorey diversity is expected to be higher in the mixed stand compared to each of the component tree species monocultures (Reich et al., 2012). Furthermore, the higher the overstorey species richness, the more tree species are shared with other stands and the smaller the understorey compositional differences among the different stands (i.e. low interstand compositional turnover and high interstand compositional nestedness). We expect the understorey species richness of a forest composed of mixed stands and their component monoculture stands to be similar to the understorey species richness of a forest that only contains the component monoculture stands.

On the other hand, a mixed overstorey may also create new conditions as a result of averaging of tree species effects or interactive effects of tree species on the environment (*novel environment creation*). In this case, the effects on the environmental conditions are true overstorey diversity effects. For example, Ball et al. (2008) found that mixing litter with different qualities may affect the decomposition rate and therefore also the soil nutrient availability and acidity compared to monoculture litter. Compared to the component tree species monoculture stands, the new environmental conditions in the mixed stand may impede the presence of understorey species for which the new environmental conditions do not match their niche requirements. However, these conditions may also provide opportunities for species that are not present in the component tree species monocultures (i.e. high level of true species turnover between the mixed stand and the component monocultures). Stand-level understorey species richness in mixed stands may thus be higher, equal or lower compared to each of the component tree species monocultures. The new environmental conditions in the mixed stand are presumably relatively homogeneous,

Table 1
Expected changes in stand-level SR and intrastand and interstand compositional turnover and nestedness when increasing stand-level tree species diversity (relative to a monoculture stand) and expected changes in forest-level SR when combining mixed and component monoculture stands instead of only monoculture stands, under the influence of environmental heterogeneity (tree identity effects) and novel environment creation (tree diversity effects; ↑ indicates an increase, ↓ indicates a decrease, ≈ indicates negligible change).

Mechanism	Stand-level SR	Intrastand comp. diss.		Interstand comp. diss.		Forest-level SR
		Turnover	Nestedness	Turnover	Nestedness	
Environmental heterogeneity	↑	↑	↓	↓	↑	≈
Novel environment creation	↑ ↓ ≈	≈	≈	↓	↑	↑

resulting in limited differences in the understory composition among the patches in a stand (i.e. low intrastand compositional turnover and high intrastand compositional nestedness, similar to monoculture stands). Stands with a higher overstorey species richness may share tree species, which may lead to similar environmental conditions and hence rather small differences in understory composition (i.e. low interstand compositional turnover and high interstand compositional nestedness). Meanwhile, combining mixed stands and their component monoculture stands within a forest is expected to increase the forest-level understory species richness above that of a forest that only contains the component monoculture stands. In mature forests, we expect a mix of environmental heterogeneity and novel environment creation to take place in diverse stands. The intensity of the interspecific interactions among the tree species in a mixed stand probably determines the relative contributions of both mechanisms (i.e. environmental heterogeneity and novel environment creation; [Ampoorter et al., 2015](#)). When trees species are present in clusters, interspecific interactions may only take place at the cluster borders and environmental heterogeneity will be more prevalent. On the contrary, tree-by-tree mixtures allow interactions at the level of each individual tree, favouring novel environment creation.

So far, studies examining the relationship between overstorey and understory diversity in mature forests based their expectations solely on the environmental heterogeneity hypothesis, but they yielded inconsistent results (e.g. [Barbier et al., 2008](#); [Vockenhuber et al., 2011](#)). Moreover, previous studies did not explore spatial scales other than the stand-level, nor did they study the effect of overstorey functional diversity on the understory. We used a unique and innovative large-scaled European research platform ([Baeten et al., 2013](#)) to test the following hypotheses:

H1. The understory composition shows interregional differences, triggered by contrasting environmental conditions and overstorey compositions.

H2. A tree-by-tree mixing pattern in mixed stands leads to the creation of novel environmental conditions with similar intrastand compositional turnover and nestedness, lower interstand compositional turnover and higher interstand compositional nestedness, higher forest-level SR and inconsistent effects on stand-level SR of the understory compared to monocultures.

H3. Overstorey functional diversity effects are different from overstorey taxonomic diversity effects.

2. Materials and methods

2.1. Exploratory set-up

This study is located in the overstorey diversity-oriented “Exploratory Platform” created within the FP7 FunDivEUROPE project. It encompasses six major forest types across Europe (boreal forest in Finland; hemiboreal, nemoral coniferous, mixed broadleaved-coniferous forest in Poland; beech forest in Germany; mountainous beech forest in Romania; thermophilous deciduous forest in Italy; Mediterranean mixed forest in Spain), from the northern boreal region to the southern Mediterranean region and along large soil and climatic gradients ([Fig. 1a](#); see [Appendix 1](#)). In this way, the representativeness of our results is high. In each region, three to five target tree species were selected that are regionally common and/or important from a silvicultural point of view. Based on this species pool, 28–43 plots were chosen per region, covering a target tree species richness (SR) gradient from monoculture stands to three- to five-species mixed stands with a tree-by-tree mixing intensity, and containing different target tree species compositions (‘Composition’) per target tree SR level ([Fig. 1b](#)). This platform allows to separate tree species identity and diversity effects. Attention was paid to avoid complete dilution, maximize evenness of tree species abundances and minimize covariation between tree SR and environmental factors within each region. Admixtures of non-target tree species were accepted as long as the summed basal area of the admixed species was below 5% of the total basal area. The plots were 30 m × 30 m large and surrounded by a buffer zone of 10 m wide with similar forest composition and structure, to avoid edge effects. For more information on the regions, plot selection criteria, and plot-level information refer to [Baeten et al. \(2013\)](#) and [Jucker et al. \(2014\)](#).

2.2. Data collection

Each plot was subdivided in nine subplots of 10 m × 10 m ([Fig. 1c](#)). In the lower left corner (usually southwestern relative to the centre), central and upper right subplots, the understory was surveyed between May and August 2012 in a 5 m × 5 m quadrat,

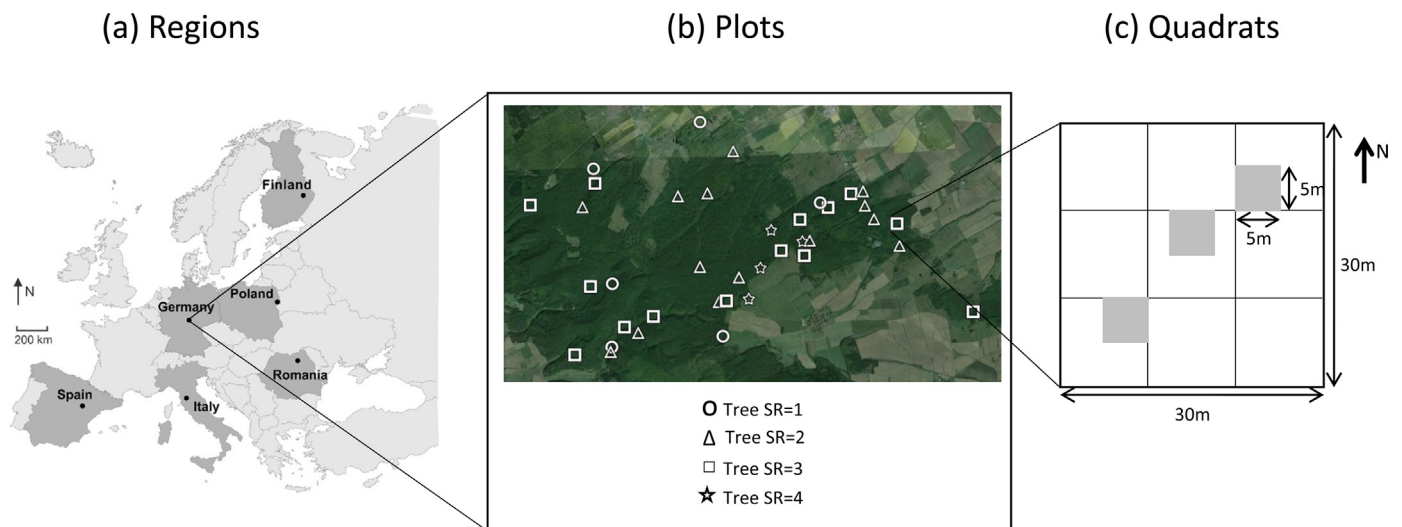


Fig. 1. Overview of the regions in the FunDivEUROPE Exploratory Platform (a), with a detailed view on the location and the tree species richness (SR) level of the plots in the German exploratory region (b), and a scheme of the plot lay-out, subdivided in nine subplots, with an indication of the quadrats where the understory was monitored (grey squares) (c).

placed at a fixed location within the subplots. In each of these three quadrats, the percentage cover of each understorey species (<1.3 m) was estimated. The plots are used as research units representing forest stands, except for the analysis of the understorey compositional variation where quadrats were compared, and the forest-level understorey SR where virtual forests were created by combining quadrats (see Section 2.3).

2.3. Data analysis

All analyses were performed in R 3.1.1 (R Core Team, 2014). First, we explored the understorey compositional variation among regions (H1). We calculated compositional dissimilarities based on the full matrix containing quadrat-level understorey data of all six regions, using the Lennon distance measure based on presence/absence (Lennon et al., 2001). The Lennon distance metric quantifies true compositional turnover and is not influenced by richness differences among quadrats that create nestedness patterns. Nonmetric Multidimensional Scaling (NMDS) was used to visualize the compositional differences among quadrats. The significance of the compositional differences among the six regions was tested with a permutational multivariate analysis of variance (PERMANOVA; *adonis* in *vegan* package; Anderson, 2001; Oksanen et al., 2013). However, dissimilarity approaches, such as PERMANOVA, confound location (compositional dissimilarities among regions) and dispersion effects (compositional dissimilarities within regions; Anderson, 2001; Warton et al., 2012). Hence, we tested separately for multivariate heterogeneity of dispersions among regions using *betadisper* (*vegan* package), a multivariate analogue of Levene's test for homogeneity of variances (Anderson et al., 2006). In case multivariate dispersion is significant, PERMANOVA results must be handled with care.

Second, we explored the understorey compositional variation within each region in a similar way. We calculated compositional dissimilarities on the matrix containing quadrat-level understorey data of one region (Lennon distance measure based on presence/absence) and visualized compositional differences among quadrats with NMDS. PERMANOVA was used in combination with *betadisper* to test the significance of the understorey compositional differences among levels of target tree SR (H2). For each region, the highest level of target tree SR (for Spain the two highest levels) was excluded from both tests as unbalanced plot numbers (see Appendix 1) can skew the results.

Third, we quantified understorey diversity at the forest-level (forest-level SR, interstand compositional turnover and nestedness) and the stand-level (stand-level SR and true diversity, intrastand compositional turnover and nestedness) (H2). The forest-level understorey SR (gamma diversity) was quantified by creating virtual forests. The following procedure was performed for each tree species composition realized in a region. First, we made a pool of the mixed quadrats with the requested tree species composition and all monoculture quadrats of the component tree species. Second, to create a more or less proportional mix of monoculture and mixed quadrats, we randomly selected five monoculture quadrats (taking into account that at least one monoculture quadrat of all component tree species should be present, also for the five-species mixtures) and three mixed quadrats (taking into account that only three quadrats were present for some tree species compositions) from this quadrat pool (120 runs; approximately equal numbers of quadrats of all component tree species present in each run); we calculated the total understorey SR of the quadrat combination for each run; and we averaged the values of all runs (forest-level $SR_{\text{mono+mix}}$). Third, we performed the same analysis but selecting eight monoculture quadrats from the quadrat pool (120 runs; approximately equal numbers of quadrats of all component tree species present in each run), resulting in the forest-level

SR_{mono} . Fourth, we subtracted the forest-level SR_{mono} from the forest-level $SR_{\text{mono+mix}}$ in order to know how many understorey species were gained on average by replacing three monoculture quadrats by three mixed quadrats of that specific tree species composition (Δ forest-level understorey SR). For one tree species in Germany and two tree species in Poland there were no monoculture quadrats, so the analysis was not performed for the tree species compositions containing these species. For the interstand compositional dissimilarity (i.e. beta diversity among stands, composed of a turnover and nestedness component), a dissimilarity matrix was calculated based on the Sørensen distance measure, using plot-level presence/absence data. The Sørensen distance measure incorporates both true compositional turnover and nestedness (Koleff et al., 2003). The mean of the pairwise compositional dissimilarities of a plot against all other plots within the same region determines its interstand compositional dissimilarity. Then, an additive partitioning of the Sørensen dissimilarity was performed to quantify the compositional turnover (using the Lennon distance measure) and nestedness (using the nestedness-resultant distance measure; Baselga, 2010) as parts of the total interstand compositional dissimilarity. Next, we calculated the stand-level understorey SR and true diversity (exponent of Shannon diversity index, using mean cover values over the three quadrats per plot; i.e. alpha diversity). The total intrastand compositional dissimilarity (i.e. beta diversity among quadrats within a plot), and its turnover and nestedness components were determined analogously to the interstand compositional dissimilarity, deriving the mean pairwise compositional dissimilarity of a quadrat against the two other quadrats within the same plot.

The effect of target tree SR on the stand-level understorey SR and true diversity and the intrastand and interstand compositional turnover and nestedness was tested using mixed models, for all regions together and separately. The models allowed for random variation across target tree species compositions which were nested within region (for the analysis of the separate regions, 'Region' was deleted from the random structure). The intercept was fitted at tree SR=1, so representing the estimated understorey diversity in monoculture plots. Starting from the full model [R-syntax: $y \sim \text{Target tree SR} + (1 \mid \text{Region/Composition})$], using *glmer* with a Poisson error distribution and log link for stand-level understorey SR (not overdispersed) and *lmer* with a normal error distribution for the other response variables, both from the *lme4* package (Bates et al., 2013), and parameter estimation via maximum likelihood, we looked for model parsimony (approach according to Zuur et al., 2009). We sequentially reduced the random structure while keeping the fixed effect term: we subsequently dropped the variance terms associated with target tree species compositions and regions [R-syntax: $y \sim \text{Target tree SR}$; using *glm* from the *stats* package with a Poisson error distribution, log link and parameter estimation via maximum likelihood for understorey species richness and with a Gaussian distribution family and maximum likelihood parameter estimation for the other response variables]. Model selection was based on Akaike's Information Criterion (AIC; Akaike, 1973). Once an optimal random structure was found, we searched for the optimal fixed effect structure by comparing the AIC of models with and without the fixed effect of target tree SR. For models with fixed effects only, the adjusted R^2 of the linear model was reported; for models that (also) contained random effects, the conditional R^2 was calculated according to Nakagawa and Schielzeth (2013) (*MuMIn* package; Bartoń, 2013), indicating the proportion of the variance explained by both the random and fixed effects.

Fourth, a similar approach was used to test the influence of functional overstorey diversity on the above mentioned response variables (H3), using community-weighted functional dispersion instead of target tree SR as a predictor in the mixed model

(Laliberté and Legendre, 2010). We selected tree traits that are expected to have strong effects on the understorey, i.e., traits related to litter decomposition and nutrient fluxes towards the soil, and that are available for most of the target tree species: leaf type (deciduous/evergreen), specific leaf area (SLA; information from the LEDA traitbase; Kleyer et al., 2008), foliar %C and %N and Ca content. The latter three traits were measured on fresh leaves that were collected in the Exploratory Platform. They were oven-dried for 48 h at 60 °C and analyzed with Near Infrared Spectroscopy, combined with a wet-chemical reference method using a CHN Elemental analyser for C and N (Flash EA1112 Series, ThermoFinnigan, Milan, Italy), and an atom absorption spectrometer for Ca concentration (AAS, ICE 3000 series, ThermoScientific, China). Community-weighted functional dispersion among target tree species was calculated by combining the trait matrix with a matrix containing basal area values of the target tree species for each plot (basal area was calculated based on an inventory of the diameters at breast height performed by the FunDivEUROPE field teams), using the function *dbFD* from the *FD* package (Laliberté et al., 2014).

3. Results

The location of the regions in the multidimensional space based on the composition of the understorey vegetation was clearly distinct (H1; Fig. 2). The quadrat-level composition was relatively similar in Romania, Germany and Poland, while the understorey vegetation in Finland and especially Spain and Italy was clearly different from the other regions. Dispersions were also heterogeneous ($p_{\text{disp}} = 0.001$), with relatively large compositional variation among the quadrats of Spain and relatively small compositional variation among the quadrats of Finland, Germany, Poland and Romania. Consequently, the significant result of PERMANOVA ($p_{\text{perm}} = 0.001$) indicates both a location and a dispersion effect.

For Finland, Germany and Italy, both PERMANOVA and *betadis-per* yielded significant *p*-values for the effect of target tree SR on the composition of the understorey community within the region (H2;

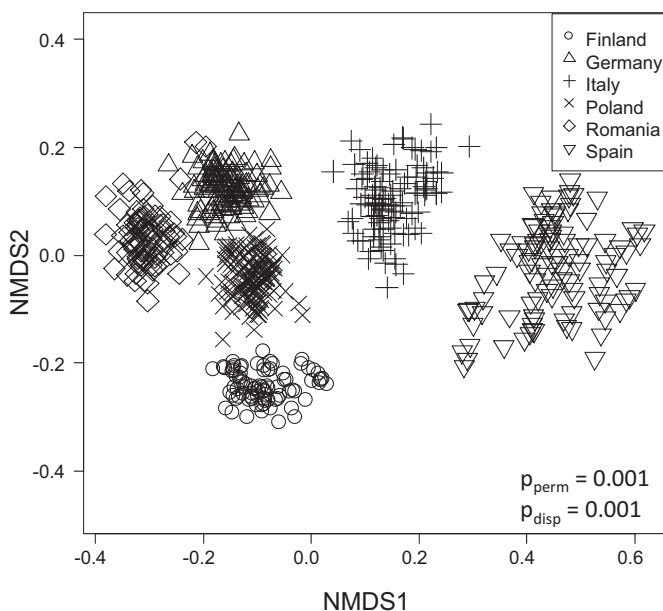


Fig. 2. Dissimilarity in understorey vegetation composition among quadrats in function of region, based on the Lennon distance measure. The p_{perm} value indicates the combined significance of the location and dispersion effect, based on PERMANOVA; the p_{disp} indicates the significance of the dispersion effect, based on the function *betadis-per* in R.

Fig. 3). As there was visually no obvious difference in understorey composition among levels of target tree SR (i.e. no clear location effect) for these regions, the significant *p*-value of PERMANOVA probably only indicated a dispersion effect, with lower compositional variation among quadrats towards higher levels of target tree SR. For Poland and Spain, dispersion among target tree SR levels was homogenous ($p_{\text{disp}} > 0.05$). The significant *p*-value from PERMANOVA therefore indicated a location effect, and hence a difference in understorey community composition between levels of Tree SR. For Romania, neither location nor dispersion effects were visible.

Adding tree species mixed quadrats to a virtual forest consisting of monoculture quadrats clearly affected the forest-level understorey SR but in an inconsistent way (H2; Fig. 4). The combination of two-species mixed quadrats with their component monoculture quadrats generally increased the forest-level understorey SR compared to the combination of only component monoculture quadrats. The combination with three-species mixtures led to higher forest-level understorey SR in Germany, Italy and especially Spain, while in Finland, Poland and Romania the effect was negligible or even negative. The combination with four- and five-species mixtures predominantly had a negative effect.

Effects of target tree SR and functional dispersion on stand-level true diversity and intrastand and interstand compositional turnover and nestedness were insignificant for all regions (H2, H3; Table 2). Target tree SR had a negative effect on the stand-level understorey SR in Romania while the effect of functional dispersion on the stand-level understorey SR was positive for Germany and Spain. However, the amount of variation explained by target tree SR and functional dispersion was very small (<10%).

4. Discussion

H1. The understorey composition shows interregional differences, triggered by contrasting environmental conditions and overstorey compositions.

The understorey composition showed a clear interregional differentiation. Differences in climate, forest structure, soil conditions and tree species composition probably all affected the understorey composition, leading to different understorey species pools for all regions (Ellenberg and Leuschner, 2010). Furthermore, the understorey showed higher compositional variation among quadrats for the Mediterranean regions compared to northern latitudes. This can in part be explained by the larger understorey species pool in Spain and Italy, but it might also be because of differences in experimental set-up. In Finland only three target tree SR levels were used and plots were all located in flat areas, in contrast with Spain and Italy that have four and five levels of target tree SR, respectively, and plots located on differing slopes and aspects (Baeten et al., 2013).

H2. A tree-by-tree mixing pattern in mixed stands leads to the creation of novel environmental conditions with similar intrastand compositional turnover and nestedness, lower interstand compositional turnover and higher interstand compositional nestedness, higher forest-level SR and inconsistent effects on stand-level SR of the understorey compared to monocultures.

Previous studies examining overstorey–understorey diversity relationships all started from the environmental heterogeneity hypothesis that predicts a positive effect of target tree SR on stand-level understorey SR and true diversity and intrastand compositional turnover and a negative effect on intrastand compositional nestedness. Aubert et al. (2004) and Vockenhuber et al. (2011) indeed showed that a more diverse overstorey featured a more diverse understorey at the stand-level. Nevertheless, our results on the effect of target tree SR on the stand-level understorey diversity did not prove the presence of environmental heterogeneity.

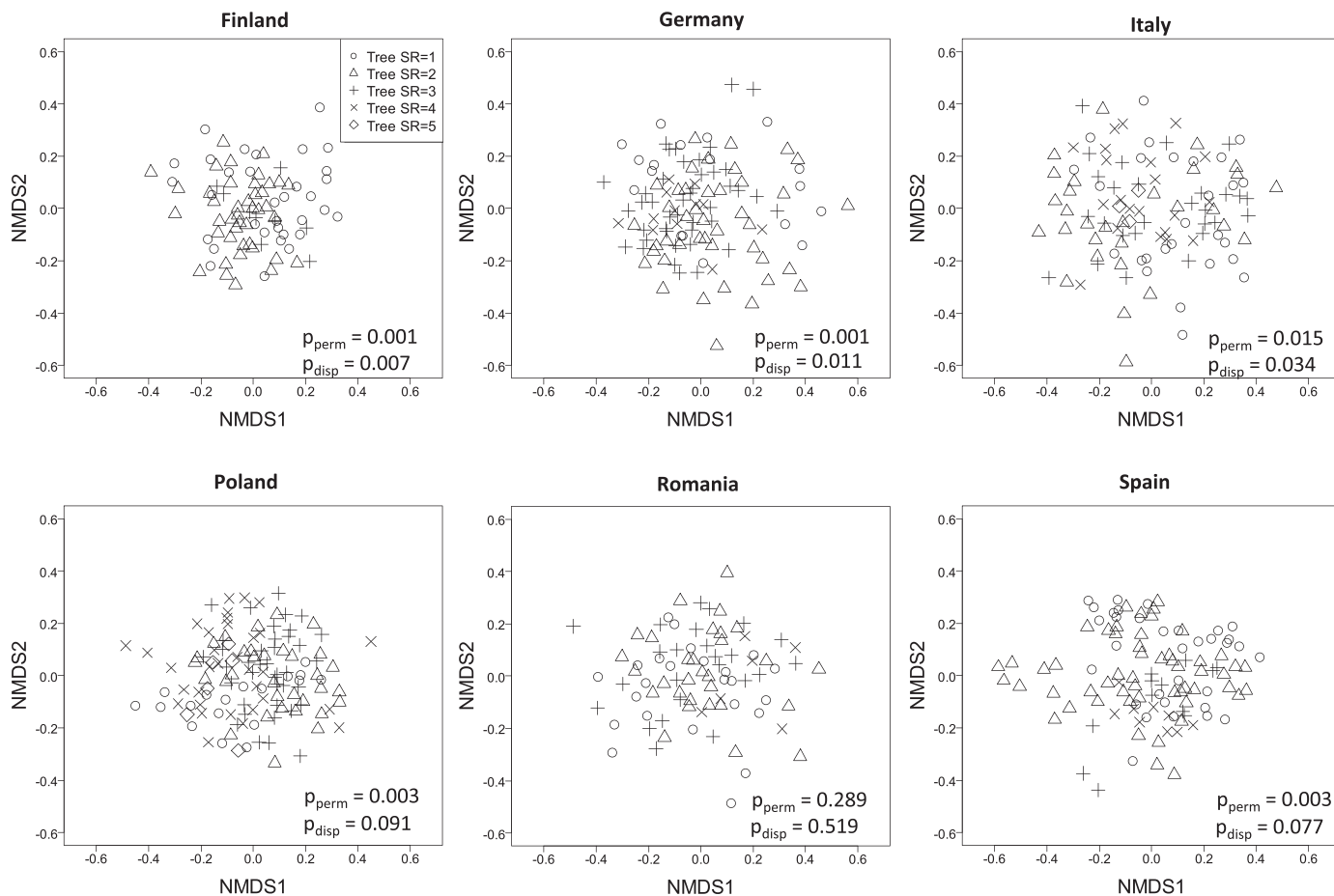


Fig. 3. Dissimilarity in understorey vegetation composition among quadrats per region in function of target tree species richness (SR), based on the Lennon distance measure. The p_{perm} value indicates the combined significance of the location and dispersion effect, based on PERMANOVA; the p_{disp} indicates the significance of the dispersion effect, based on the function *betadisper* in R. Symbols represent the target tree SR levels. The highest target tree SR level of each region (for Spain the two highest levels) was excluded from both tests (not from the figure).

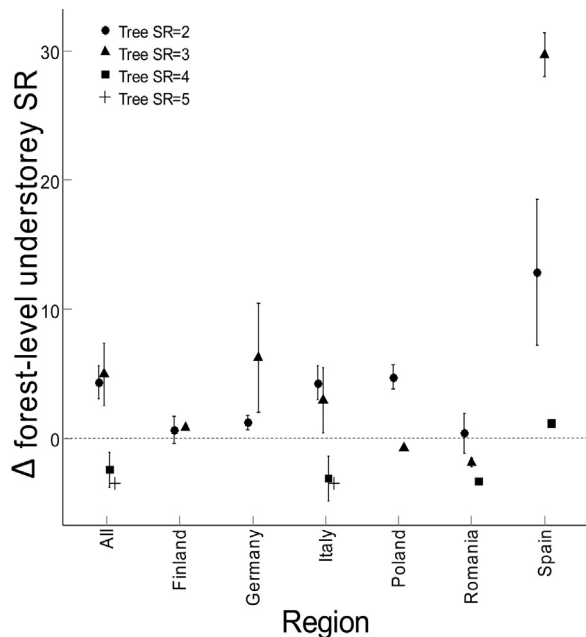


Fig. 4. Difference in forest-level understorey SR between a combination of three mixed and five component monoculture quadrats and a combination of eight component monoculture quadrats. For more information on how Δ forest-level understorey SR was calculated, see Section 2. Values represent the mean \pm standard error of all analyzed tree species compositions of a certain tree species richness (Tree SR) level in the region (for 'All' the values of all regions were analyzed together).

Both et al. (2011) did not find a clear overstorey–understorey relationship either, and Barbier et al. (2008) indicated in their review that monospecific stands may even have a higher understorey diversity than mixed stands. The inconsistency in the results of these studies may on the one hand indicate a lacking effect of overstorey diversity on the understorey, and the presence of other driving factors for understorey diversity. On the other hand, it may also demonstrate the presence of novel environment creation in some forests. Namely, trees species in mixed stands may interact (e.g. Ball et al., 2008), leading to other environmental conditions and a different understorey community compared to their component monocultures. This was demonstrated in Fig. 3 for Poland and Spain. Moreover, in case novel environment creation indeed takes place and component tree species are more or less evenly distributed over the stand as is true for the majority of the FunDivEUROPE plots, the new environmental conditions are more homogeneous compared to the pattern created by environmental heterogeneity. This may restrict the understorey compositional differences among patches within a mixed stand to the level present in monoculture stands. In this way, novel environment creation may also form an explanation for the lack of an effect of target tree SR on the intrastand compositional turnover and nestedness in the FunDivEUROPE Exploratory Platform, as an alternative to a lacking overstorey–understorey diversity relation. Bartels and Chen (2010) indicated that the lack of an overstorey–understorey diversity relationship at the stand-level might also be explained by resource quantity dominating over resource heterogeneity in affecting the understorey vegetation in mature forests.

Table 2

Optimal mixed-effects model structure relating the stand-level understorey species richness (SR) (A) and true diversity (B) and the intrastand (C, D) and interstand (E, F) compositional turnover and nestedness to the stand-level target tree SR and functional dispersion for all regions together (All) and separately. Parameter estimates are given for the intercept and fixed structure, consisting of target tree SR or functional dispersion (§ indicates if the random structure, consisting of target tree species composition nested within region or only region or target tree species composition, is significant). See Section 2.3 for details about the structure and the stepwise reduction of the full model. R^2_m refers to the marginal R^2 , i.e. the fraction of the variation explained by the fixed structure; R^2_c refers to the conditional R^2 , i.e. the fraction of the variation explained by the fixed and random structure (n : number of observations).

Country	n	Target tree SR				Functional dispersion					
		R^2_m	R^2_c	Intercept	Fixed	R^2_m	R^2_c	Intercept	Fixed		
A. Stand-level understorey SR											
All	209	–	0.549	3.167 ± 0.133	–	§	–	0.549	3.167 ± 0.133	–	§
Finland	28	–	0.245	2.861 ± 0.087	–	§	–	0.245	2.861 ± 0.087	–	§
Poland	43	–	–	3.299 ± 0.029	–	–	–	–	3.299 ± 0.029	–	–
Germany	38	–	0.071	3.147 ± 0.073	–	§	0.081	0.140	2.886 ± 0.127	2.736 ± 1.094	§
Romania	28	<0.001	<0.001	3.033 ± 0.068	–0.112 ± 0.049	–	–	–	2.910 ± 0.044	–	–
Italy	36	–	0.109	2.948 ± 0.059	–	§	–	0.109	2.948 ± 0.059	–	§
Spain	36	–	0.126	3.817 ± 0.052	–	§	0.072	0.193	3.675 ± 0.085	0.892 ± 0.399	§
B. Stand-level understorey true diversity											
All	209	–	0.510	7.251 ± 1.404	–	§	–	0.510	7.251 ± 1.404	–	§
Finland	28	–	–	4.217 ± 0.346	–	–	–	–	4.217 ± 0.346	–	–
Poland	43	–	–	6.426 ± 0.350	–	–	–	0.420	6.429 ± 0.409	–	§
Germany	38	–	–	5.524 ± 0.616	–	–	–	0.238	5.624 ± 0.726	–	§
Romania	28	–	–	6.324 ± 0.533	–	–	–	0.242	6.404 ± 0.600	–	§
Italy	36	–	–	6.730 ± 0.487	–	–	–	0.197	6.741 ± 0.509	–	§
Spain	36	–	0.301	14.038 ± 1.864	–	§	–	0.301	14.038 ± 1.86	–	§
C. Intrastand compositional turnover											
All	209	–	0.328	0.264 ± 0.028	–	§	–	0.328	0.264 ± 0.028	–	§
Finland	28	–	–	0.164 ± 0.015	–	–	–	–	0.164 ± 0.015	–	–
Poland	43	–	–	0.256 ± 0.012	–	–	–	–	0.256 ± 0.012	–	–
Germany	38	–	–	0.243 ± 0.014	–	–	–	–	0.243 ± 0.014	–	–
Romania	28	–	–	0.243 ± 0.018	–	–	–	–	0.243 ± 0.018	–	–
Italy	36	–	–	0.309 ± 0.022	–	–	–	–	0.309 ± 0.022	–	–
Spain	36	–	–	0.364 ± 0.013	–	–	–	–	0.364 ± 0.013	–	–
D. Intrastand compositional nestedness											
All	209	–	–	0.084 ± 0.004	–	–	–	–	0.084 ± 0.004	–	–
Finland	28	–	–	0.092 ± 0.009	–	–	–	–	0.092 ± 0.009	–	–
Poland	43	–	–	0.081 ± 0.008	–	–	–	–	0.081 ± 0.008	–	–
Germany	38	–	–	0.097 ± 0.009	–	–	–	–	0.097 ± 0.009	–	–
Romania	28	–	–	0.102 ± 0.013	–	–	–	–	0.102 ± 0.013	–	–
Italy	36	–	–	0.086 ± 0.009	–	–	–	–	0.086 ± 0.009	–	–
Spain	36	–	–	0.054 ± 0.008	–	–	–	–	0.054 ± 0.008	–	–
E. Interstand compositional turnover											
All	209	–	0.772	0.417 ± 0.047	–	§	–	0.772	0.417 ± 0.047	–	§
Finland	28	–	–	0.244 ± 0.009	–	–	–	–	0.244 ± 0.009	–	–
Poland	43	–	–	0.418 ± 0.008	–	–	–	–	0.418 ± 0.008	–	–
Germany	38	–	–	0.424 ± 0.010	–	–	–	–	0.424 ± 0.010	–	–
Romania	28	–	–	0.339 ± 0.014	–	–	–	–	0.339 ± 0.014	–	–
Italy	36	–	–	0.522 ± 0.011	–	–	–	–	0.522 ± 0.011	–	–
Spain	36	–	–	0.558 ± 0.012	–	–	–	–	0.558 ± 0.012	–	–
F. Interstand compositional nestedness											
All	209	–	0.287	0.115 ± 0.013	–	§	–	0.287	0.115 ± 0.013	–	§
Finland	28	–	–	0.151 ± 0.009	–	–	–	–	0.151 ± 0.009	–	–
Poland	43	–	–	0.091 ± 0.007	–	–	–	–	0.091 ± 0.007	–	–
Germany	38	–	–	0.139 ± 0.008	–	–	–	–	0.139 ± 0.008	–	–
Romania	28	–	–	0.136 ± 0.012	–	–	–	–	0.136 ± 0.012	–	–
Italy	36	–	–	0.100 ± 0.008	–	–	–	–	0.100 ± 0.008	–	–
Spain	36	–	–	0.073 ± 0.004	–	–	–	–	0.073 ± 0.004	–	–

The addition of two-species mixtures to a forest composed of their component monocultures clearly increased the forest-level understorey SR. This means that the mixtures contained understorey species that were not yet present in the component monocultures. As all understorey species have specific niches (e.g. [Ellenberg and Leuschner, 2010](#)), it indicates that the environmental conditions in the mixtures were distinct from the conditions in the component monocultures, allowing for other understorey species to survive. This may again indicate the presence of novel environment creation in the two-species mixtures. A higher understorey diversity at the forest-level may thus be attained by favouring the coexistence of two-species mixed stands with their component monoculture stands into a single forest via silvicultural management. In contrast, the effect of adding three-species mixtures on the

forest-level understorey SR was region-dependent while adding four-species or five-species mixtures predominantly had a negligible or negative effect. Assuming that novel environment creation was present, interactions among multiple tree species in mixtures may have induced ‘intermediate’ environmental conditions that showed high resemblance with the environment in one or more of component monocultures, which was in turn reflected in a similar understorey community composition.

For Finland, Germany and Italy (and marginally for Poland and Spain), the dispersion of quadrats within a target tree SR level decreased with increasing target tree SR. All tree species have a species-specific impact on the environmental conditions that the understorey encounters (e.g. [Barbier et al., 2008](#); [Reich et al., 2012](#)). As understorey species differ in their affinities to

particular environmental conditions (Ellenberg and Leuschner, 2010), this may explain the considerable understorey compositional differences among monoculture quadrats of different target tree species. The higher the target tree SR level, the more the quadrats of that level shared tree species. This results in higher similarities in environmental conditions and lower understorey compositional dissimilarities towards higher target tree SR levels, in the presence of environmental heterogeneity as well as novel environment creation. Ampoorter et al. (2014) also found stronger compositional differences in the understorey for monocultures than for mixtures for a relatively young, experimental forest plantation in Finland, but the relationship was clearer in the current study focusing on mature forests.

H3. Overstorey functional diversity effects are different from overstorey taxonomic diversity effects.

The functional dispersion among target tree species, based on SLA, foliar %N, %C and calcium content, showed a positive relationship with the stand-level understorey SR of Germany and Spain but this relationship only explained a minor part of the variation in the dataset. Similar to the overstorey taxonomic diversity effects, we did not find a significant relationship between functional dispersion on the one hand and stand-level true diversity and the intrastand and interstand compositional turnover and nestedness on the other. As mentioned above, this finding may point in the direction of novel environment creation.

5. Conclusions

In order to maintain or even extend the ecosystem functions and services provided by the forest understorey now and in the future, a diverse understorey is warranted. Overstorey diversity may be an important driver of understorey diversity. It is often hypothesized that this effect is regulated by environmental heterogeneity (i.e. the presence of a patchy matrix of environmental conditions, determined by the tree species covering the patch), leading to a positive overstorey–understorey diversity relationship at the level of the individual stand. But previous results on this relationship were far from unequivocal. We examined the possibility of an alternative mechanism, i.e. novel environment creation, to take place in mixed stands with a tree-by-tree mixing intensity. This mechanism was overlooked previously and leads to alternative hypothesized overstorey–understorey diversity relationships compared to those found when environmental heterogeneity is the driving mechanism. Our study in the large-scale FunDivEUROPE Exploratory platform, consisting of numerous plots in mature forests, showed a lack of support for the environmental heterogeneity hypothesis while some results pointed in the direction of novel environment creation. However, no indisputable proof for the presence of novel environment creation could be obtained using this set-up. Future research on the overstorey impact should therefore perform fine-scaled measurements of abiotic characteristics (soil pH and nutrient content, litter decomposition, understorey light availability, etc.) in mixed and component monoculture stands to examine the potential mechanisms of environmental heterogeneity and novel environment creation in more detail. Furthermore, it would be interesting to focus on the influence of the tree species mixing intensity on the relative contribution of both mechanisms. We also noticed that the effect of overstorey diversity on understorey diversity differs across spatial scales. Overstorey–understorey diversity relations should therefore always be evaluated at multiple spatial scales (intrastand, stand-level, forest-level, etc.).

Conflict of interest statement

All authors declare that there are no conflicts of interests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2016.02.001>.

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