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Understorey vegetation in young naturally regenerated and planted birch (*Betula* spp.) stands on abandoned agricultural land

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Abstract The abandonment of agricultural lands in Northern and Eastern Europe increases the area covered by first generation forests, which are either formed as an outcome of secondary succession or established as plantations. However, questions remain as to how these new stands develop and what kind of species they favour, which in turn has impacts on their ecological and economical value. Our aim was to compare understorey vascular plant and bryophyte vegetation characteristics between naturally regenerated and planted birch stands on abandoned agricultural sites in Estonia, focusing on the aspects of species richness and forest understorey recovery. Species richness and diversity of vascular plants were similar in both stand types but the number of forest vascular plant species was significantly higher in naturally regenerated stands. The bryophyte layer of naturally regenerated stands had a higher species richness, diversity, and number of forest bryophyte species. The higher number of forest vascular plant and bryophyte species in naturally regenerated stands can be explained by the longer undisturbed succession period. The recovery of the forest understorey was unaffected by former agricultural land use (crop field or grassland). The influence of soil properties on the recovery of the forest understorey was not detected, but the number of vascular plant species that grow in forests as well as in grasslands was negatively correlated with distance from forest. Overall, understorey vegetation of natural and planted birch stands did not reveal substantial differences. However, in the case of vigorous natural birch regeneration in the vicinity of forest land, unassisted reforestation should be favoured.

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Introduction

Transitions in land use that result in deforestation for agriculture, or in reforestation of abandoned agricultural lands have taken place throughout the history of human society (Mather and Needle 1998; Lambin and Meyfroidt 2011). Since the nineteenth century, forest transition (a shift from net deforestation to net reforestation) has occurred at different times via assisted or unassisted reforestation in most European countries, as well as in several other countries of the World (Meyfroidt and Lambin 2011). Generally the effect of land use change in the future biodiversity scenarios of terrestrial ecosystems is considered to be crucial (Sala et al. 2000).

One of the most recent examples of forest transition was initiated during the last decades of the twentieth century in Northern and Eastern Europe, when a considerable area of agricultural land was abandoned for socio-economic reasons (Peterson and Aunap 1998; Kuemmerle et al. 2011; Alcantara et al. 2012). In such areas of hemiboreal Estonia, the secondary succession of vegetation that takes place after abandonment leads to the creation of forests with pioneer tree species such as *Betula* spp. among the first arrivers. However, the inclusion of woody species could be slow when herbaceous plants exhibit intensive growth. Birches (*Betula pendula* Roth and *B. Pubescens* Ehrh.) are the most widespread and economically significant deciduous trees in this region (Hynynen et al. 2010). These species have also been used for the establishment of forest plantations on abandoned agricultural lands (Johansson 1999; Liepins 2007). There has been a recent increase in the demand for woody biomass as a renewable energy and pulpwood resource, as well as in the establishment of plantations of fast-growing deciduous trees in Northern and Eastern Europe.

Only a few studies have compared the understorey vegetation characteristics between naturally regenerated and planted stands on abandoned agricultural sites (Aubin et al. 2008; Zhang et al. 2010; Boothroyd-Roberts et al. 2013). The establishment of a monospecific even-aged tree layer, together with silvicultural treatments used for plantation management (e.g. site preparation) creates homogeneous habitat for the understorey. In natural succession, the establishment of woody species has shown a mosaic pattern, creating more heterogeneous conditions for the understorey (Ruskule et al. 2012). Therefore, differences might be expected in the understorey vegetation characteristics of plantations and naturally regenerated stands. In former mining areas in Europe the processes of active reforestation (establishment of plantations) and unassisted natural succession have repeatedly been compared in terms of biomass production and understorey vegetation characteristics (e.g. Prach and Pyšek 2001; Luud and Pensa 2004; Pensa et al. 2004; Tropek et al. 2010), leading to the conclusion that spontaneous succession has its advantages. Besides low establishment costs, spontaneously revegetated sites have exhibited higher natural value (Prach and Pyšek 2001), supporting more diverse vegetation (Pensa et al. 2004), higher species richness and diversity (Hodačova and Prach 2003), and a higher proportion of rare and endangered species (Tropek et al. 2010; Prach et al. 2011). Nevertheless, there are opposite examples; the planting of pine species increased the understorey plant diversity in comparison with unplanted control areas in a degraded Mediterranean kermes oak shrubland (Ganatsas et al. 2012). Regarding tree layer, stand growth and yield characteristics are often better in plantations established with previously selected planting material than in naturally regenerated stands.

In addition to species richness and diversity, species composition is another important aspect that helps to evaluate the vegetation cover. The formation of the tree layer should be accompanied by the gradual recovery of a unique forest understorey. The understorey of recent forest growing on former agricultural land differs from the understorey of forest that was never cleared (Flinn and Vellend 2005; Flinn and Marks 2007), since in young forest the proportion of forest species is low. As migration rates of forest species are usually quite low, distance to propagule sources is an important factor affecting the recovery of the understorey (Dzwonko and Loster 1992; Brunet and von Oheimb 1998; Brunet et al. 2000; Dzwonko 2001; Graae et al. 2003).

Several studies have demonstrated that understorey vegetation characteristics, especially species composition in the forest growing on former agricultural sites, is also influenced by the type of former agricultural use (field or grassland) (Koerner et al. 1997; Wulf 2004; Brunet 2007; Kopecký and Vojta 2009; Soo et al. 2009). The recovery of the forest understorey may be quicker in former grasslands, as a number of forest species often survive with small populations in pastures and meadows, while the colonization of forest species to former crop fields starts only after the cessation of cultivation (Wulf 2004).

Soil chemical properties may also affect the understorey of young forests (Honnay et al. 1999; De Keersmaeker et al. 2004; Graae et al. 2003). Studies from Belgium (Honnay et al. 1999; De Keersmaeker et al. 2004) indicated that soil phosphate content may have an indirect negative effect on the number of forest species, as it stimulates vigorous vegetation development leading to the exclusion of forest species by competitive species. On the other hand Graae et al. (2003) found in a study conducted in Danish oak and beech forests that, instead of soil conditions, limited seed dispersal of forest species was the critical factor explaining the slow migration of some ancient forest species.

The aim of this study was to compare understorey vascular plant and bryophyte vegetation characteristics in planted and naturally regenerated birch stands on abandoned agricultural sites in Estonia and to determine if the recovery of the forest understorey occurs similarly in both stand types. Distance to the nearest forest, the type of former land use, the concentrations of major mineral nutrients and the acidity of the soil humus horizon, the litter layer and overstorey stand characteristics were included as possible factors explaining the variation in understorey vegetation characteristics and the occurrence of forest species.

The following hypothesis was formulated: understorey vegetation of naturally regenerated birch stands is more diverse and supports higher species richness compared to planted stands.

Materials and methods

Study area

The study was conducted in Estonia, which belongs to the hemiboreal forest zone and northern temperate climate zone. Floristic data were collected from 11 silver birch (*Betula pendula* Roth.) plantations and in 11 naturally regenerated birch (*B. pendula* Roth. and *B. pubescens* Ehrh.) stands where 22 experimental plots (each 0.1 ha in size) had been previously created in order to study stand growth and biomass productivity (Vares 2005), (Fig. 1; Table 1). All stands are growing on former agricultural lands that had been

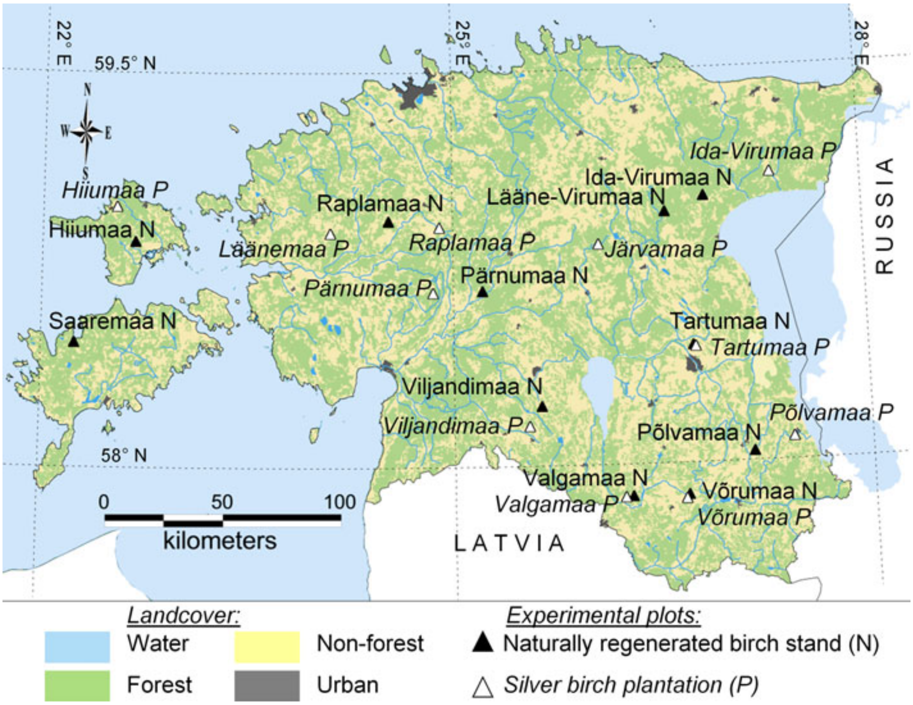

Fig. 1 Locations of the studied birch stands

abandoned in the 1990s. All silver birch plantations were established in 1999 with 1-year-old seedlings. Floristic data analysed in the current study were collected during July of the 13th growing season in 2011. The approximate age of naturally regenerated birch stands at the time of floristic data collection varied between 14 and 20 years, based on an earlier survey of these stands (Vares 2005), although younger birch trees were also present. In every experimental plot, the stem diameter at breast height (DBH) of all the trees was measured and basal area (BA) per hectare was estimated (Table 1). In natural birch stands other tree species were also represented and usually formed the second layer under birches (Table 1). Growing stock and biomass production of planted and natural birch stands was estimated and the respective results are presented in Lutter et al. (2012). In natural birch stands, usually one precommercial and one commercial thinning had been carried out, whereas no management activities had been undertaken in silver birch plantations, except Läänemaa plantation, where light thinning had been done. Using aerial photos (Estonian Land Board 2012), distance from experimental area to the nearest forest was estimated. The type of former agricultural land use (field or grassland) was determined on the basis of personal communication with landowners.

Four vegetation plots (each 2 × 2 m) were created in every experimental plot. In every vegetation plot a list of vascular plant and bryophyte species was compiled, including tree saplings growing in the field layer (defined as the herb and small shrub layer). The total percentage cover of the field layer and bryophyte layer and the percentage cover of individual species were visually estimated, using the scale of 1–100 %. Additionally a list of bryophyte species growing on the trunks of 4 trees situated near the corners of every vegetation plot was compiled. Bryophytes that could not be identified in field conditions were collected for

Table 1 Characteristics of the studied birch stands (distance: distance from the nearest forest, DBH: stem diameter at breast height, BA: basal area; M: volume)

Stand	General		Main tree layer					Secondary tree layer						Total	
	Previous land use	Distance, m	Density, trees ha^{-1}	Height, m	DBH, cm	BA, m^2 m^{-2}	M, m^3 ha^{-1}	Tree spp.	Density, trees ha^{-1}	Height, m	DBH, cm	BA, m^2 m^{-2}	M, m^3 ha^{-1}	BA total	M total
Silver birch plantations															
Hiiumaa	Field	100	1,520	4.7	3.7	2.0	7.7	–						2.0	7.7
Ida-Virumaa	Grassland	40	2,430	11.8	8.5	15.8	95.0	–						15.8	95.0
Järvamaa	Grassland	80	1,760	11.4	9.2	12.8	74.8	–						12.8	74.8
Läänemaa	Grassland	35	1,362	13.5	12.1	16.3	108.3	–						16.3	108.3
Põlvamaa	Field	20	1,960	12.8	9.2	13.4	85.8	–						13.4	85.8
Pärnumaa	Field	400	2,800	11.3	7.8	15.6	90.6	–						15.6	90.6
Raplamaa	Field	250	2,700	12.2	8.6	17.4	107.1	–						17.4	107.1
Tartumaa	Field	60	1,130	10.9	9.4	8.4	47.9	–						8.4	47.9
Valgamaa	Field	40	1,760	10.2	7.1	7.7	41.7	–						7.7	41.7
Viljandimaa	Grassland	150	1,550	12.9	10.5	13.8	88.8	–						13.8	88.8
Võrumaa	Grassland	40	1,740	10.2	8.5	11.0	59.5	–						11.0	59.5
Naturally regenerated birch stands															
Hiiumaa	Grassland	200	5,725	10.5	6.2	20.1	111.0	–						20.1	111.0
Ida-Virumaa	Grassland	100	1,820	9.4	7.3	8.9	45.8	*P. a.*[a]	400	5.3	5.0	0.8	0.6	9.7	46.4
Läänemaa	Grassland	30	3,475	12.0	7.5	16.6	100.5	*P. a.*	7,200	2.3	2.0	2.3	3.9	18.9	104.4
Põlvamaa	Field	40	4,358	11.5	6.8	17.8	104.4	*P. a.*	9,000	2.5	2.0	2.8	3.9	20.6	108.3
Pärnumaa	Grassland	15	9,067	8.7	4.6	16.6	82.3	*P. a.*	11,600	1.6	0.5	0.2	1.5	16.8	83.8
Raplamaa	Field	290	2,638	12.0	9.0	18.8	114.1	*P. a.*	2,500	2.0	1.5	0.4	1.2	19.2	115.3
Saaremaa	Grassland	30	2,844	5.2	2.5	1.6	25.0	*A. i.*[b]	14,000	7.5	6.5	46.5	186.6	48.1	211.6
Tartumaa	Field	155	1,987	11.2	8.8	13.6	78.4	–						13.6	78.4

Table 1 continued

Stand	General		Main tree layer					Secondary tree layer						Total	
	Previous land use	Distance, m	Density, trees ha^{-1}	Height, m	DBH, cm	BA, m^2 m^{-2}	M, m^3 ha^{-1}	Tree spp.	Density, trees ha^{-1}	Height, m	DBH, cm	BA, m^2 m^{-2}	M, m^3 ha^{-1}	BA total	M total
Valgamaa	Grassland	110	2,570	14.2	10.1	22.5	156.7	*P. a.*	2,500	1.7	0.5	0.05	0.3	22.5	157.0
Viljandimaa	Grassland	40	2,773	11.8	7.3	12.9	77.2	*P. a.*	800	0.7				12.9	77.2
Võrumaa	Grassland	90	2,204	13.6	9.4	17.1	114.4	*P. a.*	22,000	2.0	1.5	3.9	10.6	21.0	125.0

[a] *Picea abies*; [b] *Alnus incana*

further investigation under a microscope. The nomenclature follows the keybooks of Estonian vascular plants (Leht 1999) and bryophytes (Ingerpuu and Vellak 1998).

Leaf and branch litter was collected by hand from two subplots (each 20 × 20 cm) located at opposite sides of a vegetation plot. From the same subplots, soil samples were taken from the middle of the humus horizon. Composite samples of litter and soil from each vegetation plot were taken for laboratory analyses. Litter samples were dried at +70 °C to constant weight and weighed to the nearest 0.001 g. Litter estimates (t ha^{-1}) were then calculated for each vegetation plot. The total N in soil samples was determined by the Kjeldahl procedure using method ISO 11261 (1995). To analyse available P and K in the soil, Mehlich 3 extractant was used. Soil pH was measured in 1 M KCl at a 10 g: 25 ml ratio using method ISO 10390 (2005).

Hemispherical (fisheye) photos were taken from the centre of each vegetation plot above the understorey vegetation layer (approximately 50 cm height) using Sigma 8 mm 1:3.5 EX DG FISHEYE lens attached to a Canon EOS 5D digital camera (Canon USA, Inc., NY, USA). The photos were analysed with Gap Light Analyzer 2.0 (Frazer et al. 1999) to estimate canopy openness and the amount of below-canopy (transmitted) direct, diffuse, and total solar radiation incident on a horizontal receiving surface.

Data analysis

Floristic diversity indices

Estimates of species richness of vascular plants (S_{VP}) and bryophytes growing on the ground (S_{B_ground}) and Simpson's diversity index (D'_{VP}, D'_{B_ground}) were calculated for all vegetation plots. In the case of bryophytes growing on the trunks of trees, only species richness (S_{B_trunk}) was estimated. Species richness of bryophytes (S_B) was estimated on the basis of combined data of bryophytes growing on the ground and on tree trunks.

In order to analyse the pairwise relations between species richness, coverage and diversity estimates within the whole univariate dataset, where some non-normality was detected, Spearman correlation coefficients were computed.

Floristic composition

Based on the BIOFLOR database (Klotz et al. 2002) and the Estonian keybook of vascular plants (Leht 1999), vascular plant species were classified by habitat preference into the following categories: forest species, grassland species, fallow species, species growing in forests as well as in grasslands and species growing in grasslands as well as in fallows. Habitat preference of bryophyte species (forest species, grassland species and species growing in forests and in grasslands) was determined based on Ingerpuu et al. (1994). Frequency estimates of bryophytes were determined based on Ingerpuu et al. (2011).

Detrended Correspondence Analysis (DCA, Hill 1979) was applied with default options using PC-ORD v.4 (MjM Software, Gleneden Beach, Oregon, USA); species with less than two occurrences were excluded.

In order to assess species association with stand type (plantations or naturally regenerated stand), Indicator Species Analysis (Dufrêne and Legendre 1997) was performed, including species present in at least eight vegetation plots. Since bryophytes and vascular plants may respond differently to environmental factors (Herben 1987; Ingerpuu et al. 1998, 2001, 2003; Hokkanen 2006), vascular plant and bryophyte data were analysed separately. Combined data of ground and trunk bryophytes was used for ordination where the coverage of trunk bryophytes was considered to be 1 %. The scores of the first three DCA axes were used in further analysis.

In order to understand the ecological data underlying the DCA axes scores, Spearman rank correlations (r_s) were computed with continuous site variables. The effect of discrete factors (stand type and previous land use) on vegetation plot level DCA scores was checked using proc MIXED with SAS for Windows 9.1.3 (SAS Institute Inc., Cary, NC, USA), where experimental plot was treated as a random variable.

Modeling the effect of multiple factors on floristic attributes

Our principal aim was to analyse the effect of stand type (natural or planted) on a number of floristic variables. Being aware of many other factors that potentially might influence these attributes, we included several soil- and overstorey-related variables as explanatory confounders to the model. Stand basal area was considered as the main characteristic of the overstorey effect. Multicollinearity of the continuous explanatory variables was checked based on squared Spearman rank correlations (r_s^2). The results indicated that understorey light characteristics were strongly intercorrelated ($r_s^2 \approx 0.9$) and it was decided to use only total transmitted radiation for modelling.

There were no other strongly ($r_s^2 > 0.5$) correlated variables and they were all included as confounding covariates to the model analysing the effect of stand origin (planted or natural) and previous agricultural land use (grassland or crop field) on species richness and coverage estimates of the understorey vegetation layer.

A generalized linear mixed model with SAS proc GLIMMIX was applied to test the significance of the fixed effects of stand type and independent confounders on floristic attributes. As data was hierarchical (containing both vegetation plot and stand experimental plot level estimates), experimental plot was treated as a random effect. Species richness estimates were treated as response variables with Poisson distribution, while for coverage estimates and diversity indices, Gaussian distribution was used. The assumption of normal distribution of model errors was checked.

Results

Stand and site characteristics

The comparison of stand and site characteristics between naturally regenerated and planted birch stands revealed some significant differences (Table 2). The most significant difference was in the amount of branch litter and thinning residues, and this was three times higher in natural stands compared to plantations where no thinnings had been carried out, and grounded branches originated entirely from litter. As an exception, in the Läänemaa plantation a light thinning had been performed, however the owner had left only minor residues on site, resulting in a just slightly above average estimate of branch litter (1.66 t ha^{-1}). The average amount of leaf litter was similar in both stand types. The mean DBH of birches was higher in plantations, but as natural stands were significantly denser, there was no difference in basal area and volume of the birch layer. In the majority of natural stands a second layer of *Picea abies* had formed, resulting in a higher total basal area. As an exception, *Alnus incana* had overgrown birches in the Saaremaa stand. Canopies had almost entirely closed and light conditions of the understorey layer were

Table 2 Stand and site characteristics (±standard error, range in brackets) and the significance of stand type effect on these variables based on one-way ANOVA for stand-level variables and MIXED model (with stand as random variable) for vegetation plot-level variables

Characteristic	Stand type		Stand type effect, p value
	Plantations	Natural stands	
Determined at stand (0.1 ha experimental plot, $n = 22$) level			
Distance from forest (m)	110 ± 35 (20–400)	100 ± 26 (15–290)	0.814
Main (birch) layer[a]			
Tree density (trees ha^{-1})	1,919 ± 176 (1,130–2,800)	3,587 ± 646 (1,820–9,067)	**0.028**
Height (m)	11.7 ± 0.4 (10.2–13.5)	10.9 ± 0.7 (5.2–14.2)	0.361
DBH (cm)	9.1 ± 0.4 (7.1–12.1)	7.2 ± 0.7 (2.5–10.1)	**0.035**
Basal area (m^2 ha^{-1})	13.2 ± 1.0 (7.7–17.4)	15.1 ± 1.8 (1.6 ± 22.5)	0.371
Stand volume (m^3 ha^{-1})	80.0 ± 7.4 (41.7–108.3)	91.8 ± 10.8 (25–156.7)	0.387
Whole stand (main and secondary layer)[a]			
Basal area (m^2 ha^{-1})	13.2 ± 1.0 (7.7–17.4)	20.3 ± 3.0 (9.7–48.1)	**0.046**
Stand volume (m^3 ha^{-1})	80.0 ± 7.4 (41.7–108.3)	110.8 ± 13.4 (46.4–211.6)	0.065
Determined at vegetation plot (2 × 2 m, $n = 88$) level			
Leaf litter (t ha^{-1})	1.24 ± 0.16 (0.05–4.25)	1.91 ± 0.38 (0.04–9.23)	0.412
Branch litter (t ha^{-1})	1.11 ± 0.12 (0–3.00)	3.41 ± 0.32 (0.36–10.38)	**<0.001**
Soil humus horizon properties			
pH_{KCl}	5.5 ± 0.2 (3.9–7.3)	5.0 ± 0.1 (3.9–7.3)	0.212
Total N (%)	0.16 ± 0.01 (0.09–0.27)	0.13 ± 0.01 (0.06–0.29)	0.236
P (mg kg^{-1})	97.0 ± 13.9 (12.5–372.5	70.3 ± 7.5 (7.5–191)	0.418
K (mg kg^{-1})	141.3 ± 10.6 (18.5–289.0)	105.8 ± 11.2 (13.0–289)	0.269
Understorey light conditions			
Canopy openness (%)	13.9 ± 2.3 (3.8–67.7)	10.3 ± 0.7 (2.6–19.6)	0.459
Transmitted solar radiation			
Direct (mol m^{-2} d^{-1})	1.6 ± 0.3 (0.2–7.9)	1.2 ± 0.1 (0.2–2.6)	0.619
Diffuse (mol m^{-2} d^{-1})	2.1 ± 0.3 (0.7–9.2)	1.8 ± 0.1 (0.5–3.6)	0.682
Total (mol m^{-2} d^{-1})	3.7 ± 0.6 (1.0–16.9)	3.1 ± 0.2 (0.8–5.8)	0.650

Bold indicates significant ($p < 0.05$) effects

[a] Excluding Hiiumaa plantation, as a considerably slower growing plantation, from the comparison of stand growth characteristics

similar in both stand types. Concentrations of main mineral nutrients and the pH of the soil humus horizon were also similar in both stand types.

Species richness and diversity

Altogether 145 vascular plant species and 17 specimens identified at the genera level were found in 88 vegetation plots. Ninety-eight vascular plant species were found growing in silver birch plantations and 116 species in naturally regenerated birch stands; the number of species present in both stand types was 69. Fifty-five percent of the species that were found only in naturally regenerated stands were forest or forest and grassland species; the corresponding figure for plantations was 16 %. Rare and protected species (*Carex* *brizoides, Festuca altissima and Platanthera* sp.) grew on four experimental plots all situated in naturally regenerated stands.

Forty-five bryophyte species were found growing on the ground and on the trunks of bordering trees. Among them 35 bryophyte species were growing on the ground and 24 bryophyte species were growing on trunks, 10 species were found only on trunks. Twenty-five bryophyte species were found growing in silver birch plantations and 36 species in naturally regenerated birch stands; the number of species present in both stand types was 16. The majority of bryophyte species were either very frequent or frequent in Estonia; no rare species were found.

The mean number of vascular plant species in one stand (based on four vegetation plots) was similar in plantations and natural stands (Table 3, one-way ANOVA $F_{1,20} = 0.17$, $p = 0.898$). Vegetation plot-level estimates of S_{VP}, D'_{VP} and C_{VP} were also not affected by stand type (Table 4). The mean number of bryophyte species was significantly higher in naturally regenerated birch stands (Table 3, one-way ANOVA $F_{1,20} = 13.42$, $p = 0.002$). S_{B_ground}, D'_{B_ground} and S_B per vegetation plot were also higher in natural stands (Tables 3, 4). S_{B_trunk} and C_{B_ground} did not differ between silver birch plantations and naturally regenerated birch stands. S_{VP} was negatively affected by tree leaf litter, but other site variables did not significantly affect richness and diversity estimates (Table 4). Pair-wise correlations among vascular plant and bryophyte layer characteristics revealed a negative relationship between S_B and C_{VP} ($r_s = -0.37$, $p < 0.001$) and a positive correlation between S_B and C_B ($r_s = 0.47$, $p < 0.001$).

DCA ordination

Axis 1 scores of DCA ordination of vegetation plots with vascular plant data were significantly affected by stand type (Table 5), with silver birch plantations converged to the left side of the axes (Fig. 2). Plot and species scores of natural stands were generally more dispersed. Axis 1 scores correlated positively with stand basal area and litter characteristics and negatively with soil nutrients (Table 6). DCA2 and DCA3 scores were weakly related with distance from forest.

Table 3 Richness (S), coverage (C) and diversity (D') estimates of vascular plants (VP) and bryophytes (B) in the studied birch stands

	Plantations			Natural stands		
	Mean ± SE	Min	Max	Mean ± SE	Min	Max
S_{VP}	12.84 ± 0.73	1	22	13.20 ± 0.91	3	28
S_{VP_4plots}	24.00 ± 1.67	14	30	24.36 ± 2.26	12	36
D'_{VP}	0.70 ± 0.03	0.00	0.94	0.69 ± 0.03	0.05	0.94
C_{VP} (%)	44.09 ± 3.27	2	88	39.07 ± 2.99	1	85
S_B	2.80 ± 0.24	0	7	5.36 ± 0.27	2	9
S_{B_4plots}	6.55 ± 0.74	2	10	10.18 ± 0.66	8	14
S_{B_ground}	1.95 ± 0.17	0	5	4.00 ± 0.29	0	8
S_{B_trunk}	1.43 ± 0.23	0	5	2.36 ± 0.22	0	6
D'_{B_ground}	0.39 ± 0.04	0.00	0.75	0.65 ± 0.03	0.00	0.86
C_B (%)	4.70 ± 0.95	0	25	8.86 ± 1.53	0	40

The effect of stand type on these variables is characterised in Table 4 and in the text

Table 4 Significance (*p* values, type 3 effects) of the factors contributing to species richness (S), diversity (D') and coverage (C) estimates of vascular plants (VP) and bryophytes (B) according to the GLIMMIX model

Factor	Vascular plants								Bryophytes							
	S_{VP}	D'_{VP}	S_{VP_forest}	S_{VP_forest} grassland	$S_{VP\_grassland}$	$S_{VP\_grassland}$ fallow	S_{VP_forest}	C_{VP}	S_B	S_{B_ground}	D'_{B_ground}	C_{B_ground}	S_{B_trunk}	S_{B_forest}	S_{B_forest} grassland	$S_{B\_}$ grassland
Stand type																
(Plantation)	0.498	0.927[a]	**0.014**[a]	0.328[a]	0.288	0.554[a]	**0.014**[a]	0.627	**0.001**[a]	**0.001**[a]	**0.001**[a]	0.241[a]	0.145[a]	**<0.001**[a]	0.126[a]	0.355
(Natural)	–	–	–	–	–	–	–			–	–	–	–	–	–	–
Former land use																
(Field)	0.632[a]	0.779[a]	0.826	0.918	0.651[a]	0.462	0.826	0.603[a]	0.737[a]	0.322	0.128	0.962	0.055[a]	0.437[a]	0.906[a]	0.102
(Grassland)	–	–	–	–	–	–	–			–	–	–	–	–	–	–
Distance	0.828	0.445	0.232	**0.031**[a]	0.576[a]	0.428	0.232	0.887[a]	0.564[a]	0.488[a]	0.360[a]	0.375	0.496	0.638	0.158[a]	0.732[a]
Basal area	0.475	0.970	0.275	0.062	0.877	0.777[a]	0.275	0.282	0.121[a]	0.112[a]	0.205[a]	0.857	0.102[a]	0.233[a]	0.092[a]	0.091
Transmitted total radiation	0.885a	0.544[a]	0.573[a]	0.308[a]	0.918[a]	0.626[a]	0.573[a]	0.099	0.210[a]	0.103[a]	0.145[a]	0.650	0.341[a]	0.174[a]	0.258[a]	0.066
Leaf litter	**0.030**[a]	0.096[a]	0.294[a]	0.312[a]	**0.034**[a]	0.185[a]	0.294[a]	0.085[a]	0.631	0.601[a]	0.932[a]	0.528[a]	0.407	0.517	0.853[a]	0.285
Branch litter	0.909	0.507[a]	0.478	0.992	0.340[a]	0.346[a]	0.478	0.074[a]	0.525	0.479	0.712[a]	0.896	0.598	0.831	0.362	0.905[a]
Soil N	0.414	0.374	0.838[a]	0.573	0.216	0.628[a]	0.838[a]	0.555[a]	0.642	0.308	0.067	0.735[a]	0.286[a]	0.935[a]	0.556	0.858[a]
Soil P	0.996	0.810[a]	0.345	0.879[a]	0.808[a]	0.631[a]	0.345	0.296[a]	0.302	0.641	0.769	0.551[a]	0.243	0.352	0.257	0.336[a]
Soil K	0.315[a]	0.446[a]	0.148[a]	0.721[a]	0.708[a]	0.689	0.148[a]	0.208	0.820	0.575[a]	0.578[a]	0.663	0.852	0.576	0.850[a]	0.659[a]
Soil pH	0.406[a]	0.635[a]	0.526[a]	0.073[a]	0.353[a]	0.510	0.526[a]	0.915[a]	0.112	0.122	0.752	0.347	0.148	0.210	0.102	0.184[a]

Bold indicates significant ($p < 0.05$) effects

[a] Negative effect

Table 5 The effect of stand type and former land use on vegetation plot-level DCA scores, based on the MIXED model with experimental plot (stand) as random effect

	Stand type (plantation–natural)	*p* value	Former land use (field–grassland)	*p* value
Vascular plants				
$DCA1_{VP}$	−113.6	**0.021**	−31.9	0.549
$DCA2_{VP}$	−64.4	0.111	−27.9	0.509
$DCA3_{VP}$	13.8	0.631	−22.24	0.446
Bryophytes				
$DCA1_{B}$	58.9	**0.012**	11.2	0.661
$DCA2_{B}$	21.8	0.103	19.9	0.145
$DCA3_{B}$	40.3	0.107	47.8	0.055

Bold indicates significant ($p < 0.05$) effects

Axis 1 of DCA ordination with bryophyte data also separated naturally regenerated stands and plantations, and this effect was stronger than in the case of vascular plants (Table 5; Fig. 3). The influence of land use history remained insignificant (Table 5). In addition, bryophyte DCA scores were significantly affected by overstorey stand growth (basal area, branch litter), transmitted solar radiation and soil pH and K (Table 6).

Fig. 2 DCA ordination of vegetation plots and vascular plant species (axis 1 Eigenvalue = 0.82, axis 2 Eigenvalue = 0.63); ellipses indicate 75 % range of the plot scores. Abbreviations: Acer pla *Acer platanoides*, Achi mil *Achillea millefolium*, Aego pod *Aegopodium podagraria*, Agro cap *Agrostis capillaris*, Agro gig *A. gigantea*, Alch vul *Alchemilla vulgaris* (coll.), Alnu inc *Alnus incana*, Alop pra *Alopecurus pratensis*, Anem nem *Anemone nemorosa*, Ange syl *Angelica sylvestris*, Anth odo *Anthoxanthum odoratum*, Anth syl *Anthriscus sylvestris*, Arte vul *Artemisia vulgaris*, Betu pen *Betula pendula*, Betu pub *B. pubescens*, Cala aru *Calamagrostis arundinacea*, Cala can *C. canescens*, Cala epi *C. epigeios*, Camp glo *Campanula glomerata*, Camp lat *C. latifolia*, Camp pat *C. patula*, Care hir *Carex hirta*, Care lep *C. leporina*, Care mon *C. montana*, Care pal *C. pallescens*, Care sp *C. sp*, Care vag *C. vaginata*, Cera fon *Cerastium fontanum*, Cirs arv *Cirsium arvense*, Cirs ole *C. oleraceum*, Dact glo *Dactylis glomerata*, Desc ces *Deschampsia caespitosa*, Dryo car *Dryopteris carthusiana*, Elym rep *Elymus repens*, Epil ang *Epilobium angustifolium*, Epil mon *E. montanum*, Equi arv *Equisetum arvense*, Equi pra *E. pratense*, Fall con *Fallopia convolvulus*, Fest pra *Festuca pratensis*, Fest rub *F. rubra*, Fili ulm *Filipendula ulmaria*, Frag ves *Fragaria vesca*, Fran aln *Frangula alnus*, Frax exc *Fraxinus excelsior*, Fuma off *Fumaria officinalis*, Gale sp *Galeopsis sp*, Gale tet *G. tetrahit*, Gali alb *Galium album*, Gali uli *G. uliginosum*, Gera pal *Geranium palustre*, Geum riv *Geum rivale*, Geum urb *G. urbanum*, Hier umb *Hieracium umbellatum*, Holc lan *Holcus lanatus*, Hype mac *Hypericum maculatum*, Hype per *H. perforatum*, Impa n-t *Impatiens noli-tangere*, Impa par *I. parviflora*, Junc eff *Juncus effusus*, Knau arv *Knautia arvensis*, Laps com *Lapsana communis*, Lath pra *Lathyrus pratensis*, Leuc vul *Leucanthemum vulgare*, Luzu pil *Luzula pilosa*, Lych f-c *Lychnis flos-cuculi*, Lysi vul *Lysimachia vulgaris*, Medi lup *Medicago lupulina*, Mela pra *Melampyrum pratense*, Ment arv *Mentha arvensis*, Moeh tri *Moehringia trinervia*, Moli cae *Molinia caerulea*, Myos arv *Myosotis arvensis*, Oxal ace *Oxalis acetosella*, Padu avi *Padus avium*, Phal aru *Phalaris arundinacea*, Phle pra *Phleum pratense*, Pice abi *Picea abies*, Pinu syl *Pinus sylvestris*, Poa ang *Poa angustifolia*, Poa com *P. compressa*, Poa nem *P. nemoralis*, Poa pal *P. palustris*, Poa pra *P. pratensis*, Poa tri *P. trivialis*, Popu tre *Populus tremula*, Pote ere *Potentilla erecta*, Prim ver *Primula veris*, Prun vul *Prunella vulgaris*, Pyro rot *Pyrola rotundifolia*, Quer rob *Quercus robur*, Ranu acr *Ranunculus acris*, Ranu aur *R. auricomus*, Ranu rep *R. repens*, Rubu ida *Rubus idaeus*, Rume ace *Rumex acetosa*, Rume a-a *R. acetosella*, Saurxcin *Salix aurita* x *S. cinerea*, Sali sta *S. starkeana*, Sali phy *S. phylicifolia*, Sali cap *S. caprea*, Sali cin *S. cinerea*, Soli vir *Solidago virgaurea*, Sorb auc *Sorbus aucuparia*, Stel gra *Stellaria graminea*, Stel med *S. media*, Tara off *Taraxacum officinale* (coll.), Trif med *Trifolium medium*, Tuss far *Tussilago farfara*, Urti dio *Urtica dioica*, Vale off *Valeriana officinalis*, Vero agr *Veronica agrestis*, Vero cha *V. chamaedrys*, Vero off *V. officinalis*, Vici cra *Vicia cracca*, Vici hir *V. hirsuta*, Vici sep *V. sepium*, Viol arv *Viola arvensis*, Viol can *V. canina*, Viol pal *V. palustris*

Species composition

Among all vascular plant species growing on the vegetation plots in the plantations, 53 % were typical grassland species, 22 % fallow species, 13 % forest species, 10 % forest and grassland species and 2 % grassland and fallow species. In naturally regenerated stands 48 % of vascular plants were grassland species, 22 % forest species, 18 % forest and grassland species, 10 % fallow species and 2 % grassland and fallow species. Among all bryophyte species found in the plantations, 52 % were forest species, 39 % were forest and grassland species and 9 % were grassland species. The corresponding figures for naturally regenerated stands were 68.6 % forest species, 25.7 % forest and grassland species and 5.7 % grassland species.

The number of forest vascular plant species (S_{VP_forest}) and the number of forest bryophyte species (S_{B_forest}) were significantly higher in naturally regenerated birch stands, but were not affected by the land use history or the chemical properties of the soil humus horizon (Table 4). Stands and plantations that were situated near old forests contained a higher number of vascular plant species that usually grow in the forest as well as in grasslands ($S_{VP\_forest\ grassland}$). The number of vascular plant species growing in grasslands ($S_{VP\_grassland}$) was negatively affected by tree leaf litter.

The differences in species composition between naturally regenerated stands and plantations were revealed also from Indicator Species Analysis that pointed out 11 vascular plant species characteristic to silver birch plantations, and 8 vascular plant species (including 3 tree species) and 5 bryophyte species characteristic to naturally regenerated

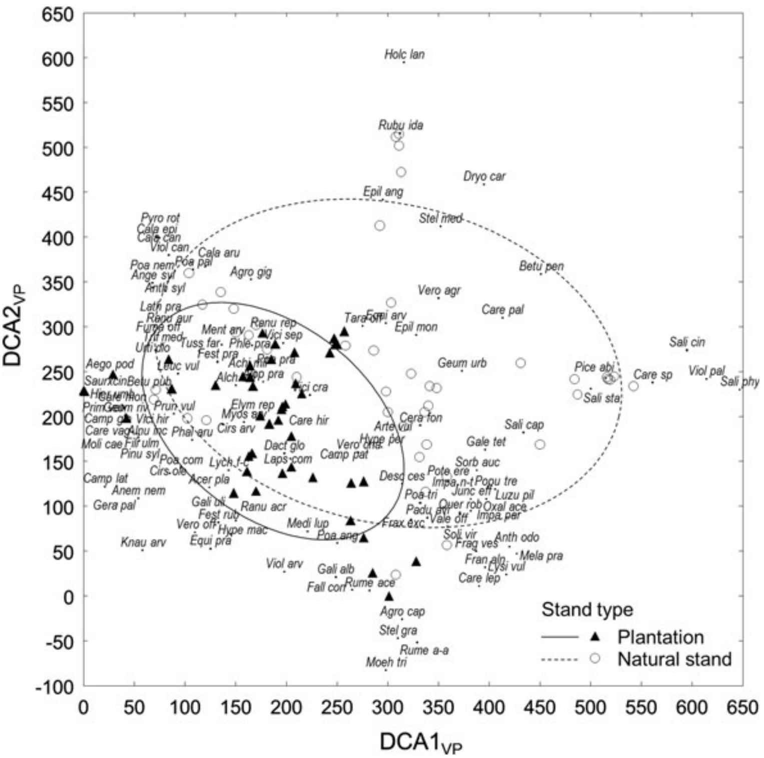

Table 6 Spearman correlation coefficients among DCA axes scores (*VP* vascular plants, *B* bryophytes) and site variables, bold indicates significant ($p < 0.05$) correlations

Variable	$DCA1_{VP}$	$DCA2_{VP}$	$DCA3_{VP}$	$DCA1_{B}$	$DCA2_{B}$	$DCA3_{B}$
Distance	−0.06	**0.27**	**−0.22**	−0.07	0.17	0.16
Basal area	**0.32**	**0.26**	−0.10	**−0.38**	−0.02	−0.03
Leaf litter	**0.28**	−0.13	**0.34**	0.14	−0.18	**−0.22**
Branch litter	**0.43**	**0.31**	0.00	**−0.34**	0.04	−0.07
Transmitted total radiation	0.13	0.02	0.10	0.01	−0.01	**−0.22**
Soil pH	**−0.37**	0.11	**−0.53**	0.03	0.18	**0.27**
Soil N	**−0.37**	−0.07	**−0.27**	0.15	−0.04	0.14
Soil P	0.14	−0.01	**0.26**	−0.01	−0.15	0.07
Soil K	**−0.24**	**0.38**	−0.15	−0.10	0.18	**0.26**

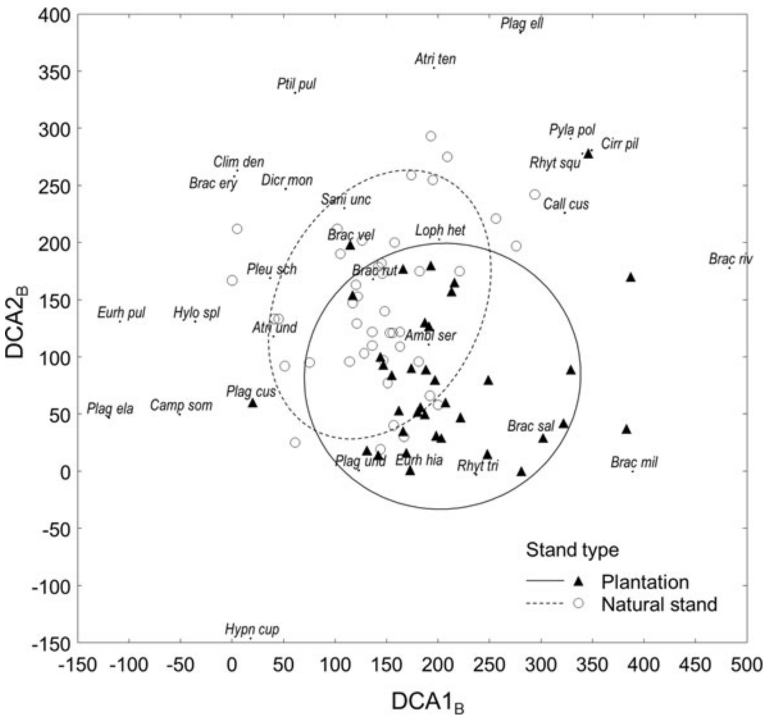

Fig. 3 DCA ordination of vegetation plots and bryophyte species (axis 1 Eigenvalue = 0.59, axis 2 Eigenvalue = 0.40); ellipses indicate 75 % range of the plot scores. Abbreviations: Ambl ser *Amblystegium serpens*, Atri ten *Atrichum tenellum*, Atri und *A. undulatum*, Brac ery *Brachythecium erythrorrhizon*, Brac mil *B. mildeanum*, Brac riv *B. rivulare*, Brac rut *B. rutabulum*, Brac sal *B. salebrosum*, Brac vel *B. velutinum*, Call cus *Calliergonella cuspidata*, Camp som *Campylium sommerfeltii*, Cirr pil *Cirriphyllum piliferum*, Clim den *Climacium dendroides*, Dicr mon *Dicranum montanum*, Eurh hia *Eurhynchium hians*, Eurh pul *E. pulchellum*, Hylo spl *Hylocomium splendens*, Hypn cup *Hypnum cupressiforme*, Loph het *Lophocolea heterophylla*, Plag cus *Plagiomnium cuspidatum*, Plag ela *P. elatum*, Plag ell *P. ellipticum*, Plag und *P. undulatum*, Pleu sch *Pleurozium schreberi*, Ptil pul *Ptilidium pulcherrimum*, Pyla pol *Pylaisia polyantha*, Rhyt squ *Rhytidiadelphus squarrosus*, Rhyt tri *R. triquetrus*, Sani unc *Sanionia uncinata*

Table 7 Characteristic vascular plant and bryophyte species of birch plantations and natural stands according to indicator species analysis, and their habitat preference

Species	Indicator value	*p*-value	Habitat
Plantations			
Vascular plants			
Agrostis capillaris	42.5	0.006	Grassland
A. gigantea	38.7	0.001	Grassland
Alopecurus pratensis	20.5	0.002	Grassland
Cirsium arvense	24.2	0.013	Fallow
Dactylis glomerata	23.2	0.028	Grassland
Elymus repens	59.7	0.002	Grassland
Equisetum pratense	18.2	0.006	Grassland
Festuca rubra	44.6	0.001	Grassland
Galium album	14.4	0.05	Grassland
Ranunculus repens	28.0	0.009	Grassland
Veronica agrestis	19.7	0.048	Fallow
Naturally regenerated stands			
Vascular plants			
Angelica sylvestris	18.2	0.008	Forest, grassland
Fragaria vesca	22.9	0.038	Forest, grassland
Geum urbanum	38.1	0.001	Grassland
Picea abies	58.2	0.001	Forest
Poa nemoralis	18.9	0.012	Forest
Quercus robur	21.2	0.029	Forest
Rubus idaeus	23.0	0.011	Forest
Salix caprea	20.5	0.004	Forest
Bryophytes			
Brachythecium rutabulum	57.1	0.001	Forest
B. velutinum	36.0	0.003	Forest
Lophocolea heterophylla	49.2	0.001	Forest
Plagiomnium cuspidatum	25.4	0.009	Forest
B. erythrorrhizon	22.7	0.001	Forest

Species present at least in eight vegetation plots were included

birch stands (Table 7). The majority of vascular plant species characteristic to naturally regenerated birch stands were forest or forest and grassland species, and all characteristic bryophyte species were forest species. In the case of silver birch plantations, the majority of characteristic vascular plant species were grassland species, with the exception of *Cirsium arvense* and *Veronica agrestis* (fallow species).

Discussion

The current study focused on understorey vegetation of first generation birch forests on abandoned agricultural lands and aimed to clarify the differences that exist in the understorey species richness and species composition between naturally and artificially established stands. We found that species richness and diversity of bryophytes were higher in naturally regenerated stands, thus confirming our hypothesis that naturally regenerated birch forests offer more favourable conditions for ground vegetation. At the same time, species richness and diversity of vascular plants did not differ between the two stand types. Bryophytes and vascular plants have significant differences in morphology and physiology, and differences in the species-richness responses of these plant groups to environmental conditions have also been observed in other studies (Ingerpuu 2002; Ingerpuu et al. 2003).

In contrast to our findings, a study conducted on abandoned agricultural lands in northwest China (Zhang et al. 2010) showed that the herb layer of secondary forests had a higher species richness than that in pine plantations. This can be explained via differences in the tree layer. In our study, tree layer characteristics were quite similar in both stand types (Table 2), while the secondary forests in northwest China had high tree layer diversity (including deciduous trees) in contrast to the monocultural pine plantations. Several studies have concluded that mixed stands may be more beneficial for understorey floristic diversity than monocultures (Barbier et al. 2008; Felton et al. 2010).

Although species richness and diversity of vascular plants were similar in both stand types (Tables 3, 4), DCA ordination with vascular plant data separated plantations and naturally regenerated stands (Table 5), indicating the compositional differences between the two stand types. Species composition of naturally regenerated stands was more heterogeneous (Fig. 2). Tree species (species of *Salix*, *Picea*, *Betula*, *Populus*, *Padus*, *Sorbus*, *Fraxinus, Quercus*) growing in the field layer were typically converged to the region of naturally regenerated stands. Rare vascular plant species were occasionally found only from the vegetation plots of naturally regenerated stands, indicating their more diverse habitat variety. The field layer of naturally regenerated stands had a higher number of forest species than plantations (Table 4) and several forest and forest and grassland species were characteristic to natural stands (Table 7). Thus the recovery of the forest understorey had progressed further in naturally regenerated stands as the colonization of forest understorey species to naturally regenerated stands could start simultaneously with birches after the cessation of agricultural land use. In plantations, however, ploughing was used for site preparation before the planting of birch trees to reduce competition with the field layer. A similar conclusion was reached in the study of Canadian plantations and naturally regenerated stands growing on former agricultural lands (Aubin et al. 2008), where the understorey of plantations was generally less developed than the understorey of naturally regenerated stands. This was attributed to the intensive site preparation method used in plantations.

In the DCA ordination of bryophyte data (Fig. 3) the stand types were separated slightly more significantly than in the case of vascular plants (Table 5). Regarding individual species scores, more species were found in the region of plots from natural stands. Similarly to the vascular plants the number of forest bryophyte species was higher in naturally regenerated stands (Table 4) that could also be attributed to the longer colonization period. Additionally, the amount of branch litter and thinning residues was higher in naturally regenerated stands (Table 2), providing habitat to species that grow on decaying wood. Bryophyte species *L. heterophylla*, *B. velutinum* and *B. erythrorrhizon* that, according to Indicator Species Analysis, were characteristic to naturally regenerated stands are often found on decaying wood (Ingerpuu et al. 1994). The abundance of decaying wood may contribute positively to the species richness of bryophytes, while being less important for the species richness of vascular plants, as demonstrated by Bartels and Chen (2012). In addition, bryophytes and vascular plants interact directly and these interactions may vary from facilitation to inhibition. In our study, a negative impact of the cover of vascular plants on the species richness of bryophytes was observed, which can be related to the competition for available resources between bryophytes and vascular plants and the physical limitation imposed by vascular plant species (Bartels and Chen 2012).

Distance to the nearest forest helped to explain the variation in plot scores of the second and third axes in DCA ordination with vascular plant data. Several studies have concluded that the joint effect of distance to forest and stand age plays a major role in the colonization of vascular plants to recent woodlands (e.g. Brunet and von Oheimb 1998; Jacquemyn et al. 2001; Verheyen et al. 2003). In our study the number of vascular plant species that grow in forests as well as in grasslands was higher in the stands situated near to old forests, but in the case of forest vascular plant species, the correlation was not statistically significant. Possible explanation may be differences in prevailing dispersal types in the case of forest vascular plant species versus forest and grassland vascular plant species in our study. In a study conducted in recent pine woods in southern Poland, Dzwonko (2001) found that, with increasing distance from the ancient woodland, the numbers of anemochores and tree species in the field layer increased, while the numbers of myrmecochores and vegetatively reproducing species decreased. Numerous woody and herb anemochores (*Acer platanoides*, *Alnus incana*, *Alnus glutinosa*, *Picea abies*, *Pinus sylvestris*, *Salix caprea*, *Populus tremula*, *Fraxinus excelsior*, *Athyrium filix-femina*, *Dryopteris carthusiana*, *Pyrola rotundifolia*) represented forest species, and several myrmechochores (*Viola canina*, *Viola palustris*, *Carex montana*) and vegetatively reproducing species (*Aegopodium podagraria*) represented forest and grassland species. This is why the influence of shorter distance was evident only in the case of forest and grassland vascular plant species.

We also studied the effect of land use history and soil properties on the occurrence of forest understorey species. In our study the number of forest species was similar in the stands developing on former grasslands and in the stands on former arable fields. Contrarily, Wulf (2004) found that a large number of forest species occurred more frequently in the stands on former grasslands in northeastern Germany. The possible reason might be differences in land cultivation practices. While Wulf analysed the data collected from stands originating from the nineteenth and twentieth centuries, our stands were established only in the 1990s.

No negative correlation between soil nutrients (N, P, K) and the occurrence of forest species was found, indicating that soil properties do no limit the colonization of forest species to new forests on former agricultural sites in Estonia (Table 4). This is in accordance with the results from Graae et al. (2004), who, based on a seed sowing experiment, concluded that soil variables did not influence the colonization of forest species to recent forests in Denmark. However, the effect of chemical soil properties on vascular plant and bryophyte vegetation was revealed from DCA ordination (Table 6).

We also analysed the effect of light conditions on the understorey vegetation attributes. Somewhat surprisingly, these effects were usually insignificant, except that total transmitted radiation explained some of the variation in DCA axes 2 scores of bryophytes (Table 6). Higher sensitivity to light conditions of bryophytes compared to herbaceous plants was observed also by Tinya et al. (2009). In addition, the understorey is likely to respond to changes in light availability with some delay (Thomas et al. 1999; Brockerhoff et al. 2003), and may therefore reflect historic rather than current light conditions. The studied stand types differed in this respect. In plantations the initial density was about 2,500 trees ha^{-1} which means that the light availability for the understorey was not greatly affected by the planted trees during several years after establishment. In naturally regenerated stands the average density was about 35,500 trees ha^{-1} before thinnings (Jõgiste et al. 2003) and probably the supression of open community species started earlier and the competition for light and nutrients between trees and herbs was stronger.

Regarding tree growth, basal area of both planted and natural birch stands was similar, however, diameter of the stems at breast height was greater in plantations (Table 2). The range of mean heights had been comparable in the same stands also 10 years earlier (Jõgiste et al. 2003). In natural birch stands usually second tree layer of *P. abies* had formed under the dominant birch layer, however its total contribution to aboveground stand volume was less than 9 % (Table 1). A second stand layer can be expected to emerge also in plantations. The establishment of shade-tolerant spruces under pioneer deciduous trees follows as part of the typical natural succession in the region. Growing mixed with spruces is regarded as beneficial for the stem quality of birches (Hynynen et al. 2010). Natural birch stands were quite dense and require repeated thinnings to produce high-quality assortments from large-dimensional stems; on the other hand, if bioenergy production is the aim, then total biomass is more important than individual stems, and from this perspective dense natural stands could outcompete sparser plantations. At the same time, natural afforestation is not always fast and even, and could also result in less valuable tree species than birch. Poor seed availability and competition with a dense herbaceous plant layer on previously fertilized agricultural lands can delay natural afforestation for a period of up to 20 years (Ruskule et al. 2012). From this perspective, planting can be recommended, since trees are able to suppress competition from shade-intolerant plant species and can thereby accelerate the restoration of forest understorey (Fortier et al. 2011; Boothroyd-Roberts et al. 2013). However, the choice of tree species needs careful consideration, as plantations with introduced tree species may lead to reduced plant diversity (Wang et al. 2011).

Conclusion

The need to clarify the consequences of assisted and unassisted reforestation for ecological restoration is relevant to various regions of the world, where forest transition has taken place as a result of changes in agricultural land use. We compared these two alternatives from the perspective of understorey vegetation. Regarding vascular plants, we did not detect a clear trend towards more diverse understorey vegetation in natural birch stands, nor were the stand growth parameters considerably better in plantations. However, observed differences in the understorey species composition between naturally regenerated stands and plantations indicated that the recovery of the forest understorey had progressed further in naturally regenerated stands already 14–20 years after stand creation. In addition bryophyte species richness and diversity were higher in naturally regenerated stands. When the aim is to establish a commercial birch forest on abandoned agricultural land, both natural succession as well as plantation establishment are possible alternatives and they offer quite similar conditions for understorey vegetation. When the aim is to facilitate the restoration of forest ecosystem on abandoned agricultural land, then for areas close to natural forests, natural succession can be recommended. This should result in a mixed stand where colonization with forest understorey species is quite fast. Otherwise the landowner's decision can be based on other aspects like economic goals and landscape context.

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