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Composition of functional groups of ground vegetation differ between planted stands of non-native *Pinus contorta* and native *Pinus sylvestris* and *Picea abies* in northern Sweden

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Highlights

- Differences in ground vegetation patterns can be linked to tree species, forest stand age and differences in canopy cover.
- Vascular plant cover was higher in stands of *P. contorta* than in stands of both native tree species.
- The overall differences and similarities between *P. contorta* and the two native conifers were not consistent over the different age classes.

Abstract

Intensified forestry increases the interest in replacing native tree species with fast growing non-native species. However, consequences for native biodiversity and ecosystem functioning are poorly understood. We compared cover and composition of major functional groups of ground vegetation between planted stands of non-native *Pinus contorta* Dougl. var. *latifolia* Engelm. and native conifers *Pinus sylvestris* L. and *Picea abies* (L.) H. Karst. in northern boreal Sweden. We quantified the ground cover of lichens, bryophytes, vascular plants and ground without vegetation (bare ground) in 96 stands covering three different age classes (15, 30 and 85 years old). Our study revealed differences in ground vegetation patterns between non-native and native managed forests, and that these differences are linked to stand age and differences in canopy cover. Total vascular plant cover increased with increasing stand age for all tree species, with *P. contorta* stands having higher cover than both native conifers. The ground cover of lichens was, although generally low, highest in stands of *Pinus sylvestris*. *P. abies* stands had a lower cover of vascular plants, but bare ground was more common compared with *P. contorta*. Our results suggest that the use of *P. contorta* as an alternative tree species in Fennoscandian forestry will influence native ground vegetation patterns. This influence is likely to change with time and future research should consider both temporal and landscape-scale effects from shifting tree-species dominance to *Pinus contorta* and other non-native tree species.

Keywords boreal forests; bryophytes; exotics; introduced species; lichens; managed forests; vascular plants

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1 Introduction

Introducing non-native tree species is a common way to increase wood production, and establishment of non-native tree plantations is expanding worldwide (Richardson 1998; Bremer and Farley 2010). The potential effects on associated native vegetation are, however, still poorly understood. To predict the consequences of tree species introductions, a deeper general understanding of how choice of tree species influences the functional composition of the vegetation is important.

Trees influence the local climate and provide important living space for other species (Lawton 1994). Influence of non-native trees on native biodiversity will largely depend on what they replace, and changes in composition of native understory species will be greater if the introduced tree species create substantial changes in canopy closure and litter composition (Brockerhoff et al. 2008; Meers et al. 2010). Another important factor is time since disturbance, e.g. generated by clear-cutting (Clark et al. 2003; Uotila and Kouki 2005; Uotila et al. 2005). The potential effects that these two factors have on functional groups of ground vegetation have rarely been examined for a range of native and non-native planted forest types (Bremer and Farley 2010).

Changes in dominance structure of functional groups of ground vegetation can influence ecosystem processes (Nilsson and Wardle 2005) and biodiversity (Suchar and Crookston 2010). Thus, ground vegetation changes may be used as an indicator of how shifts in the dominant tree species influence biodiversity and functioning of the forest (Humphrey et al. 1999; Nilsson and Wardle 2005; Suchar and Crookston 2010).

Pinus contorta Dougl. var. *latifolia* Engelm. has been planted widely outside its native North American distribution range (Sykes 2001). Despite the fact that the regional introduction of *P. contorta* has been substantial, the understanding of its consequences for native biota is limited (but see: Nilsson et al. 2008; Roberge and Stenbacka 2014). In Sweden it is now the third most common conifer after the native *Pinus sylvestris* L. and *Picea abies* (L.) H. Karst., and constitutes 1.2% of the total standing tree volume (Skogsstyrelsen 2014), In comparison to the native *P. sylvestris*, *P. contorta* allocate more of the aboveground biomass to needle production (Ågren and Knecht 2001) and reach canopy closure and limited light conditions at an earlier age (Elfving et al. 2001). *P. contorta* also produces more litter (Nilsson et al. 2008) with lower nitrogen and higher lignin concentrations than *P. sylvestris*, resulting in slower decomposition rates (Ågren and Knecht 2001). These differences suggest that species composition and cover of ground vegetation will undergo substantial change in areas were *P. contorta* have replaced the native conifers.

The objective of this study was to examine the cover and composition of functional groups of ground vegetation in a chronosequence of stand age classes of managed forests of non-native *P. contorta* and native *P. sylvestris* and *P. abies*. Specifically, the aim was to assess if cover of different taxonomic and functional groups, i.e. lichens, bryophytes and vascular plants, differ depending on choice of tree species planted, and how the composition of these vegetation groups are related to the stand age and canopy cover of the different tree species.

2 Materials and methods

2.1 Study area description

The study area (c. 2800 km^2) is located in the northern boreal zone of Sweden (64°15´N, 16°24´E) and dominated by coniferous managed forests of *P. sylvestris* and *P. abies*. The annual mean temperature is +1 °C, with mean monthly temperatures ranging from –10 °C in the winter (December–February) to +13 °C in the summer (June–August). The length of the growing season is 140–150 days. The mean annual precipitation is approximately 700 mm (data from the Swedish Meteorological and Hydrological Institute for the period 1961–1990). All of the inventoried *P. contorta* stands were in the first generation, i.e. they had all been planted after harvest of native tree species.

Stands used for inventory were selected according to the following criteria (based on data from the land owner's database): >70% of the stand volume was one of the three focal tree species, cowberry-bilberry vegetation of dry-mesic-moist ground type (after Pålsson 1998), and predominantly flat topography. Three age classes were used: 15 (±2 years), 30 (±5 years) and 85 (±5 years) years old. Most 15 and 30-year old stands had been subjected to pre-commercial thinning and the 85-year old stands had been subjected to commercial thinning.

2.2 Field methods

All stands were inventoried during the snow-free period of the three years 2009 to 2011. For each tree species, 12 stands in every age class were inventoried except for 85-year old *P. abies* (11 stands) and 85-year old *P. contorta* (1 stand). The single mature stand of *P. contorta* was the only stand of that age within the study area. Stands were on average 24.7 ha. Ground vegetation was surveyed in 24 one by one metre ground plots, evenly distributed along the longest transect through each stand, starting and ending 25 m from the edge to avoid edge effects. Average spacing between ground plots was 29 m. For practical reasons, the position of a plot was moved to the nearest acceptable position if it contained saplings taller than 50 cm, boulders covered more than 10% of the plot, or was too wet (i.e., contained water-filled holes or patches of *Sphagnum* spp.).

Within each of the 24 plots we recorded percent cover of macrolichens, bryophytes, vascular plants (ground and field layer) and ground without vegetation (bare mineral soil, needles or coarse/fine woody debris, hereafter "no vegetation"). Lichen cover was dominated by the genus *Cladonia* P. Browne. Bryophytes were recorded as total percent cover and consisted predominantly of *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Brid.) Mitt. Vascular plant cover was recorded in three groups: total vascular plants (TVP), eudicots and grasses. TVP cover includes all vascular plants in the ground- and field layer and eudicots mainly consist of the dwarf shrubs *Vaccinium myrtillus* and *V. vitis-idaea*. Grasses mainly consist of thin-leaved grasses such as *Deschampsia flexuosa* (L.) Trin. At four random points along each transect, canopy cover was estimated by the same two persons as a visual estimate of percent sky.

2.3 Statistical methods

All analyses were based on forest stand averages, both for canopy cover and ground cover data. Canopy cover was not correlated to stand age ($r=0.190$, $p=0.060$). We used beta regression models to compare the ground vegetation cover between stands of *P. contorta* and the two native conifers. As a starting point we used a full model with tree species, stand age class, canopy cover and the two-way interactions between these variables as explanatory variables. Thereafter, the least significant variables were removed one at a time (stepwise backward selection) until we achieved the lowest Akaike's Information Criterion (AIC). We defined a plausible model according to Burnham and Anderson (2002), i.e., that the alternative model's AIC (all AIC values presented in Supplementary file 3) was less than two units higher than AIC for the "best" model with the lowest AIC ($\Delta AIC < 2.0$). Differences in canopy cover between tree species within age classes was analyzed using ANOVAs with Tukey's family error rate at the 95% confidence level, i.e. we ran one separate ANOVA for each age class. Correlations and ANOVAs were tested using Minitab 16 Statistical Software, and for the beta regression the statistical software R 3.0.1 (R Development core team 2013) and the plug-in library Betareg (Cribari-Neto and Zeileis 2010).

3 Results

Tree species had a significant influence on the ground vegetation in the majority of examined cover types (Table 1). *P. contorta* stands differed from *P. sylvestris* stands in bryophyte, lichen and eudicot cover, and from *P. abies* stands in eudicot cover and no vegetation cover (Table 1, Fig. 1). Increasing stand age had a negative influence on bryophyte cover in stands of *P. contorta*, while cover of eudicots and TVP increased with stand age (Table 1). In *P. sylvestris* stands, grass cover decreased with increasing stand age (Table 1).

The overall differences and similarities were not necessarily consistent over the different age classes (Fig. 1). In general, significant differences were almost exclusively found in the two younger age classes with the exception of the cover type no vegetation (Fig. 1). The 85 year old *P. contorta* stand is not part of the significance test due to the single stand, but still included in Figure 1 for comparison. Percent canopy cover had a significant effect on grass cover that interacted with tree species (Table 1), where grass cover decreased with increasing canopy cover in *P. abies* stands (Fig. 2).

In 15 and 30-year old stands, TVP cover was lower in stands of *P. abies* than stands of *P. contorta* (Fig. 1f). There was no difference between *P. sylvestris* stands and *P. contorta* stands,

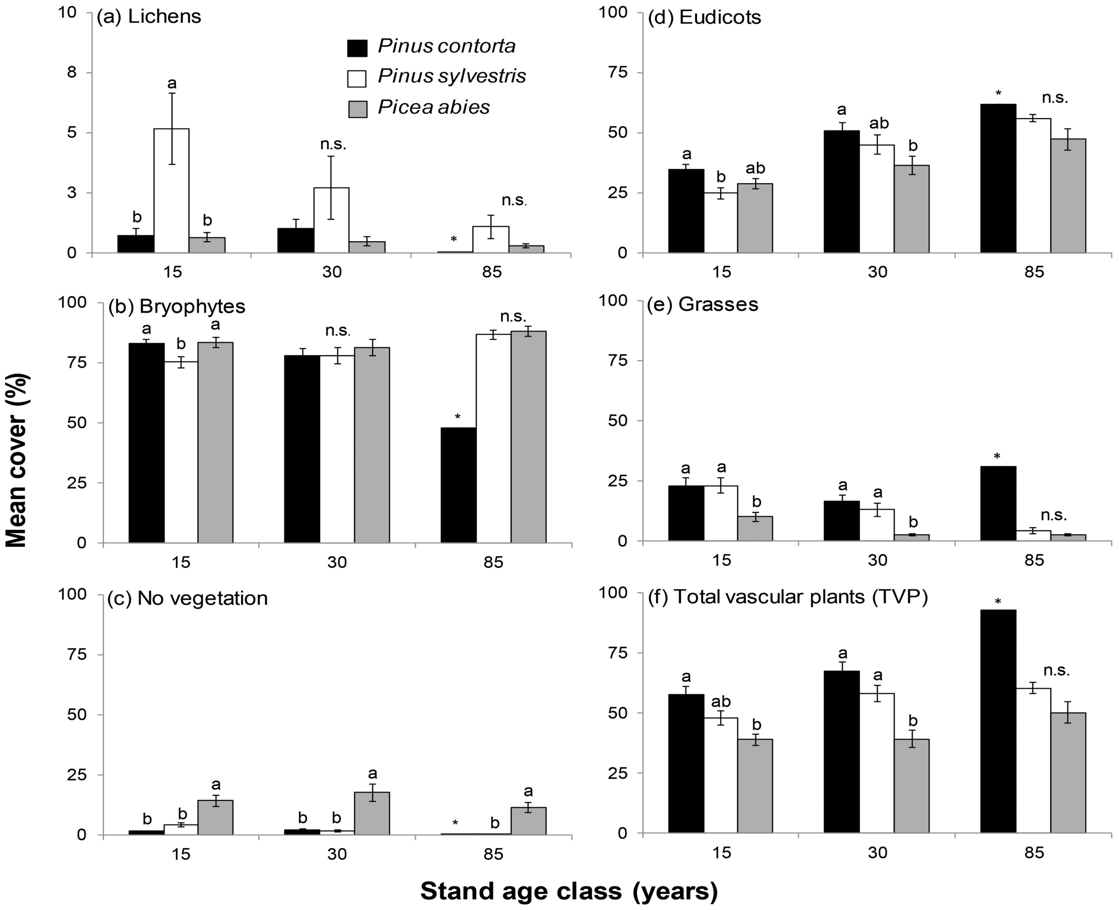

Fig. 1. Mean cover (%), ±SE, for the six different types of ground vegetation inventoried in stands of *P. contorta*, *P. sylvestris* and *P. abies* of different stand age classes. Note the different scales on the y-axes in (a) Lichens. Significant differences within age classes are indicated by different letters (Tukey's test; $p<0.05$), n.s.=not significant. The star (*) denotes the single 85 year old *P. contorta* stand which was not included in the significance test.

Table 1. Results from the beta regression models explaining average ground cover of lichens, bryophytes, eudicots, grasses, total vascular plants (TVP) and no vegetation in stands of native *P. sylvestris* and *P. abies* when contrasted to non-native *P. contorta*. Significant p-values are given in bold. The presented models represent the models with lowest AIC (see Supplementary file 3). The pseudo-R^2 value (the squared correlation of the linear predictor and link-transformed response) gives a measure of model fit.

	Estimate	SE	p-value	R_p^2
Bryophytes				0.25
Intercept	1.932	0.216	**<0.001**	
Picea abies	–0.514	0.275	0.062	
Pinus sylvestris	–0.976	0.266	**<0.001**	
Age	–0.024	0.007	**0.001**	
P. abies × age	0.030	0.008	**<0.001**	
P. sylvestris × age	0.035	0.008	**<0.001**	
Lichens				0.37
Intercept	–2.946	0.905	**0.001**	
Picea abies	–1.198	0.992	0.227	
Pinus sylvestris	2.149	0.985	**0.029**	
Age	–0.021	0.014	0.132	
Canopy cover	–0.021	0.013	0.118	
P. abies × age	0.022	0.016	0.181	
P. sylvestris × age	0.002	0.015	0.881	
P. abies × canopy cover	0.007	0.017	0.665	
P. sylvestris × canopy cover	–0.043	0.017	**0.013**	
Eudicots				0.36
Intercept	–0.611	0.112	**<0.001**	
Picea abies	–0.520	0.137	**<0.001**	
Pinus sylvestris	–0.343	0.135	**0.011**	
Age	0.015	0.002	**<0.001**	
Grasses				0.51
Intercept	–2.810	0.740	**<0.001**	
Picea abies	0.386	0.741	0.603	
Pinus sylvestris	0.527	0.770	0.493	
Age	0.022	0.015	0.137	
Canopy cover	0.026	0.012	**0.035**	
P. abies × age	0.004	0.014	0.756	
P. sylvestris × age	–0.035	0.010	**<0.001**	
P. abies × canopy cover	–0.032	0.013	**0.017**	
P. sylvestris × canopy cover	0.012	0.013	0.366	
Age × canopy cover	0.000	0.000	0.137	
Total vascular plant cover (TVP)				0.49
Intercept	–0.804	0.521	0.123	
Picea abies	0.238	0.565	0.673	
Pinus sylvestris	0.019	0.601	0.975	
Age	0.031	0.009	**<0.001**	
Canopy cover	0.011	0.008	0.145	
P. abies × age	–0.024	0.010	**0.014**	
P. sylvestris × age	–0.025	0.009	**0.006**	
P. abies × canopy cover	–0.012	0.009	0.209	
P. sylvestris × canopy cover	0.009	0.010	0.369	
No vegetation				0.68
Intercept	–3.788	0.498	**<0.001**	
Picea abies	1.928	0.442	**<0.001**	
Pinus sylvestris	0.736	0.465	0.114	
Age	–0.012	0.014	0.392	
Canopy cover	0.008	0.005	0.103	
P. abies × age	0.003	0.015	0.859	
P. sylvestris × age	–0.014	0.015	0.343	

but 30-year old *P. sylvestris* stands had higher TVP cover than *P. abies* stands of the same age (Fig. 1f). For 15 and 30-year old stands, cover of grasses was lower in *P. abies* stands than for both pine species, while there was no difference in 85-year old stands (Fig. 1e). In 15-year old stands, cover of eudicots was higher in *P. contorta* stands than *P. sylvestris* stands, while the cover in *P. abies* stands was not significantly lower than in *P. contorta* stands (Fig. 1d). In 30-year old stands, the cover of eudicots did not differ between *P. contorta* and *P. sylvestris*, while *P. abies* stands had significantly lower cover than *P. contorta* stands. The cover type no vegetation was highest in stands of *P. abies* throughout the chronosequence (Fig. 1c).

Lichen cover was generally low and the highest mean cover of lichens, 5.2%, was found in 15-year old stands of *P. sylvestris* (Fig. 1a). High canopy cover lowered lichen cover in stands of *P. sylvestris*, but had no effect in *P. contorta* and *P. abies* stands (Table 1). The most common lichen species all belonged to the genus *Cladonia* and other lichens only made up a small part of the lichen cover (Supplementary file 1).

Bryophyte cover was high with mean cover above 75% (Fig. 1b). The bryophyte cover increased with increasing stand age for both *P. abies* and *P. sylvestris*, and the highest mean cover was found in *P. abies* stands (81%–88%; Fig. 1b).

Canopy cover was highest in 15 and 30-year old *P. contorta* stands, but there was no difference from *P. abies* in 30-year old stands. In 85-year old stands, *P. abies* had the highest canopy cover (Table 2).

4 Discussion

Our study is one of few showing differences in ground vegetation patterns between managed non-native and native boreal forests, and that the differences can be linked to stand age and canopy cover. We found that the total vascular plant cover increased with stand age for *P. contorta*, which contrasts to Nilsson et al. (2008) who found no such correlation. Uotila and Kouki (2005) found that in managed *P. abies* stands, dwarf shrubs increased their cover for up to at least 80–100 years, and that herbs had a relatively constant cover, which correspond well to our study where vascular plants increased throughout the chronosequence. We also found higher cover of vascular plants in stands of *P. contorta*, which contrast the findings of Roberge and Stenbacka (2014) that reported lower cover of both dwarf shrubs and some herbs in middle-aged *P. contorta* stands compared to *P. sylvestris* stands. The use of different age classes may complicate comparisons between the studies, yet the contrasting result is surprising as there is nothing in our study that suggests a lower cover of vascular plants in *P. contorta* stands.

The response of grass cover differed between stands of *P. abies* and stands of the two *Pinus* species. For stands of *P. abies*, grass cover decreased as canopy cover increased, as also shown earlier by Widenfalk and Weslien (2009). However, for *P. contorta* and *P. sylvestris* stands we found no such correlation. The understory of stands with the two *Pinus* spp. may not have responded to increases in canopy cover because of the initially higher grass cover in these stands, and higher transmission of light to the understory vegetation in *Pinus* spp. compared to *Picea* spp. (Hart and Chen 2006). Pine stands are usually thinned later than spruce stands and are subsequently more open at later age classes (Table 2). Hence, grasses may start growing and establishing a seed bank already before final harvest in pine stands. Since it is known that the re-growth of grasses (mainly *Deschampsia flexuosa*) can be extensive after clearcutting (Uotila and Kouki 2005; Uotila et al. 2005), this likely explains the resulting higher grass cover in younger pine stands after final harvest.

Likewise, increasing canopy cover can also limit the ground cover of lichens (Coxson and Marsh 2001). This was evident in stands of *P. sylvestris* in our study, but not in stands of *P. con-*

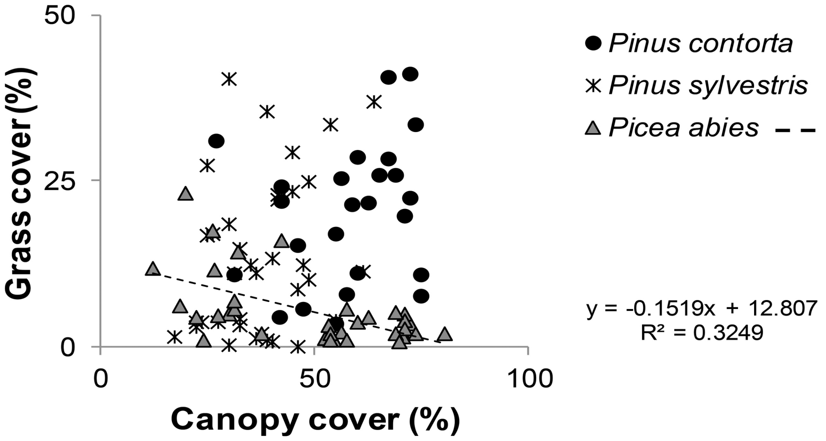

Fig. 2. Relationship between grass cover (%) and canopy cover (%). All stands included. Regression line is shown for *Picea abies*, the only tree species, under which significant correlation between grass and canopy cover was observed in the beta regression analysis.

torta and *P. abies*. Lichen cover in stands of both *P. contorta* and *P. sylvestris* has been reported to increase with increasing stand age in middle and northern boreal Sweden (Nilsson et al. 2008), but we found no significant age effect. In naturally developed pine-lichen woodlands, lichen ground cover can increase with age whereas in more productive forests where lichens are subordinate (as in our study), such response is less likely (Coxon and Marsh 2001). Although stand age and canopy cover can be important for ground cover of lichens, the effect may be obscured in forests with low and patchy lichen cover and neither time nor canopy cover are likely to have much influence under such circumstances (Uotila and Kouki 2005; Lindgren et al. 2006).

Bryophyte cover is known to increase with time since disturbance in boreal forests (Lindgren et al. 2006). In young managed forests, cover is often in the range of 40–50%, but gradually increases to about 80% in older stands (Uotila and Kouki 2005). In accordance with this, we found that bryophyte cover increased with stand age for *P. abies* and *P. sylvestris*. Roberge and Stenbacka (2014) reported significantly higher cover of bryophytes in *P. contorta* stands compared to *P. sylvestris* stands. In our study, bryophyte cover was indeed higher for *P. contorta* than *P. sylvestris*, but only in the youngest stands.

Table 2. Mean values (± SE) for canopy cover in different stand types. Significant differences within age classes are represented by different letters (Tukey's test; $p<0.05$). The star (*) denotes the single 85 year old *P. contorta* stand which was not included in the significance test.

Tree species	Age class	Canopy cover (%)
P. contorta	15	57 (4.2)^a
P. abies	15	26 (2.1)^b
P. sylvestris	15	36 (3.4)^b
P. contorta	30	62 (2.2)^a
P. abies	30	58 (4.0)^b
P. sylvestris	30	40 (3.8)^a
P. contorta	85	27 *
P. abies	85	66 (1.9)^a
P. sylvestris	85	38 (1.9)^b

We conclude that planting of non-native tree species will influence composition of the ground vegetation at the stand level. Although the effects of non-native *P. contorta* on ground vegetation in Sweden do not result in complete changes of vegetation type, it is important to point out that most *P. contorta* stands in Sweden are still younger than 50 years and represent first generations of this species. Future long-term studies are needed to establish whether the observed differences between our single old *P. contorta* stand and stands planted with native conifers is a general pattern. Hence, we stress the importance of continued monitoring of both temporal and landscape-scale effects of shifting dominance in tree-species to *P. contorta* and other non-native tree species. Furthermore, if *P. contorta* was to be introduced in other bioclimatic zones, this could potentially also affect tree growth and cause differences in the magnitude and timing of vegetation responses.

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Supplementary files

Data on lichen species, forest stand information and model AIC values are available as supplementary files at http://dx.doi.org/10.14214/sf.1321.