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Understory Vegetation Dynamics in Non-Native Douglas Fir Forests after Management Abandonment—A Case Study in Two Strict Forest Reserves in Southwest Germany

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Abstract: The non-native Douglas fir (*Pseudotsuga menziesii*) is widely distributed in Europe and promoted by forestry due to its assumed resistance against climate change. An increasing cultivation area is, however, viewed critically by nature conservation as negative effects on native biodiversity and naturalness are expected. We investigated plant species diversity and composition in two strict forest reserves (SFR) dominated by Douglas fir in southwest Germany. These reserves were established in the years 2001/2002 to study the development of Douglas fir forests after management abandonment. Vegetation surveys were conducted in 2005 and repeated in 2017. We used re-survey data from a nearby SFR dominated by native tree species as a reference. The understory vegetation showed consistent development after management abandonment, irrespective of tree species identity and origin. It became less diverse and more shade-tolerant over time due to missing soil disturbance and decreasing light availability. In contrast to a native canopy, though, Douglas fir promoted the share of generalist species. Regeneration of Douglas fir largely decreased in the SFRs underlining its competitive weakness against native tree species, mainly against European beech (*Fagus sylvatica*). Thereby, regeneration patterns of Douglas fir in the SFR were similar to those observed in the native range.

Keywords: competitive strength; forest management; nature conservation; naturalness; European beech; species diversity; invasiveness; homogenization

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1. Introduction

The potentials and risks of integrating non-native tree species into native forests of Central Europe are highly debated [1]. Stand-replacing disturbances caused by drought and windthrow in recent decades [2], as well as consequent reforestation plans that aim to complement natural succession, intensified this debate [3–5]. Among non-native species cultivated in Central Europe, the North American Douglas fir (*Pseudotsuga menziesii*) is one of the most widely distributed species [6] that is currently further promoted by forestry. The species is characterized by a higher productivity and resistance against drought compared to native coniferous tree species, mainly compared to Norway spruce (*Picea abies*), and is therefore considered as an important replacement to mitigate the effects of climate change and to secure main ecosystem services [7–12].

At the same time, Douglas fir is regarded critically among nature conservationists who see a potential for invasion with negative effects for native biodiversity in the future [13,14], further discussed in [15]. With a larger cultivation area, an increased reproduction and spread of the early reproducing Douglas fir into conservation-relevant native ecosystems is expected, as well as a shift in floristic and faunistic species composition towards conditions far from the potential natural vegetation. In native mountain forests of Spain, Broncano et al. [16] recorded a Douglas fir invasion that started already 30 years after planting. Invasion was also detected in heathland ecosystems of Europe [17]. Bindewald et al. [18] assessed national forest inventory data of Germany and detected an increase in the total stand area of Douglas fir between the years 2002 and 2012 and an increasing number of inventory plots with Douglas fir regeneration. Among conservation-relevant forest ecosystems, Douglas fir regeneration had the highest share (18% on total habitat area) in open and acidic oak forests (*Quercus* spec.) supporting results by Knoerzer [19]. For most of the inventory plots considered by Bindewald et al. [18], though, regeneration was mainly restricted to a Douglas fir canopy showing the impact of propagule pressure and dispersal limitation [20] as well as the importance of competition by other tree species in restricting the establishment of Douglas fir in Central Europe [21]. Though the potential invasiveness is evaluated differently among forestry and nature conservation [15], there is unity about the need for management and cultivation concepts that prevent a further spread into conservation-relevant ecosystems as well as potential negative effects on native biodiversity [22–24]. These concepts include the establishment of buffer zones around susceptible ecosystems and the establishment of Douglas fir only in mixture with native tree species up to a proportion of 30% [25].

The fear of invasion of Douglas fir is based on the generally strong invasiveness of species of Pinaceae (including Douglas fir) around the world that affected native flora and fauna and led to the establishment of “novel ecosystems” especially in the southern hemisphere [26–28]. The invasive success of Pinaceae species can be explained by its low seed mass associated with wind distribution, its short juvenile period, and the short intervals between mast years [27]. For Douglas fir in Central Europe, though, the ecological impact has been less severe up until now [29–31]. It was for example found that species diversity and composition often resemble native Norway spruce forests [32–34]. Nevertheless, when focusing on distinct species groups, research on the effect of Douglas fir on species diversity revealed mixed results. A reduced species diversity compared to native tree species was found for fungi [29,35], for spiders [36], for arthropods and dependent birds in the Douglas fir canopy [37], and for early successional saproxylic beetles [38]. Ground beetles, on the other hand, were more abundant and diverse in pure Douglas fir compared to European beech (*Fagus sylvatica*, hereafter beech) and Norway spruce forests and mixtures of these tree species [39]. However, the authors also state that the non-native Douglas fir seems to provide no habitat for specialized beech-associated species [39]. The understory vegetation was found to mostly benefit in terms of abundance and species richness from a Douglas fir canopy compared to native beech forests [34,40,41]; but see [42]. If this finding results from a (different) forest management of Douglas fir and beech stands or from individual traits of both tree species is, however, not completely clear yet.

Despite growing data on the effects of Douglas fir on different species groups, investigations on long-term development of Douglas fir stands and its associated diversity are largely missing in Germany and Central Europe until now. According to Eberhard and Hasenauer [43], Douglas fir regeneration requires silvicultural management to survive indicating that a natural forest development represents a natural barrier for a further spread of Douglas fir. Here, monitoring in strict forest reserves (SFR) can deliver valuable insights and might help to disentangle effects of forest management and tree species identity. SFR are formerly managed forests, where management was abandoned to conserve natural forest ecosystems and to monitor and investigate the natural forest development without human influence under changing abiotic conditions. Another important aim is to deduce nature-based management and conservation concepts for managed forests [44,45]. In SFR of Bavaria, southern Germany, regeneration of Douglas fir was recorded in 27 of 160 reserves with small abundances only, supporting a low regeneration potential in unmanaged forests and a competitive strength of native tree species [46]. There, however, Douglas fir only comprised on average 2% of the basal area. A dominance of Douglas fir in the overstorey may result in a different regeneration pattern.

Two strict forest reserves (the SFR Grünberg and SFR Eselskopf), established in the years 2001 and 2002 in the federal state of Rhineland-Palatinate in southwest Germany with areas dominated by Douglas fir can provide evidence on long-term development of Douglas fir forests without forest management in the introduced range. Next to forest inventories, vegetation surveys are part of the regular monitoring program in many SFR. The understory vegetation is the key component of plant diversity in temperate forests and contributes to element cycling and functioning of above and belowground food webs [47–49]. Due to the specific environmental requirements of most plant species, the understory vegetation is also an important indicator of abiotic conditions and its changes. Based on compositional differences in the understory vegetation found between non-native Douglas fir and native beech forests [34], contrasting vegetation dynamics after management abandonment can be expected indicating effects of tree species identity on native biodiversity.

To investigate the diversity dynamics of non-native Douglas fir forests after forest management abandonment also in comparison to native forests, we conducted vegetation surveys at two points in time in the SFRs Grünberg and Eselskopf dominated by Douglas fir and in a nearby SFR dominated by native tree species (the SFR Adelsberg-Lutzelhardt) in southwest Germany. In detail, we wanted to know (1) how vegetation structure, composition, and species richness have changed within a time span of 12 years in Douglas fir dominated unmanaged forests up to 35 years after forest management abandonment and (2) if this development differs from vegetation dynamics in a SFR dominated by native tree species. Furthermore, we focused (3) on the development of Douglas fir in different vegetation layers (tree, shrub and herb layer) compared to native tree species to draw conclusions on its natural development and regeneration over time, its competitiveness against native tree species and its potential invasiveness. Our study will contribute to the increasing knowledge on the effects of Douglas fir on native forest ecosystems and can give important indications on necessary forest management activities for mitigating the potential impact of Douglas fir on native biodiversity.

2. Materials and Methods

2.1. Study Areas

We studied vegetation dynamics in two strict forest reserves (SFR) partly dominated by Douglas fir in southwestern Germany in the federal state of Rhineland-Palatinate, the SFRs Grünberg (GB-DF) and Eselskopf (EK-DF, Table 1). With 6.4% on total forest area, the federal state of Rhineland-Palatinate has the highest share of Douglas fir in Germany (2% for whole Germany; [50]). We contrasted the vegetation development to another SFR of the region, the SFR Adelsberg-Lutzelhardt, that is dominated by native tree species (abbreviation AB-NAT; see Table 1).

The SFRs GB-DF and EK-DF are geologically formed on acidic bedrock that developed to podzolic brown soils in GB-DF, while the Lower Devonian argillite with insertions of fine sand in EK-DF weathered to mesotrophic brown soils (Table 1). The landscape around both SFR would be naturally dominated by acidic beech forests admixed with sessile oak (*Quercus petraea*, [51]). Due to the mesotrophic site character, the EK-DF area is partly in transition to slightly more nutrient rich beech forest communities ([52]; Table 1).

In both SFR, we investigated a fenced representation area of 1 ha in size (= a core area with a forest fence of 2 m height preventing entry for ungulates and European brown hares (*Lepus europaeus*)) that was established within Douglas fir dominated stands. These stands were established as pure stands ca. 120 years ago. Today, naturally regenerating beech accompanies Douglas fir in the core area of GB-DF. In the core area of EK-DF, Douglas fir was still largely dominant in the tree layer in the year 2005 with minor contributions of other tree species, mainly Norway spruce, that established after several small windthrow events in the early 1990s [52]. Windthrow and ice break also affected the core area in GB-DF in 1972 and in 1990. Regular forest management operations in the core areas had already ceased ca. 20 years before the official management abandonment in the years 2001 and 2002 (Table 1).

Table 1. Characteristics of the investigated strict forest reserves and its investigated core areas (following Gauer and Aldinger [51], BLE [53]). DF and NAT indicate the tree species dominance in the core area being Douglas fir or native tree species.

Strict Forest Reserve (SFR)	Grünberg (GB-DF)	Eselskopf (EK-DF)	Adelsberg (AB-NAT)
Geographic location	49°20′8″ N 7°58′12″ E	50°2′51″ N 6°37′11″ E	49°3′32″ N 7°30′24″ E
Forest ecoregion (and subregion)	Pfälzerwald (Middle Pfälzerwald)	Nordwesteifel (Islek and Oesling)	Pfälzerwald (Southern Pfälzerwald, Wasgau)
Reserve total size	64 ha	30 ha	192 ha
Year of establishment	2001	2002	1976
Geology	Bunter (Trifels subdivision)	Lower Devonian argillite	Bunter (Rehberg subdivision)
Soil type	Dystric Cambisol	Spodic Cambisol	Dystric Cambisol
Nutrient status	Oligotrophic	Mesotrophic	Oligotrophic
Elevation	210–420 m a. s. l.	310–440 m a. s. l.	245–399 m a. s. l.
Potential natural vegetation	Acidic beech forests (Luzulo-Fagetum)	Acidic to mesotrophic beech forests (Luzulo-Fagetum to Galio-Fagetum [52])	Acidic beech forests (Luzulo-Fagetum)
Mean annual air temperature (subregion)	8.4 °C	7.6 °C	8.8 °C
Mean annual precipitation (subregion)	933 mm	928 mm	926 mm
Tree species composition of core area (>7 cm diameter at breast height (DBH))	~73% *Pseudotsuga menziesii*, 17% *Fagus sylvatica*, 7% *Pinus sylvestris*, 3% *Picea abies* (Year 2004)	~95% *Pseudotsuga menziesii*, 4% *Picea abies*, others (Year 2006)	54% *Quercus petraea*, 30% *Tilia cordata*, 14% *Fagus sylvatica*, 2% *Carpinus betulus* (Year 2006)
Years of vegetation surveys (core area)	2005 and 2017	2005 and 2017	2000 and 2016
Number of permanent subplots (400 m^2) surveyed in the core area	13	14	29

Beyond the Douglas fir dominated core area, the SFR GB-DF was characterized by mixed forests of beech with Scots pine (*Pinus sylvestris*) or Norway spruce. According to the last forest inventory in 1995, tree species shares were 37.6% Scots Pine, 28.3% Douglas fir, 21.0% beech, 11.5% Norway spruce and others. In the SFR EK-DF, mixed forests of sessile oak with beech and hornbeam (*Carpinus betulus*) existed next to stands composed of Norway spruce and different non-native tree species (e.g., *Larix kaempferi*, *Thuja* spec., *Tsuga* spec.) that had been planted ca. 50 to 70 years ago. The last forest inventory in 1997 gave the following tree species composition in the SFR EK-DF: 49% Douglas fir, 30% Norway spruce, 5% Japanese larch, 4% hornbeam, 3% sessile oak, 3% beech and others including the mentioned not-natives.

We used a 1.5 ha fenced core area of the third SFR AB-NAT as a natural reference (Table 1). AB-NAT lies in the same forest ecoregion and is characterized by similar site conditions as the SFR GB-DF, but the reserve was already established in 1976. The tree species composition represents the potential natural tree species composition for the mountain ridges of this region with sessile oak, small-leaved lime (*Tilia cordata*) and beech [54]. The share of sessile oak was, however, largely promoted by forest management in former times [51,54]. This also accounts for the whole reserve where sessile oak was the dominant tree species (48%) in the year 2006 followed by Scots pine (25%) and beech (11%). Douglas fir made up 3% of the tree species share in the SFR AB-NAT.

2.2. Data Sampling and Analysis

The three core areas were separated into 13 (GB-DF), 14 (EK-DF) and 29 (AB-NAT) subplots of 400 m^2 (20 × 20 m) that represented the sampling unit for original vegetation surveys conducted in the years 2000 (AB-NAT) and 2005 (GB-DF, EK-DF), respectively, and for resurveys conducted 12 to 16 years later (Table 1). For the old and recent surveys, plant species were recorded separately for the tree layer (woody species >5 m), the shrub layer (woody species > 0.5 m ≤ 5 m), the herb layer (woody species $\leq$0.5 m and non-woody vascular plants) and the moss layer considering all soil dwelling bryophyte species. For the vegetation layers and all species within vegetation layers, the cover value was visually estimated directly in percent by horizontally projecting the area covered by a certain species or vegetation layer on the 400 m^2 subplots.

We contrasted the vegetation structure using vegetation layer cover values and the subplot-based species richness of vegetation layers between the first and the second survey. We also calculated the total species richness across plots for vascular plants and bryophytes. To characterize potential changes in environmental conditions over time, we used species indicator values taken from Ellenberg et al. [55]. The so called Ellenberg Indicator Values (EIV) of plant species are widely used in applied ecology in Central Europe [56]. Depending on their realized niche along ecological gradients that was defined based on field experience (=expert opinion), concurrent recordings of species and environmental variables and experimental tests, plant species of Central Europe have been given indicator values representing ordinal numbers between one and nine for moisture (M; ordinal number goes up to 12), nutrients/nitrogen (N), soil reaction (R), light (L), continentality (C) and temperature (T; [55]). By calculating averages of species indicator values at a plot-scale, the mean EIVs can represent rough surrogates for environmental conditions that are often used when direct measurements are not available [56]. For the different plant species, a value of 1 is representing species indicating dry, nutrient poor or acidic conditions as well as deep shade. Continentality and temperature values relate to the geographic ranges of species with continentality indicating the distance to the sea. C = 1 characterizes extreme oceanic species and C = 9 extreme continental species that are nearly absent from Central Europe. C values were found to correlate with frost resistance of plant species [57]. The temperature values relate to the distribution of species along elevational and latitudinal gradients with T = 1 comprising cold-adapted species of high mountains or boreal-arctic regions and T = 9 very warm-adapted species spreading from the Mediterranean into warmer places of Central Europe. An increase in the mean temperature value may indicate a thermophilization effect in the forest understory caused by global warming [58]. For vascular plant and bryophyte species of Central Europe, EIVs can be taken from Ellenberg et al. [55]. N-values for bryophytes are, however not provided. Therefore, we used the values given by Simmel et al. [59].

For analyzing dynamics in species composition, we grouped species of the field layer (=shrub, herb and moss layer) according to their forest affinity [60] and their association to broad plant communities according to Ellenberg et al. [55], Oberdorfer [61] and Nebel and Philippi [62]. In their list of forest-associated species, Schmidt et al. [60] have characterized typical forest species (category 1) into those that mainly occur in closed forests (sub-category 1.1) and those of edges and clearings (sub-category 1.2). In category 2, they have grouped species with a wider habitat preference into those species that occur both in forests and in open habitats (sub-category 2.1) and into those species that occasionally occur in forests but predominantly in open habitats (sub-category 2.2). Such species may be regarded as disturbance indicators within forests (e.g., *Cirsium vulgare*, *Stellaria media*, [63]). Species not listed in Schmidt et al. [60] were considered as open habitat species (O). As broad plant communities, we defined oak and beech (-mixed) forests (=class Querco-Fagetea), coniferous forests including the class Vaccinio-Piceetea, shrubby vegetation mainly comprising *Rubus fruticosus* agg., edges and clearings represented by the class Epilobietea angustifolii, herbaceous vegetation of disturbed sites mainly of the class Artemisietea and grass- and heathlands ranging from the class Nardo-Callunetea to mesophilous grassland of the class Molinio-Arrhenatheretea. Species that occur in a wide range of communities were categorized as indifferent (e.g., *Taraxacum officinale* agg., *Rubus idaeus*; see Table S1 in Supplementary Materials). For non-native tree species, a community preference is not defined. For each species group, we quantified their relative contribution to the species richness per subplot and contrasted numbers between surveys.

To quantify a general change in species composition within the understories of the three SFRs, we calculated a pairwise presence/absence based Jaccard dissimilarity index by contrasting each subplot to all other subplots sampled within each SFR and survey year. Changes across survey periods may indicate a homogenization or a differentiation within the understory based on local colonization or extinction of species. With diversity partitioning, we quantified the species replacement component showing real species turnover among subplots (indicating that one species is directly replaced by another species) and the nestedness component showing that a dissimilarity among subplots is caused by species richness differences [64]. A dissimilarity mainly caused by the nestedness component indicates that species in species poor subplots represent a subset of the species occurring in species richer subplots. To also integrate the abundance of species and to visualize the direction of species compositional changes between surveys, we conducted a non-metric multidimensional scaling (NMDS) on two dimensions based on Bray–Curtis dissimilarity. We conducted two different NMDS ordinations, one with data of the two Douglas fir SFRs (GB-DF and EK-DF) only and another with data from all three SFRs. We correlated the NMDS axes values with EIVs to identify the main environmental drivers of compositional changes. We additionally correlated the axes values with species richness values and the cover values of beech and Douglas fir in the shrub and herb layer to visualize changes in biodiversity and tree species regeneration.

All analyses were based on the field layer combining the shrub, herb and moss layer. Differences between surveys were tested using the Wilcoxon signed rank test or the paired t-test depending on normality distribution and variance homogeneity. For calculating the Jaccard dissimilarity and its components, we used the betapart package of the R-software [65] and the function beta.pair. The NMDS was conducted using the function metaMDS of the R Package vegan [66] and the function envfit for axes correlations. If not stated otherwise, statistical significance was assumed for $p < 0.05$. The species nomenclature follows Oberdorfer [61] for vascular plants and Nebel and Philippi [62] for bryophytes.

3. Results

3.1. Changes in Vegetation Structure, Species Richness and Environmental Conditions

In the two strict forest reserves (SFRs) dominated by Douglas fir, Grünberg (GB-DF) and Eselskopf (EK-DF), the cover of the herb layer decreased, while the moss layer increased between surveys. This pattern was contrary in the SFR Adelsberg (AB-NAT) that is dominated by native tree species. The canopy cover increased in all three SFRs but significantly only in AB-NAT (Table 2).

Consistent across all three SFRs was the decrease in mean species richness of the herb and field layer, as well as the total vascular plant species richness across plots. Total richness of vascular plants was 11 species lower in AB-NAT at the second compared to the first survey, 14 species lower in EK-DF and 18 species lower in GB-DF (Table 2).

There was no consistent pattern in the dynamics of the Ellenberg Indicator Values (EIVs) and temporal changes were generally small (<0.5 units; Table 2). In all SFRs, the light value decreased (not significantly in GB-DF). For GB-DF and AB-NAT, results show a significant increase in the moisture value, for AB-NAT also the nutrient value increased between surveys as was the temperature value, while the continentality decreased (Table 2). The three SFRs differed in temperature and continentality mainly because of differences in tree species composition also in the field layer, e.g., with Norway spruce (C = 6, T = 3) being abundant in GB-DF, while EK-DF and AB-NAT showed a higher frequency of hornbeam (C = 4, T = 6) or small-leaved lime (C = 4, T = 5).

Table 2. Vegetation layer characteristics for the first and second survey. Given are mean values with standard error in parentheses. Significantly higher values ($p < 0.05$) comparing both survey years are written in bold.

Strict Forest Reserve (SFR)	**Grünberg (GB-DF)**		**Eselskopf (EK-DF)**		**Adelsberg (AB-NAT)**	
Survey year N	2005 13	2017 13	2005 14	2017 14	2000 29	2016 29
Cover value [%]						
Tree layer	84.4 (2.6)	88.8 (1.5)	75.2 (4.2)	76.8 (3.7)	71.9 (2.9)	**82.3 (1.9)**
Shrub layer	25.7 (3.4)	20.5 (3.1)	**35.9 (5.4)**	15.4 (6.2)	10.3 (1.6)	13.9 (3.1)
Herb layer	**6.0 (1.3)**	1.9 (0.5)	**14.9 (2.8)**	5.8 (1.3)	7.6 (2.1)	**11.1 (2.0)**
Moss layer	1.9 (0.4)	**2.6 (0.4)**	17.7 (4.5)	**25.3 (6.3)**	**5.2 (1.0)**	0.9 (0.2)
Species richness/400 m^2						
Tree layer	2.9 (0.1)	2.9 (0.2)	3.2 (0.3)	3.5 (0.4)	3.0 (0.1)	**3.4 (0.3)**
Shrub layer	3.9 (0.3)	3.4 (0.2)	**5.6 (0.5)**	4.6 (0.5)	1.8 (0.2)	**2.6 (1.9)**
Herb layer	**9.5 (1.5)**	2.2 (0.4)	**14.9 (1.7)**	8.4 (0.7)	**8.5 (0.7)**	7.5 (0.5)
Moss layer	3.6 (0.6)	**4.8 (0.5)**	8.3 (0.9)	9.1 (0.8)	**4.2 (0.3)**	2.5 (0.3)
Field layer (shrub + herb + moss)	**14.7 (2.0)**	8.8 (0.8)	**27.6 (2.2)**	21.7 (1.4)	**13.2 (0.7)**	10.5 (0.7)
Total species richness						
Vascular plants	27	9	48	34	39	28
Bryophytes	11	13	16	18	24	17
EIVs [1] (Field layer)						
Temperature	3.8 (0.1)	3.8 (0.1)	4.4 (0.1)	4.3 (0.1)	4.8 (0.1)	**5.0 (0.1)**
Continentality	4.1 (0.1)	4.3 (0.1)	3.7 (0.1)	3.7 (0.1)	**3.6 (0.1)**	3.3 (0.1)
Light	4.7 (0.1)	4.5 (0.0)	**5.0 (0.1)**	4.8 (0.1)	**4.8 (0.1)**	4.7 (0.1)
Moisture	5.2 (0.1)	**5.4 (0.1)**	5.2 (0.0)	5.1 (0.0)	4.9 (0.0)	**5.1 (0.0)**
Acidity	3.7 (0.1)	3.8 (0.2)	4.2 (0.1)	4.1 (0.1)	4.1 (0.1)	4.3 (0.2)
Nutrients (Nitrogen)	4.3 (0.2)	4.4 (0.1)	5.0 (0.1)	4.8 (0.1)	4.5 (0.1)	**4.9 (0.1)**

[1] EIV = Ellenberg Indicator Value.

3.2. Changes in Field Layer Species Composition

The share of species representing different forest affinity groups developed similarly in all three reserves, even though no significant changes could be detected in AB-NAT (Figure 1). In GB-DF and EK-DF, the share of (predominantly) open habitat species significantly decreased, while in EK-DF the share of closed forest species significantly increased. Though not significant, such an increase was also found in the two other reserves.

In terms of plant community association, the two SFRs dominated by Douglas fir differed from the SFR AB-NAT dominated by native tree species (Figure 2). While the share of species characteristic for deciduous forests of the class Querco-Fagetea significantly increased in the native forest of AB-NAT, the contribution of these species decreased in GB-DF (significantly) and EK-DF (non-significantly). Indifferent species showed the opposite pattern (significant increase in GB-DF and EK-DF and decrease in AB-NAT). In all three reserves, though, there was a reduction in the accumulated share of open habitat species comprising species of disturbed sites, of edges and clearings and of heath- and grasslands (GB-DF: $p = 0.023$ for paired t-test; EK-DF: $p < 0.001$ for paired t-test; AB-NAT: $p = 0.005$ for Wilcoxon signed rank test). The latter two showed a significant decrease in EK-DF (Figure 2). In AB-NAT, an increasing frequency of *Rubus fruticosus* agg. increased the share of shrubby vegetation. Due to an overall decrease in the species richness of the field layer, the contribution of non-native tree species (Douglas fir and Weymouth pine (*Pinus strobus*) detected in two subplots of the SFR GB-DF) with no defined community association increased significantly in GB-DF (Figure 2).

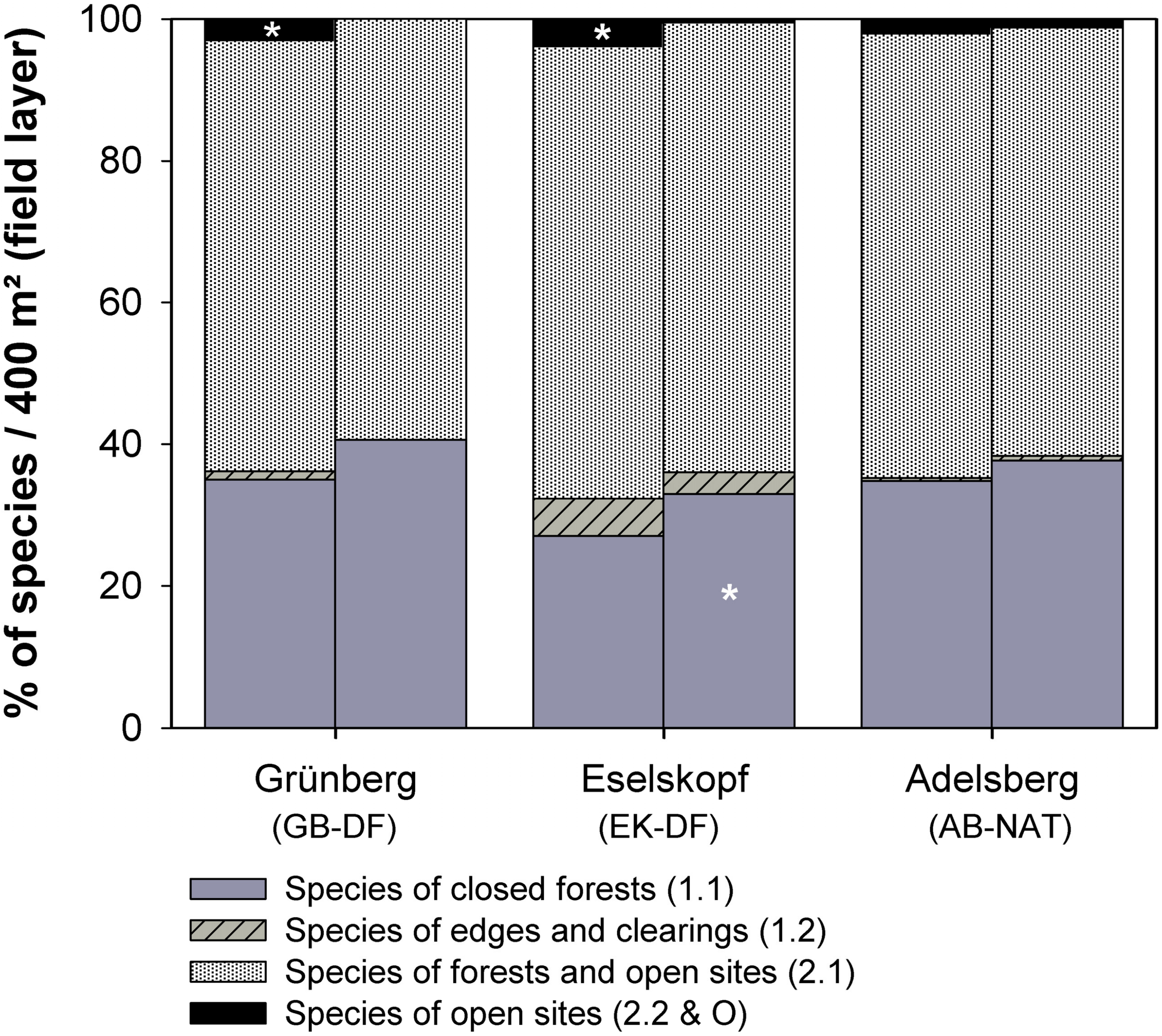


Figure 1. Percentage share of species of the field layer grouped according to their forest affinity in the three strict forest reserves. Left column = old survey, right column = recent survey. * marks significant differences between surveys ($p < 0.05$).

All three SFRs showed a significant change in species dissimilarity over time (Figure 3). While GB-DF and AB-NAT showed a homogenization in the understory with a significant reduction in the Jaccard dissimilarity index, EK-DF was characterized by a differentiation among subplots over time. The largest decrease in dissimilarity was detected in GB-DF that also showed the largest reduction in species richness (Table 2). AB-NAT additionally showed a significant increase in the nestedness component indicating that species were lost from some but not from all subplots (Figure 3).

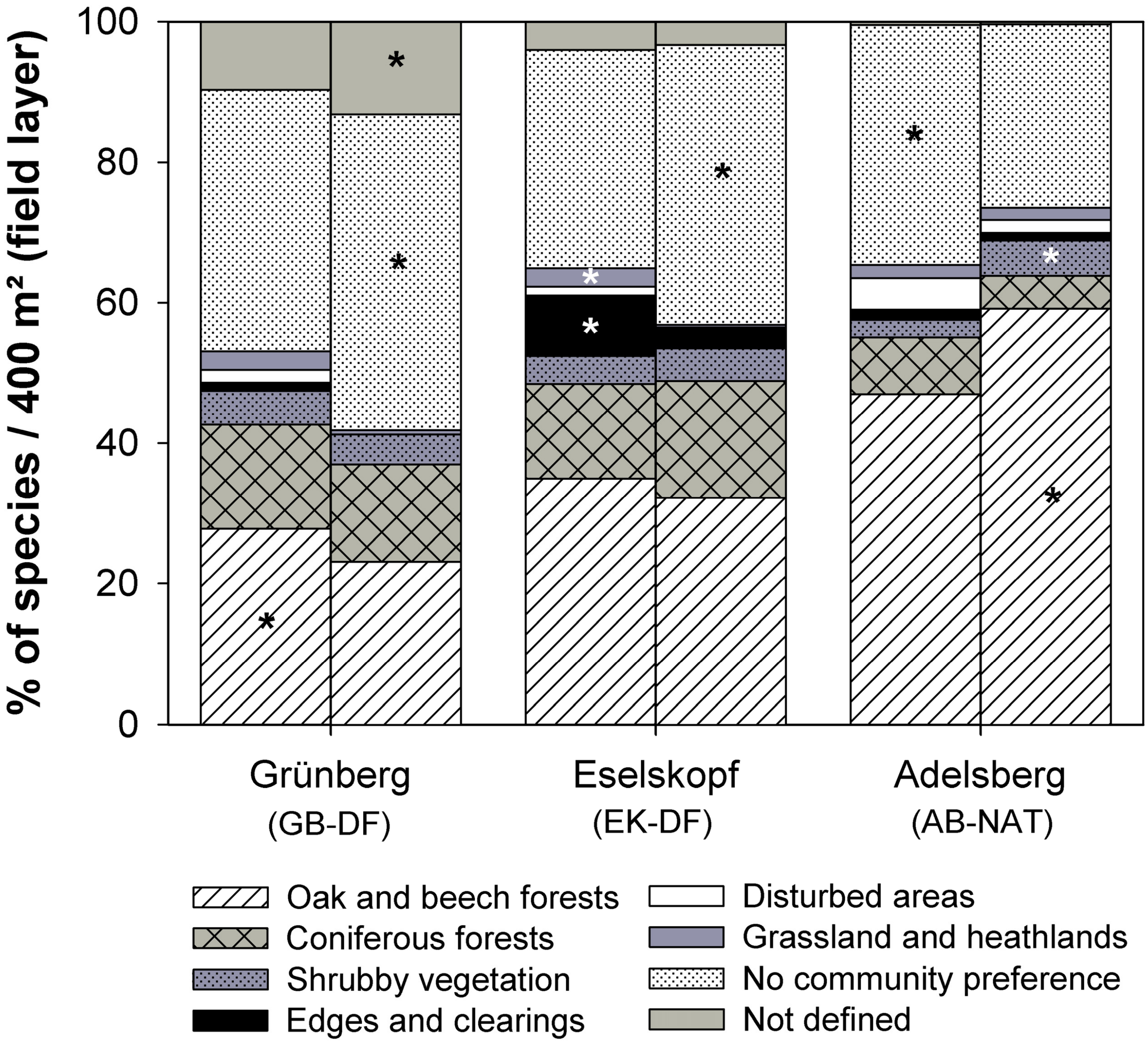


Figure 2. Percentage share of species of the field layer grouped according to their forest community preference. Left column = old survey, right column = recent survey. * marks significant differences between surveys ($p < 0.05$). See text for details.

The differing dissimilarity patterns of GB-DF and EK-DF (homogenization vs. differentiation) were confirmed by the NMDS ordination (Figure 4a). However, the ordination showed a similar direction of species compositional change with time (Figure 4a). For both Douglas fir SFRs, the axes values show a significant shift along the second axis (Table 3). GB-DF and EK-DF mainly differentiated along the first axis explained by contrasting continentality and temperature values due to differences in tree species composition in the regeneration that remained over time. Regeneration of Douglas fir (in the shrub and herb layer) and beech (in the herb layer) was associated with the first survey. The same is true for species richness and the light indicator value that was highest in EK-DF at the first survey.

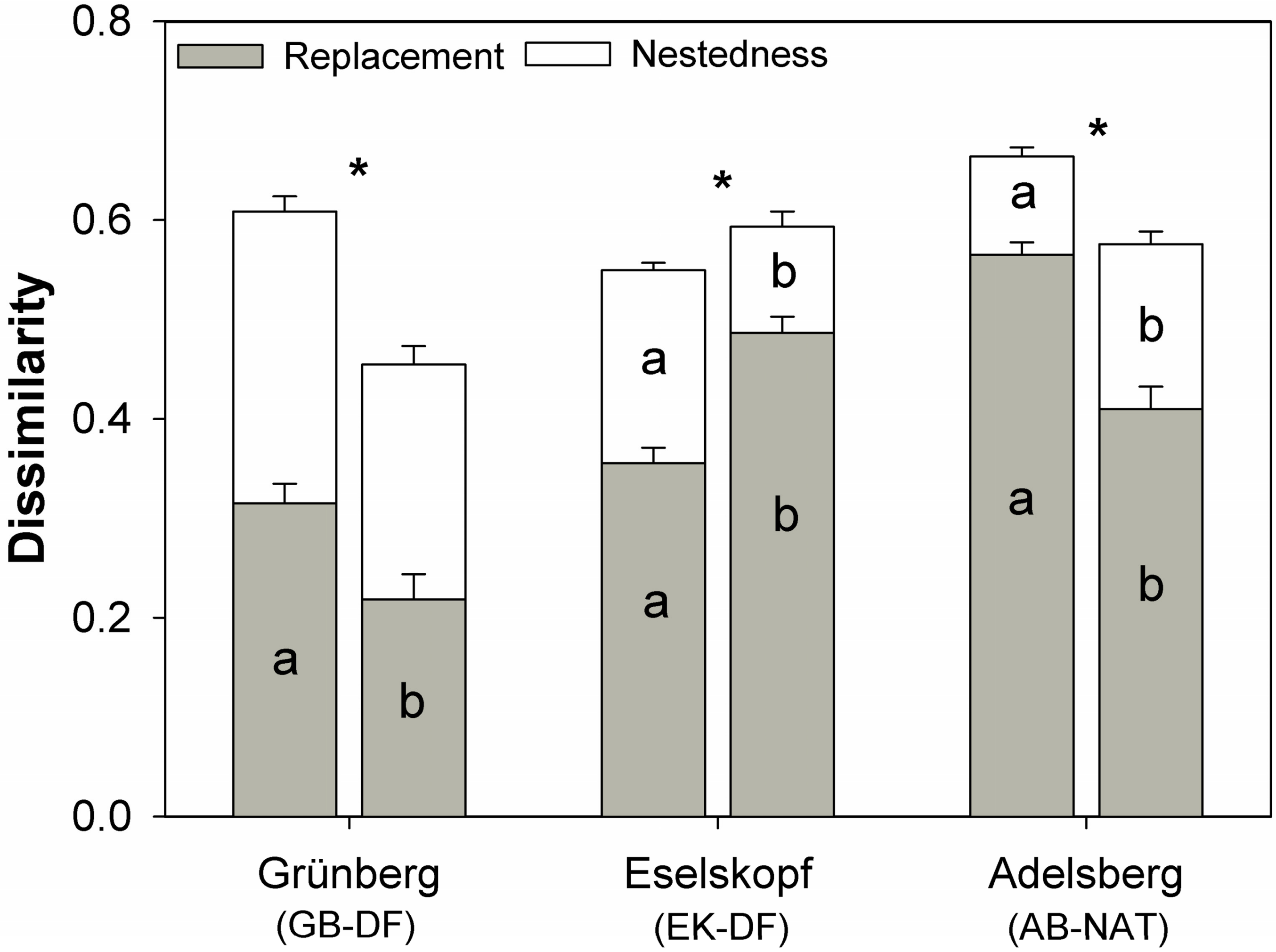
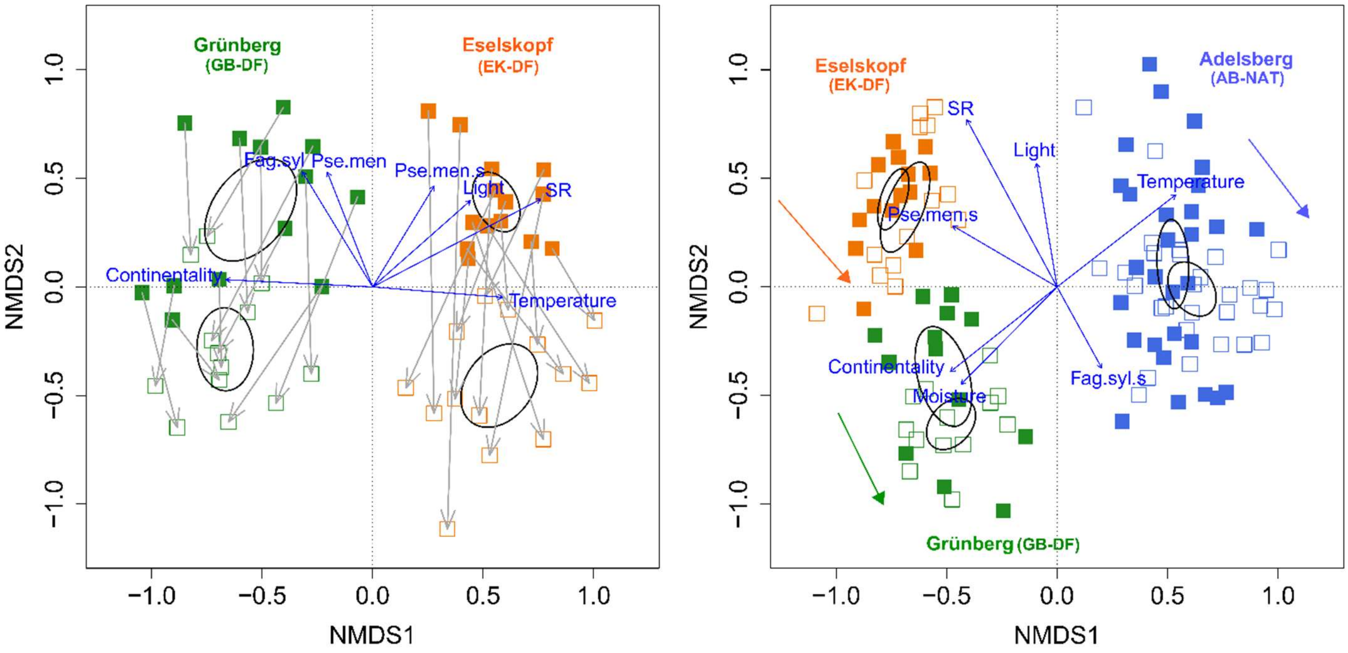


Figure 3. Mean pairwise Jaccard dissimilarity for the old (left bar) and more recent (right bar) survey in the three SFR. The dissimilarity was partitioned into the replacement and nestedness component according to Baselga [64]. * Marks a significant difference ($p < 0.05$) between the surveys for the overall Jaccard-dissimilarity. Different letters show significant differences ($p < 0.05$) for replacement and nestedness component between the old and recent survey.

The NMDS diagram of the three SFR shows a general shift of all three reserves towards a lower species richness, less light and an increasing cover of beech in the shrub layer, while Douglas fir regeneration in the shrub layer was associated with the first survey (Figure 4b). When combining both NMDS axes, we found a shift in the same direction for all three reserves, though a significant shift was only confirmed for GB-DF and AB-NAT (Table 3). The compositional separation between the two SFRs dominated by Douglas fir (GB-DF and EK-DF) and the SFR characterized by native tree species (AB-NAT) remained along the first axis over time.



(**a**) (**b**)

Figure 4. Two-dimensional NMDS ordination diagram of species abundance data of the field layer (shrub, herb and moss layer) for (**a**) the two SFR dominated by Douglas fir (stress = 0.2013) and (**b**) for all three investigated SFR (stress = 0.1899) for the two survey times. Grey arrows in (**a**) indicate the shift of individual subplots between the survey times. The colored arrows in (**b**) indicate the general shift in species composition for the respective SFRs. The ellipses give the standard error around the centroids for each observation and SFR. A bi-plot was created by correlating axes values with mean EIVs, the species richness (SR) and the cover of *F. sylvatica* (Fag.syl) and *P. menziesii* (Pse.men) in the shrub (_s) and herb layer. Only significant correlations with $p < 0.001$ are displayed.

Table 3. Mean axes scores (±SE) of the NMDS ordination for the first and second survey displayed in Figure 4. Significantly higher scores between the first and second survey according to paired t-tests are written in bold. For the ordination of the three SFR (Figure 4b), both axes were additionally combined into one axis score (NMDS1-NMDS2) to identify significant shifts across axes.

	First Survey	Second Survey	*p*-Value
NMDS of Figure 4a			
GB-DF NMDS 1	−0.552 ± 0.085	−0.668 ± 0.052	0.095
GB-DF NMDS 2	**0.355 ± 0.096**	−0.287 ± 0.078	**<0.001**
EK-DF NMDS 1	0.559 ± 0.044	0.573 ± 0.071	0.848
EK-DF NMDS 2	**0.391 ± 0.056**	−0.454 ± 0.079	**<0.001**
NMDS of Figure 4b			
GB-DF NMDS1	−0.514 ± 0.053	−0.480 ± 0.045	0.593
GB-DF NMDS2	**−0.412 ± 0.094**	−0.631 ± 0.048	**0.005**
GB-DF NMDS1-NMDS2	−0.101 ± 0.124	**0.151 ± 0.054**	**0.034**
EK-DF NMDS1	−0.741 ± 0.029	−0.687 ± 0.046	0.152
EK-DF NMDS2	0.404 ± 0.057	0.367 ± 0.085	0.613
EK-DF NMDS1-NMDS2	−1.145 ± 0.049	−1.055 ± 0.068	0.235
AB-NAT NMDS1	0.524 ± 0.030	0.611 ± 0.045	0.071
AB-NAT NMDS2	0.105 ± 0.084	−0.009 ± 0.051	0.095
AB-NAT NMDS1-NMDS2	0.419 ± 0.092	**0.620 ± 0.078**	**0.002**

3.3. Tree Species Dynamics in the Three SFRs

The cover of Douglas fir regeneration was mainly associated with the first survey period (Figure 4). Douglas fir decreased in frequency and/or cover in both SFRs dominated by Douglas fir in almost all vegetation layers, except for the tree layer in EK-DF (Table 4). In EK-DF, the shrub layer cover of Douglas fir largely decreased. In GB-DF, this was the case for both the tree and the shrub layer. Regeneration of Douglas fir in the herb layer was generally absent in all three SFRs at time of the second survey.

A different trend was found for beech. This tree species increased in the shrub layer of EK-DF and in the tree layer of GB-DF (Table 4). While beech and Douglas fir were similar in tree layer coverage at the first survey in GB-DF, beech dominated the tree layer in 2017, though underneath Douglas fir. In EK-DF, beech established in every subplot in the shrub layer from the first to the second survey. The increasing trend of beech in the tree and shrub layer is in line with the development in the SFR AB-NAT. Here, also hornbeam and sessile oak expanded in the tree layer contributing to an increase in tree layer cover (Table 2).

In contrast to Douglas fir, Norway spruce expanded in the shrub layer of GB-DF and remained constant in frequency in EK-DF.

Most tree species in the tree and shrub layer were recorded in the SFR EK-DF for both surveys. There, most species remained relatively constant or showed a shift from the shrub to the tree layer (e.g., hornbeam, hazelnut). For both SFRs dominated by Douglas fir, most woody species in the herb layer showed a significant reduction. In AB-NAT, the abundance of seedlings of sessile oak and small-leaved lime increased in the herb layer (Table 4).

Table 4. Frequency of occurrence (F) and mean cover values in % with standard error (mCV (SE)) for all woody species surveyed in the 400 m^2 subplots in the core areas of the three strict forest reserves (SFR) Grünberg, Eselskopf (both characterized by Douglas fir (DF) and Adelsberg (dominated by native tree species (NAT)) for the two surveys. Species were grouped into the tree layer, shrub layer and herb layer and were ordered according to their temporal dynamics. Significant higher cover values between surveys according to the Wilcoxon signed rank test and higher frequency values of at least 20% comparing both surveys are written in bold, +: <0.05%.

Strict Forest Reserve (SFR)	**Grünberg (GB-DF)**				**Eselskopf (EK-DF)**				**Adelsberg (AB-NAT)**			
N	**13**				**14**				**29**			
Year	**2005**		**2017**		**2005**		**2017**		**2001**		**2016**	
	F	**mCV (SE)**	**F**	**mCv (SE)**	**F**	**mCv (SE)**	**F**	**mCv (SE)**	**F**	**mCv (SE)**	**F**	**mCv (SE)**
Tree layer (>5 m height)												
Increasing												
Fagus sylvatica	100	50.1 (3.6)	100	**75.0 (5.6)**	50	1.3 (0.4)	64	3.2 (1.1)	72	17.0 (3.2)	86	**31.0 (4.1)**
Carpinus betulus					43	1.3 (0.5)	57	2.4 (0.8)	45	5.0 (1.6)	**66**	**9.4 (2.0)**
Quercus petraea					21	0.4 (0.2)	7	0.1 (0.1)	86	31.5 (3.6)	97	**40.5 (4.7)**
Corylus avellana					7	1.0 (1.0)	**50**	1.5 (0.5)				
Decreasing												
Pseudotsuga menziesii	100	**48.6 (4.5)**	100	35.9 (4.0)	100	67.6 (3.3)	100	69.1 (3.3)				
No significant change												
Pinus sylvestris	69	4.3 (1.5)	54	4.8 (1.8)								
Picea abies	23	0.7 (0.4)	38	0.9 (0.4)	29	1.8 (1.1)	36	1.8 (1.4)				
Betula pendula					21	0.4 (0.2)	14	0.3 (0.2)				
Salix caprea					21	0.4 (0.2)	7	0.1 (0.1)				
Sorbus aucuparia					21	0.4 (0.3)	7	0.2 (0.2)				
Tilia cordata									93	28.0 (3.6)	93	29.0 (3.3)
Shrub layer ($\leq$5 m height)												
Increasing												
Fagus sylvatica	100	5.6 (0.9)	100	4.3 (1.0)	79	2.0 ± 0.5	**100**	2.6 ± 0.5	72	6.8 ± 1.5	**93**	6.6 ± 1.2
Picea abies	100	7.7 (1.6)	100	**14.8 (3.2)**	64	2.3 ± 1.0	64	0.8 ± 0.2	3	+	7	0.1 ± 0.1
Rubus fruticosus agg.			**23**	0.2 (0.1)			7	+			**41**	**6.8 ± 2.8**
Tilia cordata									66	1.3 ± 0.3	**86**	1.6 ± 0.4

Table 4. *Cont.*

Strict Forest Reserve (SFR)	**Grünberg (GB-DF)**				**Eselskopf (EK-DF)**				**Adelsberg (AB-NAT)**			
N	**13**				**14**				**29**			
Year	**2005**		**2017**		**2005**		**2017**		**2001**		**2016**	
	F	**mCV (SE)**	**F**	**mCv (SE)**	**F**	**mCv (SE)**	**F**	**mCv (SE)**	**F**	**mCv (SE)**	**F**	**mCv (SE)**
Decreasing												
Pseudotsuga menziesii	100	**11.4 (1.9)**	92	1.2 (0.2)	**100**	**20.7 ± 3.4**	71	4.6 ± 2.8				
Pinus sylvestris	**54**	0.7 (0.3)										
Carpinus betulus					**86**	7.0 ± 2.9	50	5.0 ± 3.1	34	**2.2 ± 0.7**	21	0.6 ± 0.3
Quercus robur					**21**	0.2 ± 0.1						
No significant change												
Corylus avellana					86	2.8 ± 0.6	79	1.5 ± 0.3				
Quercus petraea					43	0.6 ± 0.3	43	0.7 ± 0.3			**7**	+
Acer pseudoplatanus					21	0.1 ± 0.1	14	0.1 ± 0.0				
Sorbus aria					21	0.2 ± 0.1	7	+				
Herb layer (≤0.5 m height)												
Increasing												
Quercus petraea					14	0.1 (0.0)	14	+	93	0.4 (0.0)	100	**1.9 (0.6)**
Tilia cordata									66	0.2 (0.0)	**93**	**0.4 (0.0)**
Decreasing												
Rubus idaeus	**77**	0.8 ± 0.2			**36**	0.2 ± 0.1						
Fagus sylvatica	**69**	0.4 ± 0.1	31	0.1 ± 0.1	**21**	+			**86**	0.6 ± 0.1	66	0.6 ± 0.1
Pseudotsuga menziesii	**69**	0.4 ± 0.1			**29**	+						
Cytisus scoparius	**31**	0.1 ± 0.1			**21**	+					3	+
Sambucus racemosa					**71**	0.2 ± 0.1						
Contrary development												
Rubus fruticosus agg.	**69**	1.5 ± 0.8	46	1.1 ± 0.5	100	3.2 ± 0.5	93	1.6 ± 0.5	38	1.7 ± 1.4	48	**3.6 ± 1.2**
No significant change												
Picea abies	85	0.9 ± 0.3	100	0.6 ± 0.1			14	+			7	+
Carpinus betulus					29	0.2 ± 0.1	14	+	38	0.1 ± 0.0	52	0.2 ± 0.0

4. Discussion

4.1. Vascular Plant Species Richness Declines in All Strict Forest Reserves

We detected a general decrease in the species richness of vascular plants across all three strict forest reserves (SFRs). This is in line with other studies showing a decreasing plant species richness following management abandonment [67–69]. We could further show that forest reserves either dominated by non-native coniferous species or by native deciduous tree species respond similarly to management abandonment. Reasons for a plant species richness decline are a lack of disturbance in the soil and canopy and an increasing canopy cover with a consequent reduction in light availability. A slight increase in tree layer cover, including an increase in beech in all SFRs (not significantly in EK-DF), and a decrease in light indicator values across reserves confirm an impact of reduced light availability. In addition, the share of shade-tolerant species typical for closed forests increased, while the share of light-demanding, open site species decreased between surveys.

We observed the largest reduction in species richness in the SFR Grünberg (GB-DF), where beech was the dominant tree species in the tree layer at time of the second survey (Figure S1a,c). Beech is highly competitive [70] and its spread and expansion after management abandonment can accelerate a reduction in plant species numbers [67,71]. The very low species richness observed in the SFR GB-DF is thereby typical for beech-dominated forests on acidic soils after management abandonment [67]. Low light levels below a dense beech canopy, a lack of soil disturbance, and a high leaf layer thickness due to low decomposition rates and high root competition by beech are mainly responsible for the low herb layer diversity. In mixture with other tree species, beech can even benefit from a lower intraspecific competition and can for example respond with an increased horizontal crown expansion and light absorption [72]. In the SFR GB-DF, Douglas fir was established as a pure stand and beech regenerated naturally from surrounding beech forests. The fast growth of Douglas fir and the subsequent colonization by beech led to a vertical separation of both tree species allowing sufficient light for the rather shade-intolerant Douglas fir in the upper canopy and for the shade-tolerant beech in the lower canopy. According to Thurm and Pretzsch [73], this optimized use of canopy space due to vertical niche differentiation of both tree species may result in maximum light interception. While this can increase productivity (mainly for Douglas fir [73]) and maintain a moist microclimate potentially mitigating effects of global warming [74], maximum light interception by the tree layer reduces the light availability for the herb layer and leads to a decline in its species richness and abundance.

Similar to aboveground, there is also growing evidence for belowground complementarity in mixed forests. Mixtures of complementary tree species such as early and late-successional or coniferous and deciduous species can enhance fine-root productivity by a more complete filling of the environment, including a higher horizontal volume filling [75]. Even though Lwila et al. [76] could not detect large differences in fine root biomass between pure and mixed forests of beech and Douglas fir, they found a general high belowground plasticity of beech in nutrient poor sites and a shift of beech fine roots to deeper soil layers across site conditions in mixed stands. These results confirmed research by Hendriks and Bianchi [77] that found a higher root density in deeper soil strata in mixed Douglas fir/beech stands compared to pure stands. While this belowground niche differentiation between tree species can reduce the interspecific competition and increase the exploitation of available resources for tree growth, it may increase root competition for the understory particularly on acidic sites with a low nutrient availability.

The reduction in species richness was lower in EK-DF and AB-NAT compared to GB-DF, where tree species richness was slightly higher and the share of beech much lower. This confirms results by Mölder et al. [78] who showed an increasing reduction in herb layer species richness with increasing beech share mainly due to a higher litter layer thickness.

A reduction in field and herb layer diversity and abundance was, however, also observed in the SFR EK-DF with the lowest abundance of beech in the canopy among the three SFR and a dominance of Douglas fir in the tree layer. Both in the non-native [79] and native range of Douglas fir [80], unthinned stands were species poorer in the understory compared to thinned stands. In the SFR EK-DF, Douglas fir was dominant in the shrub layer at the first survey. At the second survey, Douglas fir regeneration had largely decreased due to self-thinning processes in the shrub layer [81]. In the native range, this dense stem exclusion stage (Figure S1b,d) is characterized by a decrease in understory species richness and abundance [82].

In contrast to the herb layer, the moss layer increased in abundance and species richness (only in GB-DF) in both SFR with Douglas fir. This also supports results of the meta-analysis by Paillet et al. [68] with bryophytes benefiting from management abandonment. A stable or increasing canopy cover can create a moist microclimate including a stable soil moisture that is beneficial for the species richness of bryophytes [83,84]. An increasing EIV for moisture in GB-DF underlines an effect of management abandonment on microclimate. In addition, soil bryophytes can benefit from a coniferous canopy and a thin deciduous leaf litter layer [85–87]. This explains the highest cover values of the moss layer in the SFR EK-DF, where Douglas fir needles dominate the litter layer. The strict forest reserve AB-NAT, dominated by native tree species, showed a contrasting pattern in the moss layer with a reduction in species richness and abundance. Here, the larger amount of deciduous leaf litter because of a significant increase in canopy cover can reduce the moss layer [85]. However, also observer effects have to be taken into account as the separation between substrates (soil, deadwood and rocks) during vegetation sampling was sometimes difficult in the SFR AB-NAT. Long-term vegetation sampling beyond the fenced core area in the SFR AB-NAT showed, however, that also in this reserve the moss layer increased in species richness in plots that had been dominated by conifers between the years 2006 and 2016 [86]. On the other hand, plots dominated by deciduous tree species (oak and beech) showed no change.

4.2. Contrasting Patterns in Community Composition and Homogenization among the Three Reserves

Besides a consistent decrease in field layer species richness and in the share of light-demanding species across the three investigated SFRs, there were also distinct differences in compositional dynamics between the Douglas fir forests and the native reference. Between surveys, species typical of deciduous forests (Querco-Fagetea) showed a relative reduction under Douglas fir in GB-DF and EK-DF, but an increase in the SFR AB-NAT with native tree species. On the other hand, the share of generalist species with no community preference increased in the Douglas fir reserves. This is in line with Leitl [88], who detected less species of natural forest communities but more ruderal species within Douglas fir stands compared to native deciduous forests. Similar patterns were also observed for arthropods with Douglas fir mainly supporting generalist species [30,39]. Compositional differences in understory vegetation between forest types with and without Douglas fir have also been confirmed by other studies [29,34,40]. In forests in the Czech Republic, especially nitrophilous and ruderal species benefited from Douglas fir compared to beech, oak or Norway spruce, due to a better litter quality of Douglas fir and higher nitrogen contents in the humus and topsoil [40]. In our study, we did not find an increasing nutrient indicator value in the Douglas fir reserves, but in the SFR AB-NAT, dominated by native tree species. In the SFR AB-NAT, *Rubus fruticosus* agg. expanded between surveys and presumably benefited from fencing and the heterogeneous light conditions due to a higher species diversity in the tree layer. The lower and decreasing share of Querco-Fagetea species in the SFRs with Douglas fir compared to the SFR AB-NAT, on the other hand, may be the result of the management history. Most SFRs in Germany and Central Europe were established in ancient native forests with no tree species change in the past [45]. Thus, they have provided a continuous habitat for species of natural forest communities. Forest conversion from deciduous to coniferous forests, however, is known to cause a shift in plant species composition [89]. Further monitoring within the SFRs will show if the already observed expansion of native tree species in the shrub and tree layer of the Douglas fir reserves will cause a shift to a more natural species composition in the future. Until now, the NMDS ordination showed no convergence of field layer species composition between SFRs with and without Douglas fir, even though all three SFRs showed a similar direction of change over time towards a lower light availability and lower species richness.

We found, however, an effect of beech on understory homogenization over time. The two SFRs with a high share of beech in the tree layer, GB-DF and AB-NAT, showed a clear homogenization among subplots, while the SFR EK-DF displayed a differentiation. As all three SFRs were characterized by a decrease in species richness of the field layer, this suggests different mechanisms of local extinction and colonization as well as tree identity effects. The loss of species occurred directional in GB-DF and AB-NAT with different infrequent species disappearing from the subplots leading to a decrease in the species turnover component. Few new species colonized due to the decreasing light availability and lack of soil disturbance [90]. The SFR EK-DF was characterized by both processes. While the same species disappeared from the subplots of EK-DF (e.g., *Sambucus racemosa*, *Senecio ovatus*; Table S1), they were partly replaced by new and different species in some subplots, among them many bryophyte species that can benefit from the needle litter [34]. In total, 28 species disappeared from the field layer in EK-DF, while 16 new species colonized. Only 7 and 9 species newly occurred in the subplots of GB-DF and AB-NAT, respectively compared to 23 and 28 species that disappeared (Table S1). Besides missing disturbance, this underlines the negative effect of an increasing beech share on understory species richness [78] and supports evidence that increasing shade can lead to homogenization effects [91] also at a local scale. Natural disturbances that may affect the SFR in higher frequency and intensity in the future will presumably change this pattern.

4.3. Douglas Fir Regeneration Is Decreasing

Regeneration of Douglas fir decreased both in the shrub and in the herb layer in both Douglas fir SFRs, while the main native tree species beech and Norway spruce showed increasing or stable trends in the shrub layer. Different reasons are responsible for the decreasing regeneration of Douglas fir. In the SFR GB-DF the decreasing light availability due to an expansion of beech in the overstory seems to be the most decisive factor. According to Montigny and Smith [92], minimum gap sizes of roughly 0.3 ha are needed for a successful regeneration of Douglas fir. Mailly and Kimmins [93] mention a minimum relative light availability of 40% for a survival and growth of Douglas fir regeneration. As no larger gaps occurred between survey years, Douglas fir was clearly inferior in competition with the shade-tolerant beech. In addition, Petriţan et al. [94] showed that Douglas fir regeneration is more sensitive to root competition than beech.

Even though, the SFR EK-DF was not colonized by shade-tolerant tree species to the same degree as the SFR GB-DF, self-thinning also led to a large reduction in Douglas fir in the shrub layer (Figure S1d). According to He and Duncan [81], mortality is mainly observed in dense patches of Douglas fir regeneration leading to a regular spatial distribution of trees. Surviving Douglas fir trees partly reached the lower tree layer in the SFR EK-DF, as did some native tree species such as hornbeam, hazelnut or beech. Due to the lower share of beech in the whole area of the SFR EK-DF compared to GB-DF (according to the forest inventory from 1997 and 1995, 3% of beech in EK-DF vs. 21% of beech in GB-DF), the colonization of shade-tolerant species presumably shows a time lag and may accelerate in upcoming years at the further expense of Douglas fir.

In general, the dynamics of Douglas fir observed in the investigated SFRs reflect the dynamics in mature and old growth stands of the native range. As a pioneer tree species, Douglas fir stands often originate from catastrophic wildfires or other stand replacing disturbances [95]. In course of succession, these pioneer forests are largely shaped by self-thinning processes and are invaded by shade-tolerant tree species such as western hemlock (*Tsuga heterophylla*). The colonization by shade-tolerant tree species was found to be independent of openings that occur due to the stem exclusion of Douglas fir [81]. The increasing competition by shade tolerant tree species reaching the overstorey then hampers the successful further recruitment of Douglas fir [81]. Even in small canopy gaps within mature (100–150 years) and old-growth (>200 years) Douglas fir forests in the native range, no successful regeneration of Douglas fir was observed anymore, while the gaps were colonized by the shade-tolerant hemlock [96]. Thus, the decreasing regeneration success within the SFRs reported here is in line with the dynamics in natural Douglas fir forests in the native range and underlines the pioneer character of this tree species. As also no seedlings were found during the second survey in the SFRs, a successful germination is presumably also hampered by a dense leaf or needle litter and a dense moss layer preventing the seedlings from reaching the mineral soil [10,19,21,97]. However, most tree species showed a reduction in frequency and cover in the herb layer also suffering from decreasing light availability and an increasing litter layer thickness after management abandonment.

A competitive inferiority of Douglas fir compared to native tree species was also confirmed by Frei et al. [21] for a study in Switzerland for which 39 sites with Douglas fir planted mostly in mixture with native tree species were investigated for the occurrence and abundance of Douglas fir and native tree species regeneration. Except for some dry, nutrient-deficient sites with an open canopy where Douglas fir was able to dominate the seedling layer (<130 cm heigh) and comprised up to 23% of saplings (≥130 cm), saplings of Douglas fir were on all sites outnumbered by regeneration of beech, Norway spruce, silver fir (*Abies alba*) or other broadleaved tree species. In the SFR GB-DF, Norway spruce turned out to be more shade-tolerant in terms of survival than Douglas fir as the cover value of Norway spruce in the shrub layer significantly increased between surveys. Already in 2005, Vor [98] recorded a higher percentage (26%) of dead Douglas fir trees in the regeneration (dbh < 7 cm) compared to Norway spruce (4%). Douglas fir was, however, characterized by a greater height growth. The reduction in Douglas fir in the shrub layer between surveys confirms the finding that the light requirement of Douglas fir increases with age [10]. Despite survival, the Norway spruce regeneration showed a low vitality under the low light conditions and remained mainly below 2 m in height at time of the second survey. Mortality of Douglas fir regeneration in the SFR EK-DF showed a similar percentage as observed in GB-DF (27%) in 2005 but was much lower compared to Norway spruce (76%, [98]). Here, the faster growth rate of Douglas fir under a more open canopy seems to have outcompeted Norway spruce. However, subsequent self-thinning within the dense regeneration led to a decrease in Douglas fir in the shrub layer up to the second survey (see above).

The impact of deer is also mentioned as a limiting factor for the successful establishment of Douglas fir regeneration [10], as the tree species is often affected by browsing on spring-flush growth, by fraying from roe bucks (*Capreolus capreolus*) and by bark stripping [99]. Frei et al. [21] found browsing intensity on Douglas fir to be lower compared to ash, maple, oak or silver fir, but higher compared to beech and Norway spruce. While Douglas fir made up 10% of the number of seedlings recorded by Frei et al. [21], the species only comprised 3% of the number of saplings. A similar pattern was found for the browsing sensitive silver fir (dropping from 17 to 10%), while beech and Norway spruce showed the opposite (beech: from 29 to a 48% share, spruce: from 6 to 9%). This supports an impact of deer on the regeneration establishment of Douglas fir. According to Spellmann et al. [10], deer browsing and bark fraying or stripping can cause a complete loss of Douglas fir natural regeneration. However, as the core areas of the SFRs investigated here were fenced, our results indicate that deer seems not to be a major factor explaining failing Douglas fir regeneration. Rather light availability, litter layer thickness and the successional position of Douglas fir in relation to other tree species are likely causes. Outside fenced areas, though, the impact of deer seems to further decrease the competitive strength of Douglas fir compared to native tree species [21]. Outside the fenced areas of the SFRs, few individuals of Douglas fir (>0.5 m) were detected, most were affected by browsing (personal observation).

While most tree species decreased in abundance in the herb layer in the Douglas fir SFRs, sessile oak and small-leaved lime increased in the herb layer in the SFR AB-NAT. The increasing frequency of masting years observed in recent years is one reason for the increased abundance of seedlings [100]. The increasing frequency of both tree species in the regeneration is also responsible for an increasing temperature value in the SFR AB-NAT (T-values of 5 to 6). Further monitoring in this and in other SFRs will show if climate change with increasing temperatures and changes in the precipitation regime will promote a further growth of oak and lime at the expense of beech.

5. Conclusions

We observed similar vegetation dynamics in Douglas fir-dominated forests and forests dominated by native tree species after management abandonment irrespective of the tree species identity and origin, as diminished soil disturbance and a decreasing light availability were more important. The understory vegetation became less species-rich and more shade-tolerant over time.

Tree species identity, however, affected species compositional changes across survey periods and had an effect on understory homogenization. While a Douglas fir canopy promoted the relative share of generalist species, a native canopy promoted typical species of the class Querco-Fagetea. In addition, the expansion of beech led to a homogenization of the understory mainly due to species losses, while a canopy dominated by Douglas fir led to a differentiation mainly due to the colonization of bryophytes. This suggests that certain tree species characteristics, such as the shade-casting ability of beech and its dense leaf litter vs. a well decomposable needle litter of Douglas fir, shape the understory vegetation characteristics irrespective of forest management. However, all strict forest reserves (SFR) showed an increasing share of typical closed forest species.

Dynamics of the tree species Douglas fir in the unmanaged SFRs reflect its successional position in the native range. As a pioneer species, it does not show a successful regeneration in mature stands of the native range and similarly, regeneration also decreased between observation periods in the investigated SFRs. This supports the finding that a successful regeneration of Douglas fir requires silvicultural management or severe disturbances [43] and that the competitive strength against native, particularly shade-tolerant tree species, is low. However, in the native range, Douglas fir can build self-perpetuating forests at very dry sites, where shade-tolerant species such as hemlock fail [81]. This underlines the invasive potential of Douglas fir at dry sites in Europe [18,19,21] and stresses the need for further monitoring of Douglas fir stands under changing abiotic conditions also without forest management. Under current site conditions though, our study shows that, even in pure stands, the regeneration potential of Douglas fir seems to be low when left for natural forest development. As the seed production of the old Douglas fir trees may not have reached its maximum yet [101], uncertainties concerning its future regeneration potential remain. Regarding the long lifespan of Douglas fir in the native range [96], it can be expected that Douglas fir will be dominant in the upper canopy of the SFR in the future with native, shade-tolerant tree species colonizing below and shaping the environment for the understory. Regular monitoring in the SFRs with and without Douglas fir will provide important knowledge on this assumption in the future and on the competitive strength of Douglas fir under changing abiotic conditions.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14100795/s1, Table S1. Frequency of occurrence (F) in % and mean cover values and standard error in % (mCV±SE) for all species surveyed on the 400 m^2 subplots in the core areas of the three strict forest reserves Grünberg, Eselskopf and Adelsberg for two observation times; Figure S1. Impressions from the core areas of the strict forest reserves (SFRs) dominated by Douglas fir.

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