

Management options for the conversion of allochthonous coniferous forest patches towards more natural species composition in the Vorpommersche Boddenlandschaft National Park, NE Germany

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Abstract

The conversion of coniferous tree plantations towards natural self-regenerating forests is one of the targets of forestry in Europe and particularly desirable in national parks. The aim of this study was to evaluate the effectiveness of different conversion approaches (conducted once) on natural forest development in man-made spruce plantations. We studied the effects of three distinct management options (partial-cutting [PC], clear-cutting with timber removal [CC] and clear-cutting with timber remaining [CCr]) six years after application on tree regeneration (sapling identity, abundance, height, browsing intensity) and understorey species composition in former spruce plantations within the Vorpommersche Boddenlandschaft National Park in Northeastern Germany. An unmanaged spruce [M] and near-natural beech [N] stands were considered as local references. The sites differed significantly in tree regeneration and understorey species composition. The abundance of native tree saplings was highest at site CCr, their height did not differ among sites, while browsing intensity was most pronounced at site CC. Understorey species composition of all management options was equally dissimilar to site N. However, site CCr contained more species that are typically abundant in local beech forests. Clear-cutting of spruce plantations with dead wood remaining on site favoured the natural regeneration of native trees and understorey vegetation compared to clear-cutting with timber removal, partial-cutting and no management. Herbivore browsing detrimentally affected tree regeneration independent of the treatment. Clear-cutting with timber removal promoted the dominance of competitive herbaceous species that may hamper long-term forest regeneration. We conclude that progression of site CCr appears to proceed fastest towards natural forest conditions. Further long-term data is required to derive clear trends regarding time and direction of forest regeneration.

Keywords: forest conversion, spruce plantations, beech forest, natural tree regeneration, understorey species composition, deer browsing

Introduction

Considerable parts of the Central European forest area comprise anthropogenic plantations of coniferous tree species such as Norway spruce (*Picea abies* (L.) Karst.) (Spiecker 2003, Kreyer and Zerbe 2006). The conversion towards more natural and self-regenerating forests has recently become a target of forestry in Europe (Klimo et al. 2000, Ammer et al. 2011). Native forest ecosystems may be more resilient against confounding effects of pest outbreaks or climate change and may improve the capability

of accompanying ecosystem services such as ground water purification and carbon storage (Zerbe 2009). Taking coniferous plantations out of management may not be sufficient to enable a prompt development towards natural forests due to lasting alterations of site conditions (e.g., acidic litter layers) and persistent regeneration of coniferous tree species (Jahn et al. 1990, Cannell 1999). Forest conversion modifies the canopy cover, altering the abiotic conditions and availability of resources (light, water, nutrients) for rejuvenating trees and understorey vegetation (Augusto et al.

2003, Barbier et al. 2008). Depending on the intensity and severity of conversion, the influence on tree regeneration and understorey species composition can differ considerably (Hérault et al. 2004, Fischer et al. 2016).

Concerning tree regeneration, many studies ascertained that seedling and sapling abundance of pioneer tree species such as silver birch (*Betula pendula* Roth) and European rowan (*Sorbus aucuparia* L.) among others increased with decreasing canopy density (Modrý et al. 2004, Dobrowolska 2008) or increasing gap size (Yamamoto 2000, Huth and Wagner 2006). In contrast, the naturally dominant climax tree species in Central Europe is *Fagus sylvatica* (Leuschner et al. 2006), which is also in accordance with our study area (LFG MV 2002, Berg et al. 2004). This species is shade-tolerant and can survive in small gaps or at larger gap edges (Emborg 2007, Fischer et al. 2016). Both, autochthonous pioneer tree species and European beech are considered as target tree species for the transformational process towards more natural forests (Raspé et al. 2000, Zerbe and Kreyer 2007).

Concerning understorey species composition, forest conversion may lead to instant changes in abundance and cover of herb layer species (Zerbe and Kreyer 2007, Heinrichs and Schmidt 2009). With increasing conversion intensity, shade-tolerant species were shown to be largely displaced by more light-demanding fast-growing species (Hannerz and Hånnel 1997, Heinrichs and Schmidt 2009).

Partial-cutting of spruce may accelerate the formation of late-successional forest structures (Hannerz and Hånnel 1997) and favour tree regeneration of (intermediate) shade-tolerant species (Wagner et al. 2011). It may emulate gap disturbance, which is principally in accordance with regeneration properties of beech (Wagner et al. 2010). Although regeneration of light-demanding tree species such as pine (*Pinus sylvestris* L.) is possible with shelterwood systems, however, partial-cutting may not ascertain a major regeneration of native tree saplings (Huth and Wagner 2006, Fischer et al. 2016).

In contrast, clear-cutting may aim for an entire shift in tree species composition due to the hindrance of additional *in-situ* seed dispersal by non-target species and may be applied to favour light-demanding successional tree species to promote restoration of native broadleaved forests (D'Antonio and Meyerson 2002, Heinrichs and Schmidt 2009). In particular, clear-cutting of small patches of spruce plantations was found to decelerate spruce regeneration and to increase the abundance of pioneer tree species (Jonášová and Matějková 2007, Heinrichs and Schmidt 2009). Nevertheless, studies also identified high light intensity to promote the expansion of competitive herbaceous species (Mayer et al. 2004, Wagner et al. 2011) that may hamper tree regeneration (Löf and Welanders 2004, Priewasser 2013).

Height increment of different tree species has been shown to positively correlate with increasing light avail-

ability (Chrimes and Nilson 2005, Madsen and Hahn 2008). However, species-specific study results are ambiguous. Priewasser (2013) has shown that pioneer tree species in wind-disturbed forests were significantly taller compared to late-successional species such as beech and spruce, while Goen (2010, unpubl.) identified an opposite trend for the Vorpommersche Boddenlandschaft National Park.

Forest conversion may also promote browsing by ungulates (Reimoser 1986), which is a key factor impeding forest regeneration (Ammer 1996, Zerbe and Kreyer 2007). Ungulate habitat use and browsing impact is markedly influenced by and depends on silvicultural treatments because the inherent changes in understorey vegetation alter food supply, i.e. quantity, quality and seasonal fluctuation. The availability of lying dead wood may shelter regenerating trees against browsing by herbivores due to its physical and visual barricade function (de Chantal and Granström 2007, Hagge et al. 2019). Further, dead wood accumulation increases the diversity of light regimes and creates distinct ecological niches (Honnay et al. 2002). This may lead to more heterogeneous tree regeneration and may facilitate a species composition of natural forest communities (Müller and Büttler 2010, Hagge et al. 2019).

To date, natural regeneration of autochthonous tree species in anthropogenic forests is of particular interest for national parks, where (restoring) native plant communities and ecosystem processes is the ultimate goal (Fischer et al. 2002). However, direct comparisons of natural tree regeneration and understorey species composition among different once-performed conversion approaches combined with spatial references are rare to our knowledge. Thus, three distinct management options have been applied on otherwise comparable mature spruce stands in the Vorpommersche Boddenlandschaft National Park in the years 2012/13: partial-cutting [PC], clear-cutting with timber removal [CC] and clear-cutting with timber remaining [CCr]. In 2018, we studied the effects of these treatments on tree regeneration (sapling identity, abundance, height, browsing intensity) as well as on understorey species composition and compared them with a spruce stand without treatment [M] and a beech stand [N] that represents the reference of a near-natural forest in the region.

We hypothesise that

- (i) Management option CCr results in the greatest abundance, height and least intense browsing of target tree saplings among all different management options.
- (ii) No management option leads to successful restoration of the understorey species composition within the observed period. Successful regeneration would be indicated by no significant difference in understorey species composition in comparison to the near-natural reference stand (N). Still, management options might differ in their (dis-)similarity to site N and we expect site CCr to come closest.

Material and methods

Study area

The study area was in the Vorpommersche Boddenlandschaft National Park (NE Germany), particularly in Neudarß area with coordinates N 54.44947, E 12.49989 (Figure suppl. 1). According to the Köppen-Geiger climate classification system (Köppen 1936), the area has a “temperate oceanic climate” (Cfb). Mean annual temperature at adjacent village Born am Darß (over about 7 km) is 8.3°C and mean annual precipitation is 563 mm for the reference period 1982–2012 (Climate-Data.Org 2019). The substrate consists of marine sandy deposits that indicate past dynamic coastal processes. Hence, soil formation is in an early state and may be classified as young podzols in the study area. The relief is characterized by a variety of barrier ridges (“Reffen”, small ridges) and depressions (“Riegen”, hollows), which were deposited consecutively in east-west direction. The depressions are highly influenced by seasonal groundwater level fluctuations and exhibit alder swamp forests. In contrast, the elevated barrier ridges are characterized by relatively drier conditions and harbour acidic nutrient-poor beech-forests under natural conditions (Berg et al. 2004). However, many barrier ridges have been re-planted with coniferous tree species after a wind throw event in 1967/68 (LFG MV 2002).

Study design and data collection

The experimental design comprised of five distinct forest stands that were exclusively located on barrier ridges (Figure suppl. 1, 2). Each stand size was ca. 0.5 ha, situated within a maximum linear distance of 500 m from each other and exhibited similar abiotic conditions (described below). Four stands were planted with coniferous tree species (i.e., *Picea sitchensis* and/or *Picea abies*) between 1969 and 1973. Between November 2012 and February 2013 three of the stands were transformed with the following distinct management options: (i) partial-cutting [PC], (ii) clear-cutting with timber removal [CC] and (iii) clear-cutting with timber remaining [CCr]. The felled timber volume was 63.4 m³/ha for PC, 109.2 m³/ha for CC and 110.0 m³/ha for CCr. Tree cutting methods included the operation of a forest harvester for PC and CC and a motor-manual chainsaw application for CCr. The fourth coniferous stand [M] was planted in 1970, not transformed and was characterized as a local reference for unmanaged spruce plantations. The fifth stand [N] consisted exclusively of European beech planted in 1835 and was characterized as near-natural reference considering the stand age, time without management and the expected local climax state of forest succession (Berg et al. 2004). Stand ages and data on conversion were supplied by the local National Park Authority in Born a. Darß.

Within each stand (hereafter site), 20 sampling plots (each 5 m × 5 m, $n = 100$) were selected with a random walk plot selection approach (Krasny et al. 2003), whereas

geographic location of each sampling plot (hereafter plot) was determined in the field via a GPS device (Garmin eTrex 30x) and photographs from two cardinal directions (east, west) per plot were taken. Tree regeneration, i.e., species identity, abundance, height (in cm) and browsing intensity of tree saplings, was examined in four subplots (each 1 m × 1 m, $n = 400$) nested within the corners of each 5 m × 5 m sampling plot due to the high density of saplings in the study area. Browsing intensity was assessed by using a categorical scale according to Mirschel et al. (2006) (Table 1).

Table 1. Scale for the assessment of browsing intensity of tree saplings

Value	Characteristics
0	No visual damage according to browsing evaluation
1	Low damage: main shoot unaffected, max 1/3 of lateral shoots are browsed
2	Medium damage: main shoot affected and/or 1/3–2/3 of lateral shoots are browsed
3	High damage: main shoot affected and > 2/3 of lateral shoots are browsed

Understorey assemblage of vascular plants, i.e., species identity and species cover values (in %) and cover values (in %) of vegetation layers (i.e., moss, herb, shrub, canopy, overall), dead wood and dead bracken fern (*Pteridium aquilinum* L. Kuhn) were determined for every plot. Additional emphasis on *P. aquilinum* results from its extensive dominance in the herb layer in parts of the study area (LFG MV 2002). Cover values less than 1 % were standardized to 0.5 % for the purpose of statistical analysis. Additionally, relative ground level height differences among all plots (in cm) were measured with a water level gauge in each plot. Measurement inaccuracy amounted to 9 cm. The results were converted into values of absolute height above mean groundwater table considering measurements of a permanent gauge adjacent to the study sites taken between 2013 and 2017 (unpubl. data). Sites CC and CCr were higher above mean groundwater table compared to sites PC and N, while site M was not significantly different from all other sites (Figure suppl. 3). Furthermore, soil samples from five randomly selected plots per site ($n = 25$) as a composite sample from three insertions per plot separated by soil horizons were taken with a Pürckhauer drill to detect pH values. These values for every horizon were measured in the laboratory with a WTW pH315i measurement device assembling a testing probe SenTix 41 and using a 3 M KCL solution. Humus pH values were highest for site N, lowest for sites M and PC, while values for sites CC and CCr turned out to be intermediate and not significantly different from each other (Figure suppl. 4). This is not surprising and indicates that the site differences in humus pH are due to the pre-treatment with coniferous spruce species. In contrast, no differences in pH were detected for the upper mineral soil horizons (Table

suppl. 1), which reflects site similarity with respect to soil type. Field sampling was conducted in April, May and June 2018.

Data analysis

The data analysis on tree regeneration was generally characterized by a separation into target and non-target tree species with respect to the aim of the experiment, i.e., identifying the most effective management option to facilitate a development towards more natural forests and ultimately to promote regeneration of *Fagus sylvatica* as the presumed dominant climax tree species (Berg et al. 2004). However, time between management implementation and sampling, i.e., six years, may not have been sufficient to identify a clear trend towards the regeneration of beech forest. Hence, target tree saplings included the tree species locally occurring during succession towards local acidic nutrient-poor beech forests, i.e., *Alnus glutinosa* L., *Betula pendula* Roth, *Betula pubescens* Ehrh., *Fagus sylvatica* L., *Pinus sylvestris* L., *Quercus robur* L. and *Sorbus aucuparia* L. (LFG MV 2002, Berg et al. 2004). Non-target tree saplings embraced the species *Picea abies* (L.) Karst. *Picea sitchensis* (Bong.) Karr. and *Prunus serotina* Ehrh. In addition, the tree species were partially considered individually to delineate the species-specific responses due to the different management options. In this respect, species-specific analyses of *Quercus robur* and *Prunus serotina* were generally limited due to a small sample size.

Differences in sapling abundance, cover values of tree sapling species and environmental attributes, i.e., cover of vegetation layers, dead wood and dead bracken fern as well as humus/upper mineral soil pH values and absolute height above mean groundwater, table among the five sites were tested using simple linear models (Chambers and Hastie 2017).

Differences in sapling height among the five sites were tested using linear mixed-effect models (Bates et al. 2015) accounting for spatial nesting due to the abundance of multiple plots per site (Schielzeth and Nakagawa 2013) by using plot ID within site as random effect.

After fitting simple linear and linear mixed-effect models, followed by ANOVA-testing, Tukey's post hoc tests for pair wise comparisons (TukeyHSD) among sites were performed to avoid multiple testing (Benjamini and Hochberg 1995). The response variables (sapling abundance/height/cover values and environmental attributes) of aforementioned models had to be rank-transformed because they did not meet all parametric assumptions.

The importance of environmental attributes on the abundance and median height of tree saplings was quantified by boosted regression trees (BRT, Elith et al. 2008). The terminal models were chosen due to minimal evaluated cross-validated deviance acquired by adjusting the tree complexity to 2 and the bag fraction to 0.75. The learning rate differed among the models and is

provided in the results section. The cross-validated correlation was utilised to reveal the correlation among environmental variables and sapling abundance or height. For each environmental variable, its comparative significance in explained variance is supplied. Here, BRT were computed with the function *gbm.step* of package *dismo* (Hijmans et al. 2017).

Differences in sapling browsing intensity among the five sites were tested using Pearson's Chi-squared test accounting for categorical dependent variables, followed by Chi-square post hoc tests for pairwise comparisons among the sites (Mangiafico 2015).

An analysis of similarity (ANOSIM) was computed to test for potential differences in understorey species composition among the different sites. Test statistics delineate the distinction among the groups of sampling units: *R* is based on the difference of mean ranks between and within groups, *P* describes the significance levels. The Bray-Curtis dissimilarity was used as the dissimilarity measure due to its sturdiness with vegetation data (Faith et al. 1987). In this context, ANOSIM was computed with the function *anosim* of package *vegan* (Oksanen et al. 2018), followed by pairwise direct testing with Bonferroni correction due to a lack of post hoc tests for ANOSIM.

Furthermore, understorey species compositions (cover values of each species) in each plot were compared between the treatments by ordination [Non-metric Multidimensional Scaling (NMDS)] to graphically demonstrate the variation in understorey composition within and among the five different sites. In this regard, the NMDS was executed according to the method advised by Faith et al. (1987), which is premised on the algorithm delineated by Kruskal (1964) and Mather (1976) with multiple random starts to detect the best general solution. NMDS was computed with two dimensions using the function *metaMDS* of package *vegan* (Oksanen et al. 2018). Stress values smaller than 0.20 principally result in viable interpretations (Clarke 1993).

To test the affiliation of individual species to specific sites, an Indicator Species Analysis (Dufrêne and Legendre 1997) on species-specific cover values was conducted with the function *indval* of package *labdsv* (Roberts 2016). All statistics were performed using R 3.4.2 (R Core Team 2018).

Naturalness of understorey vegetation

Generally, the naturalness of Central European forests is difficult to determine due to a lack of primeval undisturbed forests as reference (Kaplan et al. 2009). Various indicators attempt to measure naturalness concerning forest development (reviewed by McRoberts et al. 2012). In this study, the degree of naturalness was assessed by comparing the understorey species composition of each converted spruce plantation with near-natural beech (N) and man-made spruce (M) forest as local references. In addition, the sampled plant species that revealed a significant Indicator

Value were reconciled with a list of native plant species that are disproportionally abundant in acidic nutrient-poor beech forests (*Luzulo luzuloidis-Fagion sylvaticae*) in the federal state of Mecklenburg Western-Pomerania (Berg et al. 2004).

Results

Tree regeneration

Abundance of tree saplings

Overall, 1696 tree saplings from nine different species were sampled within 400 subplots (equal to 0.04 ha) among the five sites of which ca. 56 % can be classified as target and ca. 44 % as non-target tree saplings. The abundance of target tree saplings was significantly different among the five sites (ANOVA: $P \leq 0.001$, $F = 18.2$). Site CCr showed the greatest abundance among all sites. Site N comprised significantly higher abundance compared to site M. Sites PC and CC were intermediate to and not significantly different from site M and site N (Figure 1). Abundance of *Fagus sylvatica* was significantly different among the sites (ANOVA: $P \leq 0.001$, $F = 28.3$). Beech saplings were most common at site N (TukeyHSD: all $P \leq 0.001$), whereas abundance was not significantly different among all other sites (TukeyHSD: all $P \geq 0.930$). The abundance of non-target tree saplings was also significantly different among the five sites (ANOVA: $P \leq 0.001$, $F = 6.6$). The sites M and PC were not significantly different to one another, however, comprised significantly higher abundance than site CC. Site CCr was intermediate to and not significantly different from all other sites. Abundance was not computable for site N due to small sample size of non-target tree saplings ($n = 1$) (Figure 1). Besides abundance, also cover values of each sampled tree sapling species considered solitarily showed

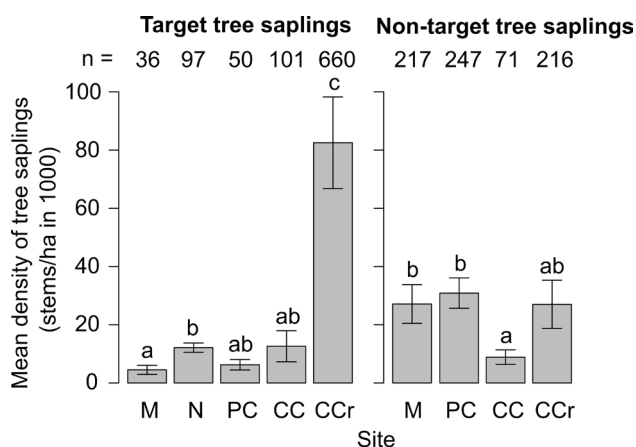


Figure 1. Mean density [stems/ha in 1000] of native target ($n = 944$) and locally non-native non-target ($n = 751$) tree saplings with standard errors for unmanaged spruce plantation (M), near-natural beech forest (N), partial-cutting (PC), clear-cutting with timber removal (CC) and clear-cutting with timber remaining (CCr).

Bars with different characters are significantly different (TukeyHSD post hoc comparisons).

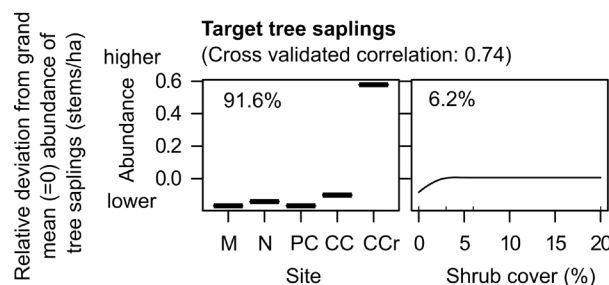


Figure 2. Relative deviation from grand mean (= 0) abundance of native target tree saplings (determined by BRT) for 944 target tree saplings as explained by environmental attributes

Learning rate was set to 0.01. Ticks below the curve show 10 % increments of the data points. Percentage in each plot indicate the proportion of overall explained variance that is explained by the single environmental attributes.

significant differences among the sites, except for *Quercus robur* (Table suppl. 2). Target tree species *Alnus glutinosa*, *Betula pendula*, *Pinus sylvestris* and *Sorbus aucuparia* had significantly highest cover values at site CCr (TukeyHSD: all $P \leq 0.050$), while *Fagus sylvatica* revealed the significantly highest cover values at site N among all sites (TukeyHSD: all $P \leq 0.001$). Environmental attributes had a pronounced effect on the abundance of target tree saplings (BRT: cv. corr. = 0.74, SE = 0.10). Here, the site/silvicultural treatment (91.6 % of explained variance) and the cover of the shrub layer (6.2 %) were most important (Figure 2). In contrast, the abundance of non-target tree saplings was only marginally influenced by environmental attributes (BRT: cv. corr. = 0.11, SE = 0.09).

Height of tree saplings

The majority (> 99 %) of tree saplings did not reach breast height yet. However, the target tree saplings that were grown above breast height ($n = 11$) solely occurred at site CCr. Mean height of target tree saplings was not found to be significantly different among the sites (ANOVA: $P = 0.827$, $F = 0.4$, Figure 3). The only target tree species with significant differences in sapling height among the sites was *Sorbus aucuparia* (Table suppl. 3). In this regard, individuals at site CCr were significantly taller compared to those at site M (TukeyHSD: $P = 0.047$) and PC (TukeyHSD: $P \leq 0.001$). The height of *Sorbus aucuparia* saplings at sites N and CC were not significantly different from each other (TukeyHSD: $P \leq 0.993$) and all other sites (TukeyHSD: all $P \geq 0.05$). In comparison, mean height of non-target tree saplings were significantly different among the sites (ANOVA: $P \leq 0.001$, $F = 46.6$). Site CCr and CC had significantly taller non-target tree saplings compared to site M and PC. Site PC comprised significantly taller non-target tree saplings compared to site M. The mean height of non-target tree saplings was not computable for site N due to small sample size ($n = 1$) (Figure 3). Environmental attributes had a pronounced effect on both, height of target (BRT: cv. corr. = 0.54, SE = 0.09) as well as non-target tree saplings (BRT: cv. corr. = 0.75, SE = 0.06). While the former was greatly influenced by browsing in-

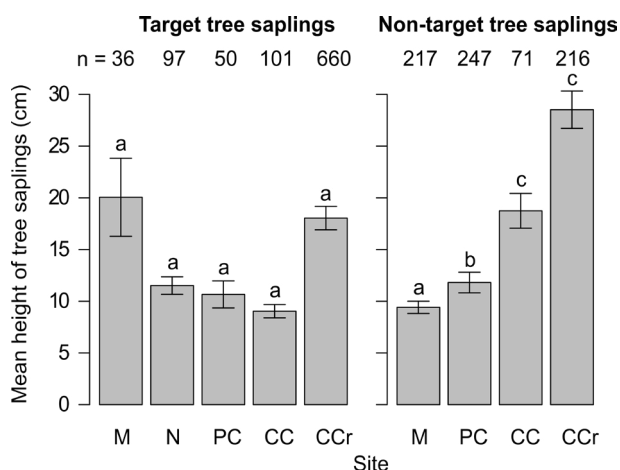


Figure 3. Mean height of native target ($n = 944$) and locally non-native non-target ($n = 751$) tree saplings with standard errors for unmanaged spruce plantation (M), near-natural beech forest (N), partial-cutting (PC), clear-cutting with timber removal (CC) and clear-cutting with timber remaining (CCr)

Bars with different characters are significantly different (TukeyHSD post hoc comparisons).

Figure 4. Relative deviation from grand mean ($= 0$) height of tree saplings (determined by BRT) for 944 native target and 751 locally non-native non-target tree saplings as explained by environmental attributes

Learning rate was set to 0.001 for both target and non-target tree saplings. Ticks below the curves show 10 % increments of the data points. Percentage in each plot indicate the proportion of overall explained variance that is explained by the single environmental attributes

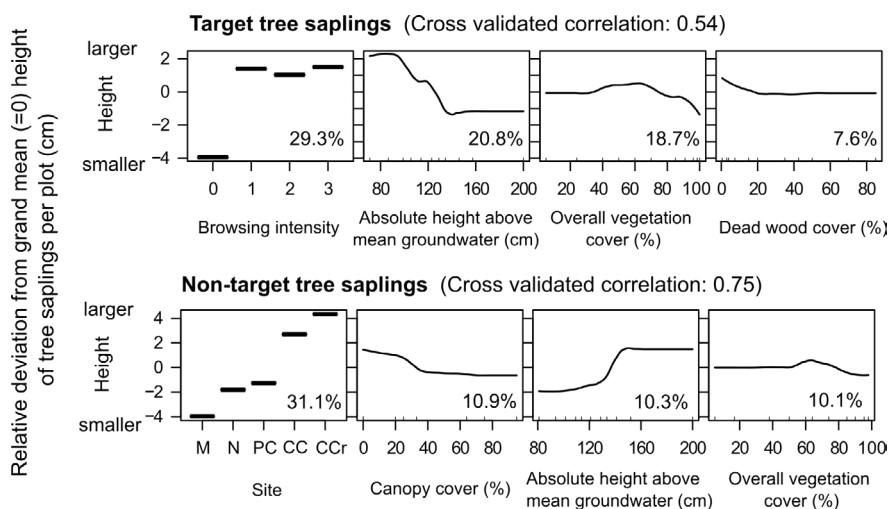


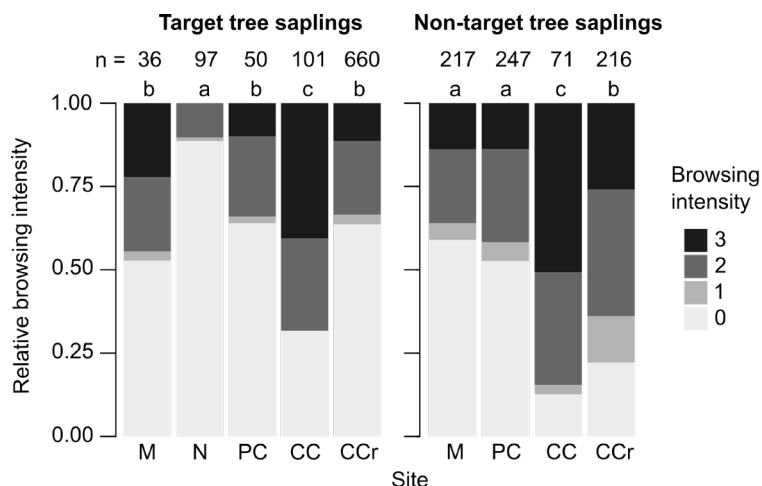
Figure 5. Relative browsing intensity of native target ($n = 944$) and locally non-native non-target ($n = 751$) tree saplings for unmanaged spruce plantation (M), near-natural beech forest (N), partial-cutting (PC), clear-cutting with timber removal (CC) and clear-cutting with timber remaining (CCr)

Bars with different letters are significantly different (Chi² post hoc comparisons).

tensity (29.3 %), absolute height above mean groundwater table (20.8 %), overall vegetation cover (18.7 %) and dead wood cover (7.6 %), the latter were mostly affected by site/silvicultural treatment (31.1 %), canopy cover (10.9 %), absolute height above mean groundwater table (10.3 %) and overall vegetation cover (10.1 %) (Figure 4).

Browsing intensity of tree saplings

About half of all sampled tree saplings were affected by browsing (ca. 47 %). Browsing intensity of target tree saplings was significantly different among the five sites (PEARSON'S CHI² TEST: $P \leq 0.001$, $X^2 = 110.2$). Site CC exhibited the most intense browsing, while site N comprised the significantly least intense browsing among the sites. Browsing intensity was not significantly different among sites M, PC and CCr (Figure 5). In comparison, browsing intensity of non-target tree saplings was also significantly different among the five sites (PEARSON'S CHI² TEST: $P \leq 0.001$, $X^2 = 126.8$). Site CC revealed the most intense browsing among all sites. Sites M and PC, both not significantly different from each other had significantly less intense browsing compared to site CCr. Here, browsing intensity was not computable for site N due to small sample size of non-target tree saplings ($n = 1$).

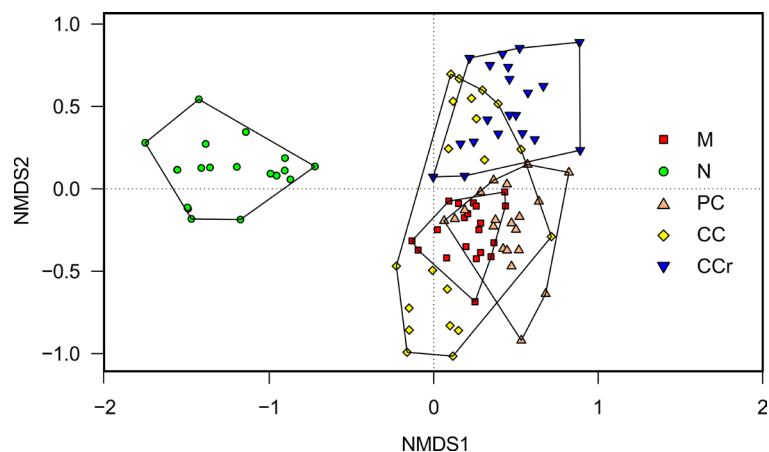


Understorey species composition

There were significant differences in understorey species composition among all five sites (ANOSIM: $P \leq 0.001$, $R = 0.81$). Particularly, sites M, PC, CC and CCr each individually exhibited a strong separation to site N (ANOSIM: all $P \leq 0.001$, $R \geq 0.99$). Furthermore, PC was significantly dissimilar to CC (ANOSIM: $P \leq 0.001$, $R \geq 0.94$). Site PC was assessed very similar to reference site M (ANOSIM: $P = 0.078$, $R \geq 0.06$). Site M was rather dissimilar to sites CCr (ANOSIM: $P \leq 0.001$, $R \geq 0.61$) and CC (ANOSIM: $P \leq 0.001$, $R \geq 0.76$).

Figure 6. Non-metric multidimensional scaling (NMDS) ordination based on the understorey species composition for the five different sites (using the Bray-Curtis dissimilarity, final stress for 2-dimensional solution: 1.9)

The graph shows all sampled plots among the five sites: unmanaged spruce plantation (M), near-natural beech forest (N), partial-cutting (PC), clear-cutting with timber removal (CC) and clear-cutting with timber remaining (CCr).



Species	M	N	PC	CC	CCr	P
<i>Fagus sylvatica</i>	0	0.98	0	0	0	0.001
<i>Alnus glutinosa</i>	0	0	0	0.02	0.87	0.001
<i>Betula pendula</i>	0.01	0	0.01	0.07	0.82	0.001
<i>Aira praecox</i>	0	0	0	0.02	0.76	0.001
<i>Rubus fruticosus agg.</i>	0.01	0	0.02	0.11	0.72	0.001
<i>Trientalis europaea</i>	0.35	0	0.60	0.01	0.01	0.001
<i>Dryopteris carthusiana</i>	0.50	0	0.12	0.10	0.12	0.001
<i>Oxalis acetosella</i>	0.46	0	0.39	0.02	0.07	0.001
<i>Picea abies</i>	0.44	0	0.29	0.01	0.06	0.001
<i>Pteridium aquilinum</i>	0.20	0.02	0.02	0.41	0.24	0.001
<i>Rumex acetosella</i>	0	0	0	0.07	0.41	0.001
<i>Carex canescens</i>	0	0	0	0	0.40	0.001
<i>Deschampsia flexuosa</i>	0.08	0	0.38	0.03	0.29	0.001
<i>Sorbus aucuparia</i>	0.19	0.03	0.20	0.04	0.35	0.001
<i>Rubus idaeus</i>	0	0	0.34	0.04	0	0.001
<i>Lonicera periclymenum</i>	0.02	0	0.06	0.15	0.32	0.001
<i>Molinia caerulea</i>	0	0	0	0.01	0.32	0.001
<i>Epilobium angustifolium</i>	0	0	0.01	0	0.27	0.001
<i>Picea sitchensis</i>	0.13	0	0.42	0	0.09	0.002
<i>Carex pilulifera</i>	0	0	0	0.09	0.26	0.002
<i>Hedera helix</i>	0.01	0	0.26	0.02	0.02	0.002
<i>Moehringia trinervia</i>	0.17	0	0.28	0.06	0.20	0.005
<i>Agrostis canina</i>	0	0	0	0	0.20	0.005
<i>Luzula pilosa</i>	0.15	0	0.33	0.14	0.23	0.007
<i>Calamagrostis epigejos</i>	0	0	0	0	0.20	0.007
<i>Pinus sylvestris</i>	0.02	0	0.03	0.18	0.22	0.013
<i>Prunus serotina</i>	0	0.16	0	0.01	0	0.021
<i>Agrostis stolonifera</i>	0	0	0	0	0.15	0.026
<i>Stellaria media</i>	0	0	0.16	0.01	0.03	0.036
<i>Carex diandra</i>	0	0	0	0	0.15	0.036
<i>Deschampsia cespitosa</i>	0	0	0.02	0.04	0.16	0.040
<i>Gymnocarpium dryopteris</i>	0.20	0	0.26	0.06	0.06	0.043

Table 2. Significant ($P < 0.05$) Indicator Values (0–1) of sampled plant species for the five sites sorted by increasing significance value

Note: In bold – the highest Indicator Value per species.

From the 32 understorey species with a significant Indicator Value, only two species were indicative of site N, in particular the target tree species *Fagus sylvatica* and non-target tree species *Prunus serotina*. 17 out of 32 species were characteristic to management option CCr. Four out of five target tree species showed a significant preference for this site. Furthermore, ten out of 32 species with a significant Indicator Value showed a preference for site PC, comprising the non-target tree species *Picea sitchensis*. Three out of 32 species were indicative for site M, including the non-target tree species *Picea abies*. The only species indicative for the management option of site CC was the fern species *Pteridium aquilinum* (Table 2).

Discussion

Tree regeneration

Abundance of tree saplings

Our first hypothesis can be partially confirmed. CCr management option substantially increased abundance of target tree saplings. CCr management resulted in an association of pioneer species following disturbance and indicates an accelerated process towards more natural forests compared to the other treatments (Raspé et al. 2000, Zerbe and Kreyer 2007). Especially, lying dead wood may have favoured a more heterogeneous and natural forest development, as proposed by other studies (Müller and Büttler 2010, Hage et al. 2019). Nevertheless, simultaneous abundance of non-target tree species should not be neglected and may also be an indication for the phenomenon of direct regrowth as suggested by other studies within the context of natural forest disturbances (Priewasser 2013, Kramer et al. 2014). Concerning beech regeneration, only few saplings were sampled beyond the near-natural beech forest. Generally, this species is highly dependent on the availability of seed-throwing trees in near proximity for regeneration due to its limited dispersal range (Wagner et al. 2011). As local seed trees are missing in the former spruce plantations, beech regeneration is particularly dependent on dispersal vectors (Wagner et al. 2010, Fischer et al. 2016), thus, colonisation may take substantial amount of time (Čavlović et al. 2008). Nevertheless, it has been demonstrated that this species is capable to establish spontaneously in former managed coniferous plantations even without directly adjacent seed trees (Zerbe and Kreyer 2007).

Height of tree saplings

Vertical growth of tree saplings likely proceeded at a slow rate as many saplings were below breast height. This study revealed that browsing had a tremendous hampering effect on tree regeneration, confirming findings by other authors (Ammer 1996, Zerbe and Kreyer 2007). Deer browsing may have had a pronounced inhibiting effect on the increment of target tree saplings due to its preference to forage on nitrogen-rich broadleaved species (Prien

1997). However, when focussing on species level, *Sorbus aucuparia* was significantly taller at site CCr compared to sites M and PC. This result probably underlines the species persistency to browsing damage as concluded from extensive research on browsing from anthropogenic coniferous forests in NE Germany (Nessing and Zerbe 2002). In addition, the abundance of *Alnus glutinosa*, which is the only species whose recruits exceeded breast height exclusively at site CCr, may indicate an accelerated development towards pioneer forest stage compared to the other sites. This assumption seems additionally convincing if one considers the species habitat requirements in relation to the site mean height above groundwater table, which is rather elevated compared to many sites (Figure suppl. 3). Although site CCr is quantitatively dominated by target tree species, a greater mean height of non-target tree species indicates that even this site may possibly be heading towards a stand development dominated by pre-disturbance species, i.e., spruce. However, the combination of pioneer and climax tree species appears to be the standard in early stages of succession after disturbance in Central European forests, also concluded by Priewasser (2013).

Browsing intensity of tree saplings

Surprisingly, browsing intensity at site CCr was not significantly different from site M as well as site PC, and was even higher compared to site N. The effect of lying dead wood to prevent browsing by herbivores may have thus been previously overestimated, as also supported by Kupferschmid and Bugmann (2005). Possibly, site CCr fulfils – besides diverse food supply – a shelter function for ungulates under disturbances (Reimoser and Gossow 1996) such as seasonal hunting or touristic activities within and adjacent to the Vorpommersche Boddenlandschaft National Park (LFG MV 2002) that may have led to increased browsing pressure. Nevertheless, browsing intensity was significantly most pronounced at site CC for both target and non-target tree saplings. This result is in accordance with other studies that assigned the greatest impact of game browsing to clear-cuts (Reimoser and Gossow 1996, Priewasser 2013). In contrast, the lowest browsing intensity at site N may be due to its scarce food supply for browsing herbivores and due to the hall-like forest structure that may not fulfil sufficient cover for ungulates (Reimoser and Gossow 1996).

Understorey species composition

Our second hypothesis can be confirmed. Understorey species composition was found to differ significantly among mature beech forest and all other sites, which is an indication that the recovery of understorey vegetation is not clearly quantifiable yet for none of the management options six years after silvicultural disturbance. The floristic similarity of sites M and PC, both simultaneously dissimilar to sites CC and CCr, demonstrates that rapid

changes in understorey species composition are highly affected by the method of conversion. This may especially be due to pronounced differences in light availability among the sites (Barbier et al. 2008). Our study indicates that sites with high light availability (CC, CCr) favoured the establishment of various light-demanding pioneer species, which is in accordance with other studies (Hannerz and Hännel 1997, Heinrichs and Schmidt 2009). The highest mean cover values of the herb and shrub layer at site CCr suggests an accelerated development towards pioneer forest stage compared to all other sites (Figure suppl. 5, 6). In contrast, our data showed that highly competitive and dominant bracken fern was strongly favoured by clear-cutting with timber removal and may have inhibited or decelerated growth of many other species. Other studies found that this species can dominate converted forest patches for decades that may potentially be predicted for site CC (Kupferschmid and Bugmann 2005, Royo and Carson 2006).

Site CCr was inhabited by many species typically abundant in acidic nutrient-poor beech forests, particularly the indicative graminoid *Molinia caerulea* (Berg et al. 2004). The herb *Trientalis europaea* as typical coniferous forest associate was shown to be outcompeted at site CCr. Furthermore, most sampled pioneer tree species and graminoids were found to be indicative for this site. In this regard, intermediate successional stages of beech forests in the Vorpommersche Boddenlandschaft National Park were described to comprise an increased percentage of *Sorbus aucuparia* and *Betula pendula* as well as various light-demanding species (LFG MV 2002). In addition, *Alnus glutinosa*, which is the only species whose recruits exclusively exceeded breast height at site CCr, may be considered as a key pioneer tree species that indicates an accelerated natural forest development. Overall, the abundance of dead wood may have facilitated a progression towards species composition most like natural forest communities, as proposed by other studies (Müller and Bütler 2010, Hagge et al. 2019). In contrast, both spruce species were found to be indicative for sites M (i.e., *Picea abies*) and PC (i.e., *Picea sitchensis*). These findings highlight the influence of adjacent seed trees on tree regeneration (Priewasser 2013), underline both site man-made character and questions the effectiveness of these management options.

Study limitations

Treatments not being replicated led to spatial nesting and pseudoreplication (Hurlbert 1984) in our sampling approach. Davies and Gray (2015) conclude that large-scale ecological experiments are often constrained by pseudoreplication, however, they may be valid if scientists integrate solutions to their experimental designs and statistical analyses. In this study, replication of the treatments was not feasible due to managerial limitations of the National Parks authorities. Thus, spatial nesting was partly dealt with by a statistical solution using linear mixed effect models with plot ID within site as random effect (Schielzeth and Na-

kagawa 2013, Bates et al. 2015). It was acknowledged that spatial nesting may limit statistical inference and to increase potentially limited reasoning a variety of plots per site were assessed. Here, we attribute the observed differences in tree regeneration and understorey species composition among the sites to the silvicultural treatments rather than due to differences in environmental site conditions. This is for instance corroborated by the BRT analyses, which revealed that soil pH values did not have measurable effects on tree regeneration. BRT also demonstrated that the relative deviation from mean abundance of target and mean height of non-target tree saplings was best explained by the silvicultural treatments among all tested parameters. Furthermore, browsing intensity was found to have a pronounced effect on the height of target tree saplings. However, absolute height above mean groundwater table was found to differ among the sites (Figure suppl. 3) and to affect the height of tree saplings (Figure 6). In this regard, additionally performed linear mixed-effect models that acknowledged height above groundwater table still revealed significant effects of the study sites on all tested environmental attributes (Table suppl. 4). Therefore, pronounced effects of the silvicultural treatments on tree regeneration and understorey vegetation are most likely, nonetheless, the influence of groundwater may not be entirely excluded from consideration.

Conclusion

This study suggests that the different silvicultural approaches for the conversion of spruce plantations towards native deciduous forests altered tree regeneration and understorey species composition. Natural regeneration of *Fagus sylvatica* in former spruce plantations, however, was not favoured by any treatment. Native pioneer tree saplings were most abundant at site CCr (clear-cutting with timber remaining) and indicate an accelerated development towards natural deciduous forests. Regardless, it must be stated that the detrimental influence of herbivore browsing on the increment of target tree saplings may currently outweigh the aforementioned accelerating effects. In terms of understorey species composition, the management options did not differ in mean similarity to reference site N (near-natural beech forest). However, site CCr appeared to anticipate a development towards a more natural forest compared to the other treatments in terms of both tree regeneration and understorey species composition. This study also exemplifies that clear-cutting with timber removal can lead to the dominance of competitive herbaceous species like bracken fern that can hamper forest development, potentially for decades. Continued monitoring and data analysis may reveal long-term effects of the different conversion approaches on natural forest development in former spruce plantations and may provide useful implications for further alternative forest management, particularly in national parks.

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Appendix: Supplemental material

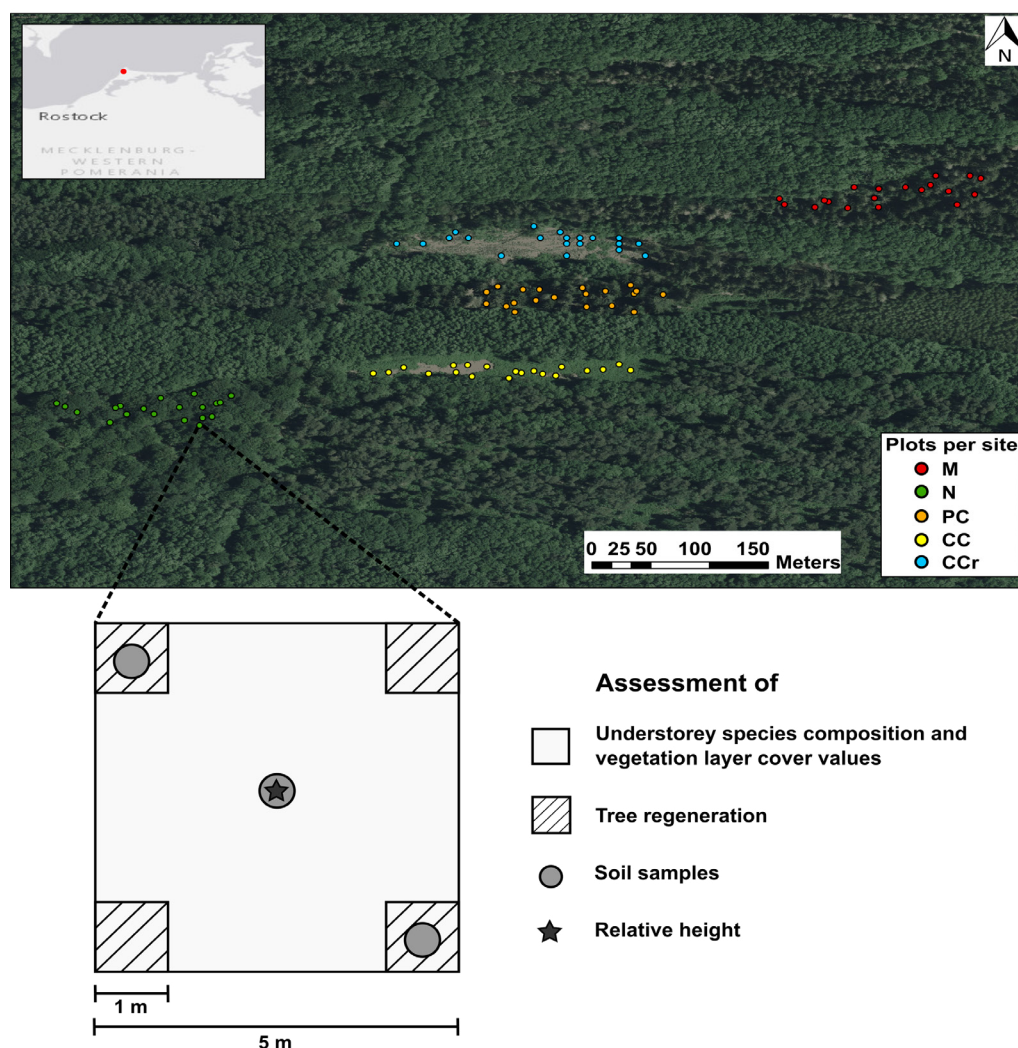


Figure suppl. 1. Location of the study area in Mecklenburg Western-Pomerania (upper left corner), arrangement of sampling plots per study site (upper extent) and the schematic design of an exemplary plot including assessed parameters (bottom extent)

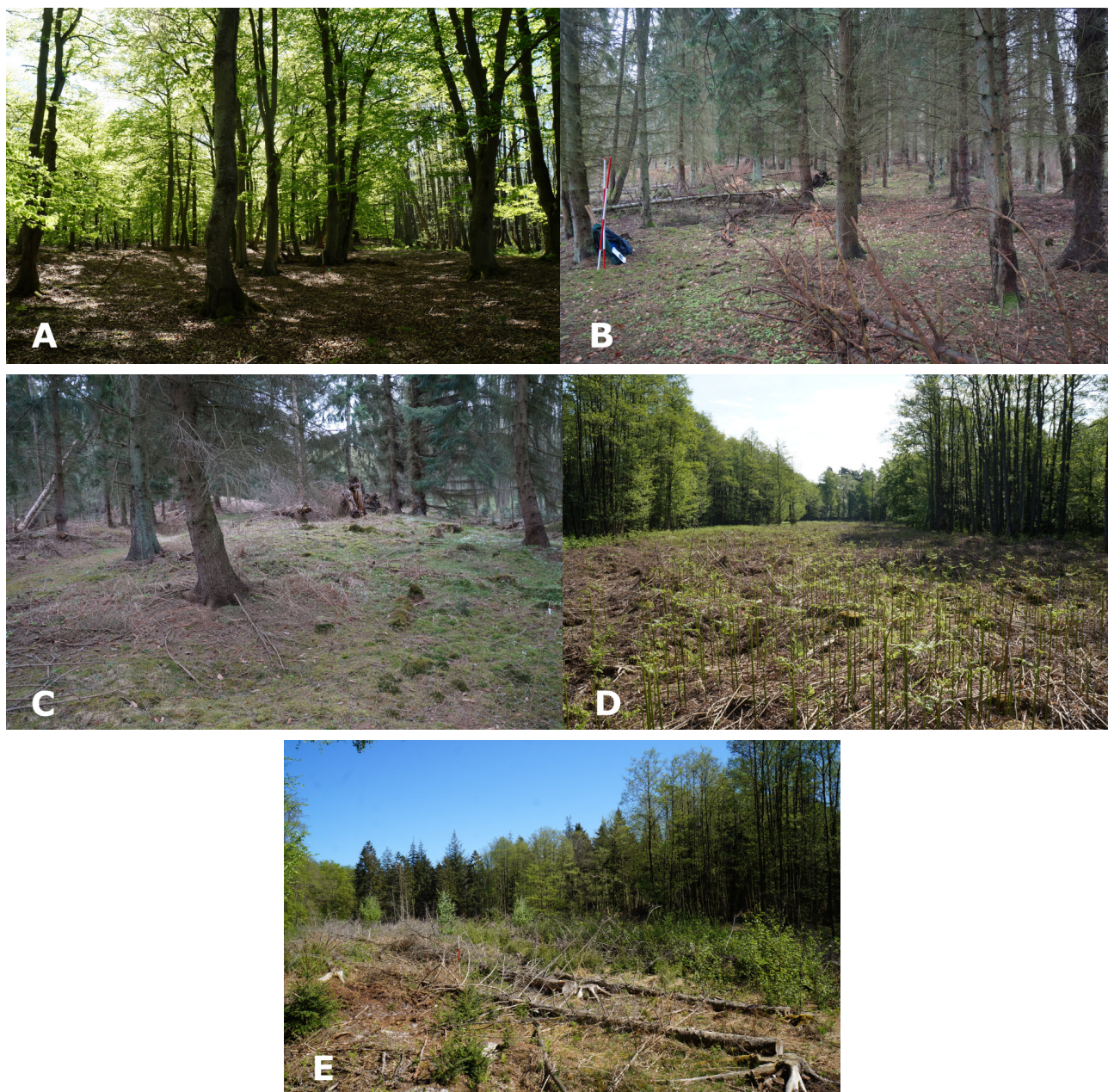


Figure suppl. 2. Overview picture of all different study sites taken in June 2018

Site N – near-natural beech forest (A), site M – unmanaged spruce plantation (B), site PC – partial-cutting (C), site CC – clear-cutting with timber removal (D), site CCr – clear-cutting with timber remaining (E).

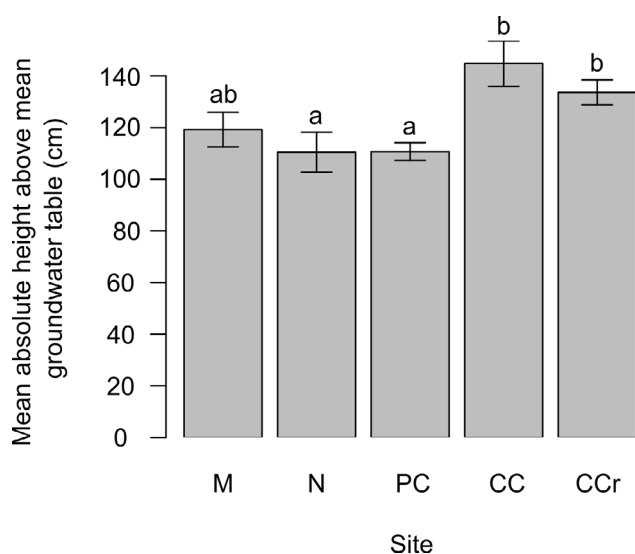


Figure suppl. 3. Mean absolute height above mean groundwater table (cm) with standard errors for coniferous reference (M), near-natural beech forest (N), partial-cutting (PC), clear-cutting with timber removal (CC) and clear-cutting with timber remaining (CCr)

Bars marked with different characters are significantly different (TukeyHSD post hoc comparisons).

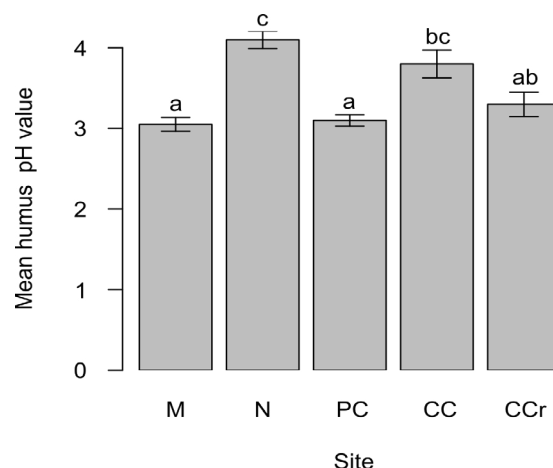


Figure suppl. 4. Mean humus pH value ($n = 25$) with standard errors for coniferous reference (M), near-natural beech forest (N), partial-cutting (PC), clear-cutting with timber removal (CC) and clear-cutting with timber remaining (CCr)

Bars with different letters are significantly different (TukeyHSD post hoc comparisons).

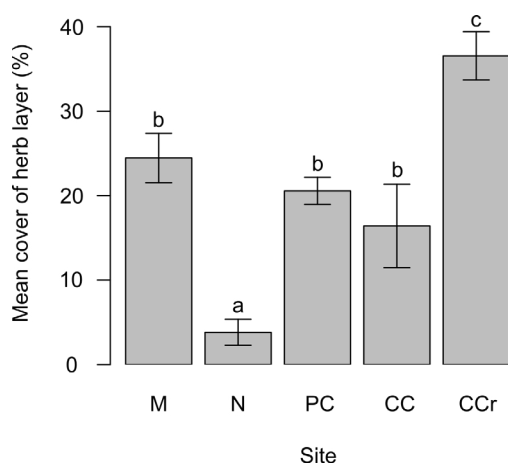


Figure suppl. 5. Mean cover of herb layer (%) with standard errors for coniferous reference (M), near-natural beech forest (N), partial-cutting (PC), clear-cutting with timber removal (CC) and clear-cutting with timber remaining (CCr)

Bars marked with different characters are significantly different (TukeyHSD post hoc comparisons).

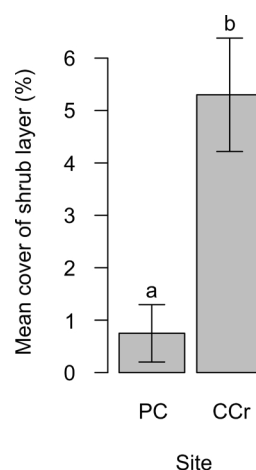


Figure suppl. 6. Mean cover of shrub layer (%) with standard errors for partial cutting (PC) and clear-cutting with timber remaining (CCr). Mean cover of shrub layer was not computable for the other sites due to non-existent shrub layer

Bars with different letters are significantly different (TukeyHSD post hoc comparisons).

Table suppl. 1. Effect of sites on environmental attributes, i.e. moss, herb, shrub and canopy as well as overall, dead wood and dead bracken fern cover, absolute height above mean groundwater table, humus pH and upper mineral soil pH detected by ANOVA

Response variable	Model and transformation	Df	F-value	p-value
Moss cover	Lm, rank	4	47.0	≤ 0.001 ***
Herb cover	Lm, rank	4	40.5	≤ 0.001 ***
Shrub cover	Lm, rank	4	34.9	≤ 0.001 ***
Canopy cover	Lm, rank	4	131.5	≤ 0.001 ***
Overall cover	Lm, rank	4	72.5	≤ 0.001 ***
Dead wood cover	Lm, rank	4	43.9	≤ 0.001 ***
Dead bracken fern cover	Lm, rank	4	29.6	≤ 0.001 ***
Absolute height above mean groundwater table	Lm, -	4	8.4	≤ 0.001 ***
Humus pH	Lm, rank	4	13.1	≤ 0.001 **
Upper mineral soil pH	Lm, -	4	1.3	0.289 ns

Note: The effects of sites on environmental attributes were tested using simple linear models (Lm). Significant effects are marked with asterisks: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

Table suppl. 2. The effect of sites on cover of each tree sapling species detected by ANOVA

Response variable	Df	F-value	p-value
<i>Alnus glutinosa</i>	4	46.2	≤ 0.001 ***
<i>Betula pendula</i>	4	47.0	≤ 0.001 ***
<i>Betula pubescens</i>	4	6.1	≤ 0.001 ***
<i>Fagus sylvatica</i>	4	29.9	≤ 0.001 ***
<i>Picea abies</i>	4	17.5	≤ 0.001 ***
<i>Picea sitchensis</i>	4	17.9	≤ 0.001 ***
<i>Pinus sylvestris</i>	4	6.8	≤ 0.001 ***
<i>Prunus serotina</i>	4	3.4	0.012 *
<i>Quercus robur</i>	4	2.4	0.059 ns
<i>Sorbus aucuparia</i>	4	15.3	≤ 0.001 ***

Note: Species-specific cover was tested using simple linear models with rank-transformed response variable. Significant effects are marked with asterisks: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.

Table suppl. 3. The effect of sites on the height of each tree sapling species detected by ANOVA

Response variable	NumDf	F-value	p-value
<i>Alnus glutinosa</i>	3	2.0	0.142 ns
<i>Betula pendula</i>	3	0.7	0.540 ns
<i>Betula pubescens</i>	1	0.1	0.821 ns
<i>Fagus sylvatica</i>	4	0.8	0.515 ns
<i>Picea abies</i>	3	36.9	≤ 0.001 ***
<i>Picea sitchensis</i>	2	10.0	≤ 0.001 ***
<i>Pinus sylvestris</i>	3	0.5	0.682 ns
<i>Sorbus aucuparia</i>	4	7.9	≤ 0.001 ***

Note: Species-specific heights among the five sites were tested using linear mixed-effect models using plot ID within site as random effect and rank-transformed response variable. Significant effects are marked with asterisks: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$. Tree species *P. serotina* and *Q. robur* were excluded due to deficient sample size.

Table suppl. 4. The effect of sites on environmental attributes, i.e. moss, herb, shrub and canopy as well as overall, dead wood and dead bracken fern cover, humus pH and upper mineral soil pH detected by ANOVA

Response variable	Model and transformation	Df	F-value	p-value
Moss cover	Lmer, rank	4	47.4	≤ 0.001 ***
Herb cover	Lmer, rank	4	40.5	≤ 0.001 ***
Shrub cover	Lmer, rank	4	41.2	≤ 0.001 ***
Canopy cover	Lmer, rank	4	131.5	≤ 0.001 ***
Overall cover	Lmer, rank	4	72.8	≤ 0.001 ***
Dead wood cover	Lmer, rank	4	43.9	≤ 0.001 ***
Dead bracken fern cover	Lmer, rank	4	29.6	≤ 0.001 ***
Humus pH	Lmer, rank	4	13.1	≤ 0.001 ***
Upper mineral soil pH	Lmer, rank	4	10.6	≤ 0.001 ***

Note: The effects of sites on environmental attributes were tested using linear mixed-effect models (Lmer) using absolute height above groundwater table within the site as random effect. Significant effects are marked with asterisks: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$.