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ORIGINAL ARTICLE

Consequences for bird diversity from a decrease in a foundation species—replacing Scots pine stands with Norway spruce in southern Sweden

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Abstract

Forest ecosystems are often defined by their dominant foundation tree species, which dictate forest structure and ecosystem processes. In southern Sweden, concerns are being raised because production stands of a foundation tree species, Scots pine (*Pinus sylvestris*), are being converted to Norway spruce (*Picea abies*) stands. Such conversions may lead to biodiversity loss, though the specific nature and extent of such losses remain unknown. Here, we assess the potential biodiversity impacts by contrasting the bird communities of 55- and 80-year-old Scots pine and Norway spruce production stands. We also determine the extent to which these production stands capture the available species pool by surveying conifer-dominated reserves. Our results indicate that Scots pine and Norway spruce production forests support overlapping but nevertheless distinct bird communities, though only few recordings were made of the species unique to either stand type. Among the production stands, the 80-year spruce stands had the highest average bird species richness, and largest total number of species recorded. We suggest that the higher diversity can be explained by a higher proportion of broadleaves and higher volumes of dead wood. Although the bird diversity found in the reserves was lower than expected, they benefit gamma diversity at landscape scales as they collectively supported a higher diversity of bird species than the production forests. In summary, the conversion of Scots pine to Norway spruce is likely to increase the homogeneity of the bird communities in this region.

Keywords Biodiversity · Forest management · Forest reserves · Forest structure · Plantation forests

Introduction

Forest ecosystems are regularly defined by their dominant tree species. These foundation species (sensu Dayton 1972) dictate forest structure and ecosystem processes, with flow-on implications for biodiversity and the ecosystem services provided. Foundation trees are decreasing world-wide, due to pathogens, overharvesting, and additional factors (Ellison et al. 2005). In southern Sweden, there are concerns about a potential long-term decline in the foundation species Scots pine (*Pinus sylvestris*). Although still common, the active regeneration of Scots pine has reduced in favor of Norway spruce (*Picea abies*), due in part to financial incentives and the risk or perceived risk of browsing damage to Scots pine by large herbivores (Anonymous 2010; Lodin et al. 2017). Whereas the conversion of Scots pine to Norway spruce involves shifting from one type of even-aged intensively managed production forest to another, concerns can nevertheless be raised regarding the potential biodiversity implications from these conversions (Felton et al. 2016b). Despite both trees being native conifers, Scots pine is a light demanding species, while Norway spruce is shade tolerant, with resulting differences in the understory micro-climate created by their distinctive crowns, branches, and needles (Barbier et al. 2008; Jonsell et al. 1998). In addition, they also differ in their bark and dead wood characteristics (Kuusinen 1996). The resultant

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differences in the resources and environments provided are in turn linked to differences in the species communities and biodiversity supported. For example, differences between Norway spruce and Scots pine stands have been found in the community composition or diversity of epiphytic lichens (Bäcklund et al. 2016; Marmor et al. 2013), macrofungal communities (Ferris et al. 2000), and bryophytes (Augusto et al. 2003; Bäcklund et al. 2015). Concerns may thereby be raised that the conversion of Scots pine stands to Norway spruce may lead to changes to forest biodiversity in southern Sweden, though the specific nature of such impacts and their extent remains largely unknown.

The lack of knowledge regarding the potential biodiversity implications of these conversions is particularly acute for forest birds. Birds are an important study species when assessing the potential implications of changing forest management regimes for biodiversity for several reasons (Fischer et al. 2007). First, birds fulfill a diverse and vital range of ecological functions, including seed dispersal, pest control, pollination, and ecosystem engineering (Sekercioglu et al. 2016). Birds are also visually and acoustically conspicuous (Whelan et al. 2008), which enables efficient surveying. Finally, bird diversity and community composition is often responsive to changes of forest management practices (Ram et al. 2017), including changes to the dominant tree species (e.g., Bibby et al. 1989; Lindbladh et al. 2017; Nilsson 1997). All of these aspects make bird species particularly useful and important indicators for assessing the implications of different forest management regimes on biodiversity and ecosystem processes (Fischer et al. 2007).

Here we contrast the bird communities of Scots pine and Norway spruce production stands, and infer the potential implications of landscape scale decreases in Scots pine. To do so, we conducted bird surveys within 55- and 80-year-old production stands of both Scots pine and Norway spruce. We chose stands of this age as they could be expected to hold a high diversity compared to lower ages (Lindbladh et al. 2017). In order to determine the extent to which these production stands were capturing the available species pool of conifer associated bird species, we also surveyed conifer-dominated reserves found within the region. We were specifically interested in determining (i) which bird species occupied these forest habitats during the breeding season; (ii) how bird species richness and composition differed among the production and protected forest categories; and (iii) to what extent stand and landscape level structures influenced the bird species composition of these forests. We place our results within the larger context of how production forest stands may contribute to or detract from regional avian biodiversity.

Material and methods

Study area

Surveys were conducted in the hemi-boreal zone of southern Sweden (Ahti et al. 1968). The mean temperature (1961–1990) in the area is approx. − 3 °C in January, and 16 °C in July, and the precipitation is 500–600 mm/year. Forests cover 63% of the land area in southern Sweden (Götaland). Production forestry dominates, and only ~ 2% of the productive forest land (timber production capacity > 1 m^3 ha^{-1} $year^{-1}$) is formally protected (Table 1.5 in Nilsson and Cory 2016). In the region, Norway spruce dominates (49% of volume), followed by Scots pine (29%) (Nilsson and Cory 2016). Data from the National Forest Inventory show that the proportion of 5–20-year-old Scots pine-dominated forest plots have fallen in the region from just over 20% in 1965 to less than 5% 2007 (Urban Nilsson in prep). Norway spruce- and Scots pine-dominated forests today are generally planted and managed using clear-cutting and even-aged stands which are pre-commercially and commercially thinned two to three times during a rotation. Stands are harvested after a rotation period of between 45 and 70, and 60 and 100 for Norway spruce and Scots pine, respectively, depending on site conditions. Other common trees in the region are birch (*Betula pendula/pubescens*; 11%), oak spp. (*Quercus robur/petraea*; 3.3%), aspen (*Populus tremula*; 2.6%), alder (*Alnus glutinosa*; 2.4%), and beech (*Fagus sylvatica*; 1.6%).

Stand selection

We surveyed the bird communities of 50 forest stands in the counties of Kronoberg and Kalmar in south-eastern Sweden. Ten of these stands were conifer-dominated reserves. The remaining 40 stands belonged to either Scots pine or Norway spruce even-aged production forests of 55 or 80 years of age (10 stands in each tree species and age category). Stands were selected from a forest data-base with tree species composition, forest age, and site fertility. Fertility was gauged using site index (SI) (Hägglund and Lundmark 2013). Stands were selected to have >80 % of the focal tree species by volume, and based on their suitability for conversion from Scots pine to Norway spruce. On this basis, we excluded sites with exceptionally low fertility (unsuitable for Norway spruce), and exceptionally high fertility (unlikely to be used for Scots pine). A subset of these stands was then selected to ensure a relatively even distribution in the area to help reduce potentially confounding biogeographic factors on outcomes.

All available coniferous-dominated forest reserves (> 75% basal area of coniferous trees) located in the same area as the production stands were included in the study. The reserves used were Bockaskruv (established 2005), Hedasjön (2010), Kärngöl (2000), Skårtaryd (1996), Smedjevik (2006), Stocksmyr (2012), Storasjö (1985), Tiafly (1996), Vackerslät (1998), and Vithult (2014). Based on the reserves' management plans and maps, we selected an area (80 × 80 m, see below) within the reserve possessing the oldest forests. It was not possible to core the trees, but according to management plans, the reserves harbored a large number of trees over 100 years of age, in many cases > 120 years, and occasionally up to 200 years of age. The reserves varied in size between 31 and 1368 ha. All stands and nature reserves were located > 1000 m apart, and no closer than 500 m from the nearest water surface.

Bird surveys

We used the point count method to survey breeding bird communities (Bibby et al. 2000). Point counts are an effective means of surveying bird communities, with the abundance estimates provided acting as indices that are correlated with the true abundance of the bird species present. We used a survey radius of 40 m. This threshold distance limits the birds assessed to only those located within the stand and reduces the risk of double counting birds at two survey points. A laser rangefinder was used to calibrate distance assessments during surveys. Furthermore, this radius is less than the maximum distance observers that are estimated to be able to differentiate the distance to calling birds (i.e., 65 m, see Alldredge et al. 2007). Four survey points were located within each stand (each of the four points were surveyed four times), with the proviso that the distance between two survey points was 80 m, and at least 40 m from the stand edge. Points were concentrated within the center of each stand, to reduce the influence of birds using the transition zone of vegetation at the edge of the study site. This constraint also helped to ensure that survey points were not displaced over larger areas in larger stands, which could have increased bird community diversity in such stands due to an increased range of environments surveyed. Survey points were located beforehand using aerial photos and the aforementioned decision rules, to avoid onsite selection bias. Whereas modeling approaches can be used to address detectability issues in point count data, these approaches themselves introduce additional concerns and uncertainties (Barry and Welsh 2001; Johnson 2008). In this study, we adopt an a priori approach to minimizing problems of detectability in the field via multiple elements of our sampling design.

We surveyed each of the study sites four times: twice in early spring (late March/early April) and twice in late spring (late May). We chose these survey periods to coincide with annual peaks in singing activity of breeding resident and migrant passerines, respectively. Notably, the majority of the tropical migrant passerines surveyed have not arrived in this region at the time of the first survey period. Daily surveys began at dawn, at approximately 6:00 a.m. in early spring and 4:30 a.m. in late spring, and finished at 9:00 a.m. and 7:30 a.m., respectively. This period overlapped with the daily peak in bird vocal activity. On each survey day, the same person surveyed two stands. The order in which the stand types were visited was varied systematically to ensure that no stand types were weighted towards early morning or late morning survey times. Surveys were only conducted in suitable weather for conducting bird surveys (i.e., minimal wind, no rain), to minimize environmental influences on detectability and lower bird activity due to the weather.

All point count surveys were conducted by ornithologists (AF, ML, and Thomas Nyberg) experienced with both bird identification and point count surveys, a combination of skill sets which are important for repeatability (Farmer et al. 2012). The stand types were randomized among the observers, and each point was surveyed for 5 min (Bibby et al. 2000). Most identification was made acoustically rather than visually. In cases of uncertainty with respect to the number of individual birds calling (e.g., was it a single individual that sang from two separate locations, or two individuals singing in sequence), the most conservative estimate of abundance was used. Birds observed flying overhead were not included in the survey. All other birds encountered were noted, but only individuals performing territorial behavior (song in almost all cases) were included in the analyses of the results.

As an estimate of the abundance of each bird species in a given stand (based on the four survey points combined in each stand), we used the highest value attained from the four separate surveys conducted in each stand. We adopted this approach, as research indicates that true avian abundance is best correlated with maximum rather than average abundance data from repeated surveys (Toms et al. 2006). This approach also accounts for seasonal differences in the song activity (and therefore detectability) of resident and migrant bird species.

We also evaluated the conservation status and ecological characteristics of the bird species encountered. To do so, we assessed the current threatened status of each species encountered using the Swedish Red List (Gärdenfors 2015). Bird species migratory status, food guilds, nest site, and forest preferences were derived from the Birds of the Western Palearctic (del Hoyo et al. 2017) and are presented in Appendix.

Stand level structures

Ten plots in each stand were surveyed for living trees, living shrubs, and dead wood. Four of the plots were the same as the bird plots; see above. The remaining six were randomly distributed 30 m from the bird plots. The DBH (diameter at breast height) was measured, and basal area calculated, for all living woody species > 1.3 m tall within a radius of 10 m from the center of the plot; in a few cases 7 or 15 m from the center, if the stand was unusually dense, open, or heterogeneous. The volume of dead standing trees and snags > 10 cm DBH were calculated from DBH and height, also within 10-m radius. All lying CWD > 10 cm in diameter within a 5.64 m radius was surveyed for volume estimates. Only the part of the log within the 5.64 was included. Stems of all woody vegetation 0.3–1.3 m tall (not dwarf shrubs) within 5.64 m from plot center were counted and identified to species. To assess structural complexity, the coefficient of the variation in tree sizes (DBH) was calculated as the ratio of the standard deviation to the mean. Shannon's diversity based on the basal area distribution between tree species was used as an indicator of tree species diversity. To estimate the fertility of the sites, soil samples were taken. Using a soil sampler, a 10-cm deep soil core was extracted from the four bird plots, after removing surface foliage down to root level. In shallow humus layers, several samples had to be taken to achieve the same volume. Carbon levels were determined by "loss of ignition" (KLK 1965:1 mod) and a conversion factor of 1.9 (Pribyl 2010). Total N (Dumas) was assessed using a Leco FP-428 analyzer.

Landscape level vegetation structures

To assess the influence of the landscape context on bird communities within stands, we used a spatially explicit dataset (pixel size 25 × 25 m) of forest land, developed from satellite imagery and inventory data provided by the National Forest Survey of Sweden, using the kNN-method (k-Nearest Neighbors algorithm) (Reese et al. 2003). For our analysis, the volumes from 2010 for Norway spruce, Scots pine, Birch, Oak, and Beech were used. Additional deciduous species were lumped into a single "other deciduous" category. Forests found within circles surrounding the center of each stand (i.e., the center of the four survey points) with radii of 2000 m were used to define landscape vegetation in terms of different tree species' proportions of the total standing wood volume. The proportion of forest land in the total land area was also determined for each radius.

Statistical analyses

All statistical analyses were done in R 3.4.1 (R_Core_Team 2017). The effect of stand type on all univariate response variables (species richness, abundance, etc.) was modeled using Generalized Linear Models (GLM). Negative binomial error distribution was used, due to detected overdispersion, on all response variables except species richness where a Poisson distribution was used, both with log-link. Planned pair-wise contrast between stand types was applied for the following pairs when an ANOVA on the GLMs indicated a significant effect of stand type: reserves vs. Pine55, Pine80, Spruce55 and Spruce80, Pine80 vs. Spruce80 and Spruce55, and Spruce55 vs. Spruce80. The contrasts were performed with the glht function in the multcomp package (Hothorn et al. 2008) and corrected for multiple comparisons with the fdr (false discovery rate) correction. All GLMs were checked for over-dispersion by calculating the dispersion parameter, and for patterns in the residuals by plotting the Pearson residuals against the fitted values. To analyze the effects of stand type on bird communities, an unconstrained ordination, non-metric multidimensional scaling (NMS), was performed on the bird community data by applying the metaMDS function in the Vegan package (Oksanen et al. 2017). The correlation between site locations in ordination space, environmental variables, and the stand type centroid was analyzed by the envfit function in Vegan and projected on the final NMS solution with 95% confidence intervals. The NMS and projection of the environmental variables were done with Bray–Curtis dissimilarity and 999 permutations. This dissimilarity index gives higher weight to more abundant than less abundant species and is a robust measure of ecological gradients (Faith et al. 1987).

Results

Birds

A total of 558 individual birds belonging to 32 species were recorded exhibiting territorial behavior during the surveys. The highest total number, the γ (gamma) diversity, of species was recorded in the reserves collectively, followed by Spruce80, Spruce55, Pine55, and Pine80 (26, 18, 16, 16, and 13, respectively). Of the pair-wise comparisons in the GLM analysis, the Reserves had a higher richness than both Scots pine types, and Spruce80 had higher richness than Pine80 (Table 1). There was a significant difference in abundance between the Reserves and Pine55, with more individuals in the former. No difference was found for resident birds. Migratory birds were more common in the Reserves compared to Pine80, and Spruce80 compared to Pine80. More insectivores were found in Reserves compared to Pine55, more Omnivores in Spruce55 compared to Spruce80. No other significant differences in richness or abundance were found between the stand types.

The NMS unconstrained ordination resulted in a solution requiring only two dimensions. The ordination diagram shows a difference in ordination space along the first dimension for the Scots pine stand types vs the Norway spruce types and thus indicated differences in the species composition of their respective bird communities, according to the 95% confidence intervals (Fig. 1). The reserves are located centrally in the ordination space between the Norway spruce and Scots pine

Table 1 Mean (SE) species total richness and abundance and richness for functional groups. The effect of stand type on these variables was estimated by Generalized Linear Models (GLM). A significant effect (P < 0.05) of stand type from the GLM was followed by planned pairwise contrasts. Significant contrasts are in italic. R reserves, P55 and Pine55 Scots pine stands 55 years old, S55 and Spruce 55 Norway spruce 55 years old, etc.

	Mean (SE)					GLM	Contrasts (p values)						
	Reserves	Spruce80	Spruce55	Pine80	Pine55	P value	R vs S80	R vs S55	R vs P80	R vs P55	S80 vs P80	S55 vs P80	S80 vs S55
Species richness	8.9 (0.6)	7.9 (0.8)	6.9 (0.7)	5.1 (0.8)	4.6 (0.7)	<0.001	0.441	0.158	*0.005*	*0.002*	*0.035*	0.158	0.441
Total abundance	13.5 (0.9)	11.6 (1.4)	13 (1.4)	10 (2)	7.7 (1.7)	0.036	0.626	0.839	0.405	*0.035*	0.626	0.405	0.638
Resident	3.9 (0.6)	2.6 (0.5)	3 (0.5)	2.8 (0.9)	1.6 (0.5)	0.089							
Migratory	3.9 (0.6)	4.1 (0.7)	2.3 (0.4)	1.9 (0.4)	2.3 (0.4)	0.007	0.823	0.062	*0.036*	0.062	*0.036*	0.627	0.062
Part migratory	5.7 (0.7)	4.9 (0.9)	7.7 (1)	5.3 (0.9)	3.8 (1.1)	0.053							
Insectivores	9.1 (0.9)	8.5 (1.1)	7.3 (1)	6 (1.4)	4.5 (0.9)	0.011	0.733	0.494	0.173	*0.012*	0.241	0.517	0.539
Omnivores	3.8 (0.3)	2.8 (0.4)	5.4 (0.7)	3.9 (0.6)	3.1 (0.8)	0.036	0.308	0.284	0.909	0.467	0.308	0.284	*0.034*
Cavity Nesters	4.6 (0.6)	3.5 (0.6)	3.7 (0.6)	2.8 (0.9)	2 (0.6)	0.058							
Off ground nesters	7.4 (0.7)	6.6 (1)	8.3 (1)	5.8 (1)	4.2 (1.3)	0.035	0.594	0.594	0.486	0.108	0.594	0.34	0.486
Conifer associated	4.4 (0.6)	4 (0.9)	4.3 (0.8)	2.4 (0.8)	1.9 (0.7)	0.029	0.936	0.936	0.156	0.084	0.195	0.156	0.936

types and was not significantly different to any of the other stand types.

Chaffinch was the most common bird species and was found in all stands (Table 2). Of the ten most common birds (found in > 15 stands), many of them are located in the center of the ordination space (Fig. 1b), indicating that they are not associated specifically with any of the stand types assessed. However, there were also species found in Scots pine that were not encountered in Norway spruce production stands. Six species were unique to Scots pine, including Tree pipit and Spotted flycatcher, whereas seven were unique to Norway spruce, including Blackcap, Dunnock, and Wood pigeon, all of which were located close to their respective stand type in the ordination space. Of the species not unique to either stand type, Song thrush were more common in Spruce80, and Robin and Wren were more common in both Spruce stand types. Many of conifer specialists were more common the Spruce stands than the Scots pine stands, in particularly Goldcrest, Willow tit, Dunnock, and Coal tit. Among the relatively common birds, Great spotted woodpecker, Pied flycatcher, Crested tit, Treecreeper, and Mistle thrush were more common in the Reserves compared to the production stands, which further differentiated the bird communities of these forest types. The red-listed species recorded in the different forest types included Goldcrest (VU; recorded in all stand types), Black woodpecker (NT; one individual in a Reserve), and Goshawk (NT; one in Spruce80).

Vegetation

In terms of differences in vegetation, the stands differed significantly in the majority of structural measures assessed (see Fig. 1, Table 3). For example, variation in tree diameters was larger in the Reserves compared to the other stand types (Table 3), indicating greater structural heterogeneity. There were small differences between the Spruce80 and the Scots pine types in this regard, whereas Spruce55 had the lowest variation in tree diameters. Tree species diversity also differed between the stand types, with the highest diversity also found in the Reserves, whereas few differences occurred between the production stand types. Specifically, there were more broadleaves stems and higher broadleaved basal area (1.9 and 1.3 m^2 ha^{-1}) in the Reserves and Spruce80 as compared to the other stand types, in which broadleaf tree species were largely absent. The shrub layer was also more developed in the Spruce80 and Reserves (1107 and 845 stems ha^{-1}) as compared to the other stand types. In particular, Spruce55 had few shrubs (135 ha^{-1}). More dead wood was recorded in the Reserves (49.8 m^3 ha^{-1}) compared to the production stands (1.8–10.0 m^3 ha^{-1}), with Spruce80 having the largest volumes among the later. Large trees (> 40 cm DBH) were

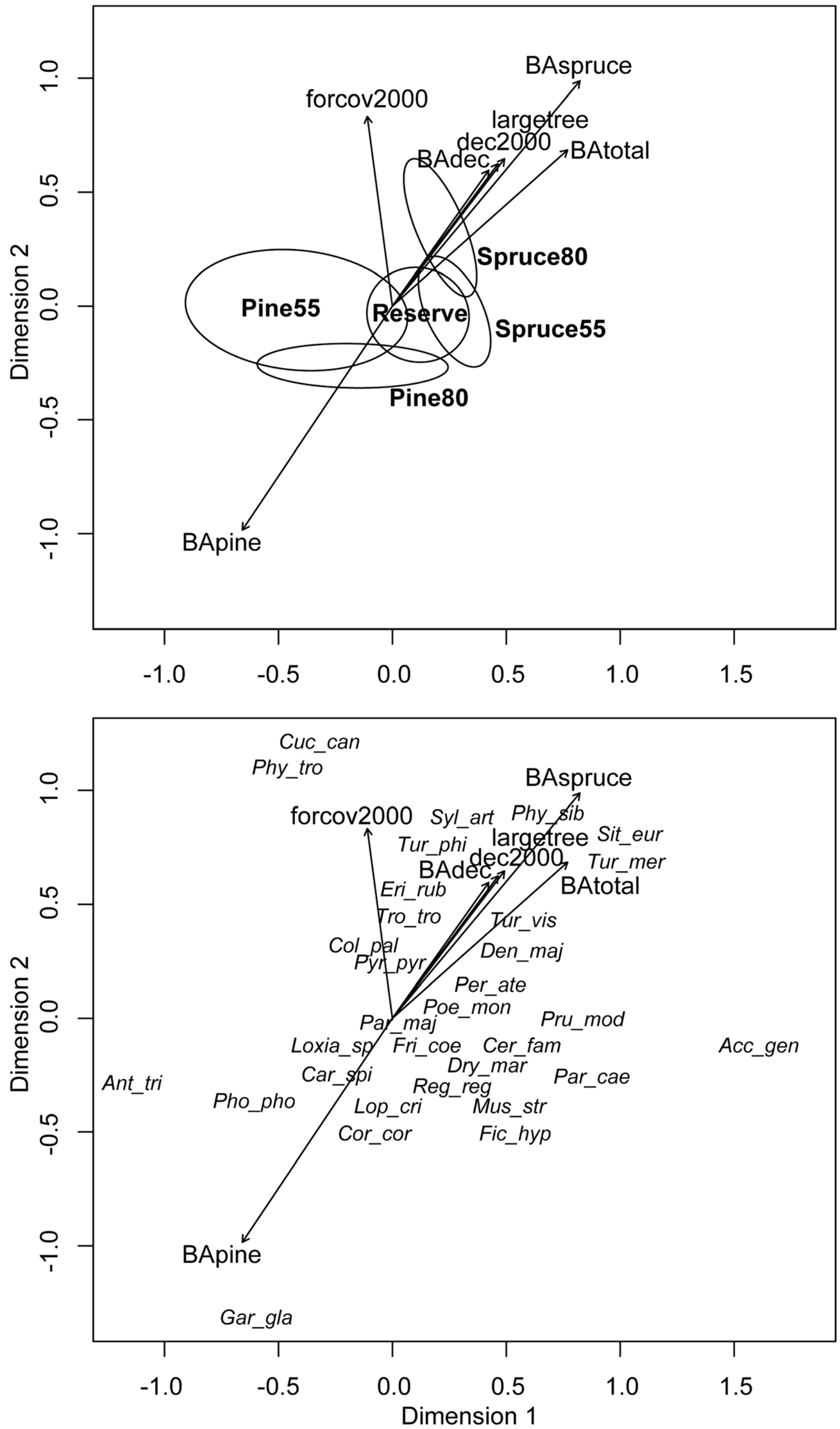

Fig. 1 Ordination diagrams from the non-metric multidimensional scaling showing the two-dimensional final solution with and explanatory/correlative variables (upper panel), and species (lower panel). The significant ($P < 0.05$) explanatory variables from a post hoc fit are shown as arrows (continuous), or location in ordination space (stand type) with 95% confident intervals. Forcov2000 is % forest cover within 2000 m, BA is basal area, Largetree is number of trees dbh ≥ 40 cm, Dec2000 is % broadleaves within 2000 m, and BAdec is broadleaves basal area. Abbreviations for bird species scientific names correspond to the three first letters in the species and genus name. See Table 2 for full names

common in the Reserves (23 ha^{-1}) and Spruce80 (38 ha^{-1}), but rarer in the other stand types (0–8 ha^{-1}). Scots pine was the most common tree in the 2000 m radius surrounding the Scots pine stands and the Reserves, while Norway spruce was more common around the Spruce stands, but the overall differences between the stand types were small. Spruce80 had the lowest soil carbon/nitrogen ratio (29.8), but the difference with the other stand types was small.

Discussion

Bird diversity in Scots pine and Norway spruce production stands

The results of our surveys indicated that Scots pine and Norway spruce production stands support overlapping but nevertheless to some degree distinct bird communities.

Table 2 Average number of individuals performing territorial behavior per hectare in the different stand types, in parenthesis the share of stands in which the species was encountered. "All prod" is all 40 Norway spruce and Scots pine stands lumped. Asterisk denotes coniferous specialists according to del Hoyo et al. (2017). When applicable, the current red-list status in Sweden is shown after the species name. VU is "vulnerable" and NT is "Nearly Threatened"; a category is assigned if the species is likely to qualify for a threatened category in the near future

	Reserves	All prod	Spruce 80	Spruce 55	Pine 80	Pine 55
Chaffinch (*Fringilla coelebs*)	2.59 (1)	2.64 (1.0)	2.09 (1.0)	3.28 (1.0)	2.69 (1.0)	2.49 (1.0)
Goldcrest* (*Regulus regulus*) VU	1.00 (0.8)	1.08 (0.7)	1.39 (0.9)	1.69 (0.9)	0.85 (0.6)	0.40 (0.4)
Treecreeper (*Certhia familiaris*)	0.65 (0.9)	0.42 (0.6)	0.60 (0.8)	0.50 (0.9)	0.50 (0.6)	0.10 (0.2)
Crested tit* (*Lophophanes cristatus*)	0.55 (0.7)	0.27 (0.5)	0.15 (0.3)	0.30 (0.5)	0.40 (0.6)	0.25 (0.5)
Great tit (*Parus major*)	0.50 (0.5)	0.49 (0.5)	0.70 (0.7)	0.30 (0.4)	0.65 (0.7)	0.30 (0.3)
Wren (*Troglodytes troglodytes*)	0.45 (0.9)	0.37 (0.6)	0.60 (0.9)	0.45 (0.8)	0.20 (0.3)	0.25 (0.5)
Robin (*Erithacus rubecula*)	0.35 (0.4)	0.27 (0.5)	0.45 (0.7)	0.35 (0.7)	0.10 (0.2)	0.20 (0.2)
Blackbird (*Turdus merula*)	0.30 (0.5)	0.19 (0.3)	0.40 (0.6)	0.25 (0.5)	0	0.10 (0.2)
Eurasian jay (*Garrulus glandarius*)	0.30 (0.4)	0.14 (0.2)	0.25 (0.4)	0.15 (0.2)	0.05 (0.1)	0.10 (0.2)
Great spotted woodpecker (*Dendrocopos major*)	0.30 (0.5)	0.10 (0.2)	0.15 (0.3)	0	0.15 (0.3)	0.10 (0.2)
Willow tit* (*Poecile montanus*)	0.30 (0.5)	0.29 (0.5)	0.30 (0.6)	0.50 (0.7)	0.15 (0.3)	0.20 (0.4)
Tree pipit (*Anthus trivialis*)	0.25 (0.5)	0.27 (0.4)	0	0	0.55 (0.9)	0.55 (0.8)
Eurasian siskin* (*Spinus spinus*)	0.20 (0.3)	0.31 (0.3)	0.20 (0.4)	0.15 (0.2)	0.45 (0.4)	0.45 (0.3)
Song thrush (*Turdus philomelos*)	0.20 (0.4)	0.14 (0.3)	0.40 (0.8)	0.10 (0.2)	0	0.05 (0.1)
Mistle thrush* (*Turdus viscivorus*)	0.20 (0.4)	0.04 (0.1)	0.10 (0.2)	0	0	0.05 (0.1)
Dunnock* (*Prunella modularis*)	0.15 (0.2)	0.05 (0.1)	0.15 (0.3)	0.05 (0.1)	0	0
Crossbill spp.* (*Loxia* ssp.)	0.15 (0.3)	0.16 (0.1)	0	0.05 (0.1)	0.60 (0.4)	0
Woodpigeon (*Columba palumbus*)	0.15 (0.3)	0.09 (0.2)	0.15 (0.3)	0.20 (0.3)	0	0
Coal tit* (*Periparus ater*)	0.15 (0.3)	0.24 (0.4)	0.40 (0.7)	0.30 (0.5)	0.15 (0.2)	0.10 (0.2)
Nuthatch (*Sitta europaea*)	0.15 (0.2)	0.00 (0)	0	0	0	0
Pied flycatcher (*Ficedula hypoleuca*)	0.15 (0.3)	0.00 (0)	0	0	0	0
Spotted Flycatcher (*Muscicapa striata*)	0.10 (0.1)	0.09 (0.1)	0	0	0.30 (0.4)	0.05 (0.1)
Blue tit (*Cyanistes caeruleus*)	0.05 (0.1)	0	0	0	0	0
Willow warbler (*Phylloscopus trochilus*)	0.05 (0.1)	0.05 (0.1)	0.10 (0.2)	0.05 (0.1)	0	0.05 (0.1)
Capercaillie (*Tetrao urogallus*)	0.05 (0.1)	0.01 (0.03)	0	0.05 (0.1)	0	0
Black woodpecker (*Dryocopus martius*) NT	0.05 (0.1)	0	0	0	0	0
Redstart (*Phoenicurus phoenicurus*)	0.05 (0.1)	0.01 (0.03)	0	0	0	0.05 (0.1)
Bullfinch (*Pyrrhula pyrrhula*)	0	0.04 (0.1)	0	0.15 (0.2)	0	0
Wood warbler (*Phylloscopus sibilatrix*)	0	0.01 (0.03)	0.05 (0.1)	0	0	0
Blackcap (*Sylvia atricapilla*)	0	0.06 (0.1)	0.15 (0.3)	0.05 (0.1)	0.05 (0.1)	0
Yellowhammer (*Emberiza citrinella*)	0	0.01 (0.03)	0	0	0.05 (0.1)	0
Goshawk (*Accipiter gentilis*) NT	0	0.02 (0.1)	0.05 (0.1)	0	0.05 (0.1)	0
Raven (*Corvus corax*)	0	0.01 (0.03)	0	0	0.05 (0.1)	0
Woodcock (*Scolopax rusticola*)	0	0.02 (0.1)	0.05 (0.1)	0.05 (0.1)	0	0
Nutcracker (*Nucifraga caryocatactes*)	0	0.01 (0.03)	0	0	0	0.05 (0.1)
Common cuckoo (*Cuculus canorus*)	0	0.01 (0.03)	0.05 (0.1)	0	0	0

Hence, converting Scots pine production forests to Norway spruce in this region's context may result in a more homogenous and less diverse bird community at the landsape scale. Whereas abundant species, including Chaffinch, Goldcrest, and Crested tit, were encountered in Norway spruce and Scots pine stands of both age categories, other less common species helped to distinguish these stand types. This includes the six species unique to Scots pine production stands encountered in the study, including Tree pipit and Spotted flycatcher, and the seven species unique to Norway spruce, including Blackcap, Dunnock, and Wood pigeon. Additional differences were also observed in the diversity of bird species encountered, with Scots pine stands supporting lower species diversity relative to similarly aged Norway spruce stands. This finding mirrors that of Jansson and Andrén (2003), which likewise found that Scots pine-dominated survey points in

Table 3 Stand data from the forest categories. The last colum describe the signifance level regarding the diffrences between the stand types. NS is Not Significant

	Reserves		Spruce80		Spruce55		Pine80		Pine55		Significance
	Mean	Standard error of mean	Mean	Standard error of mean	Mean	Standard error of mean	Mean	Standard error of mean	Mean	Standard error of mean	
Variance stem dbh	.84	.06	.68	.08	.35	.02	.61	.15	.57	.06	**
Shannon tree diversity	.65	.05	.22	.04	.16	.03	.18	.03	.10	.01	***
Pine stems ha^{-1}	217	31	9	3	25	6	447	102	426	18	***
Spruce stems ha^{-1}	644	100	759	88	749	81	131	29	132	32	***
Broadleaves stems ha^{-1}	223	85	166	35	37	15	34	14	93	28	*
Total stems ha^{-1}	1084	138	934	101	811	89	611	115	651	44	*
Pine basal area (m^2 ha^{-1})	14.4	1.6	.9	.4	1.1	.2	20.9	1.2	16.3	.9	***
Spruce basal area (m^2 ha^{-1})	8.0	1.1	29.5	2.4	24.1	2.3	1.5	.4	.3	.1	***
Broadleaves basal area (m^2 ha^{-1})	1.9	.7	1.3	.5	.2	.1	.2	.1	.1	.0	**
Total basal area (m^2 ha^{-1})	24.2	1.2	31.7	2.4	25.4	2.3	22.6	1.3	16.6	.9	***
No of woody shrubs (0.3–1.3 ha^{-1})	845	152	1107	166	135	65	693	371	619	168	*
Dead wood (m^3 ha^{-1})	49.8	10.8	10.0	1.9	1.8	.5	4.3	1.6	3.6	2.7	***
% forest cover <2000 m	81	3	88	2	81	4	81	2	80	4	NS
% Pine <2000 m	42	2	34	3	36	2	44	3	42	2	*
% Spruce <2000 m	48	3	54	3	53	2	47	3	48	2	NS
% Broadleaves <2000 m	10	1	12	1	11	1	9	1	9	1	*
No trees dbh ≥ 40 cm	22.9	4.4	37.6	9.0	1.3	.9	7.8	2.5	.0	.0	***
Soil C/N	35.1	.9	29.8	1.3	34.3	.8	37.3	.9	36.2	.8	***

Sweden supported lower species richness than those dominated by Norway spruce. The result is different than a similar study in Norway where species richness was higher in native Scots pine forest than in Norway spruce plantations (Gjerde and Saetersdal 1997). However, that assessment had different aims and did not evaluate Scots pine plantations specifically.

Our results need to be interpreted with some caution. Most of the unique species in the respective stand types were recorded rarely and consisted of a limited number of few individuals. Eight of the 13 species unique to either spruce or Scots pine production stand types were represented by only one or two individuals. Of the six species unique to Scots pine, only Tree pipit and Spotted flycatcher were recorded in higher numbers. Both species are associated with open forest conditions with higher understory light levels (del Hoyo et al. 2017) provided by forests with a lower basal area, such as that found in the Scots pine stands (Table 3). It is important to note that both birds species are among the ten most common birds in the country, with national abundances of over 1 million pairs (Ottosson et al. 2012). Furthermore, both species have stable populations at national and regional levels (Green et al. 2018; Lindbladh et al. 2017), and are known to breed in habitats other than conifer production stands. For this reason, it is difficult to argue that the decrease in Scots pine poses an imminent risk to any particular bird species.

Nevertheless, according to national surveys, several conifer-associated bird species found in southern Sweden do appear to have population strongholds in Scots pine forests, including Redstart, Woodlark, Crested tit, Willow tit, Mistle thrush, and Parrot crossbill (Ottosson et al. 2012). Of these, Crested and Willow tit were found in both Scots pine and Norway spruce production forests, with Crested tit more common in Scots pine and Willow tit more common in Norway spruce stands. Redstart and Mistle thrush are also associated with Scots pine stands, but the former was only encountered in a single Scots pine stand, and Mistle thrush was rarely encountered in any production forest types. The rarity of both species was not expected as each has been exhibiting strong population increases in the region over recent years (Green et al. 2018; Lindbladh et al. 2017). We had also expected to find Wood lark in Scots pine stands, due to its breeding association with open and semi-open habitats on well-drained soils (del Hoyo et al. 2017), an environment broadly similar to that provided by Scots pine stands in our study. However, no individuals of this species were recorded, despite Wood lark having a population stronghold in the eastern part of our study region. We suspect that its absence stemmed from a preference for bare ground or very sparse short vegetation for feeding (del Hoyo et al. 2017), something lacking in most of our stands and reserves. Furthermore, studies conducted in Poland indicate that woodlark occur in young Scots pine plantations (0–10 years post-harvest) (Zmihorski 2012), which suggests that their absence in our studies may also result from our focus on later stages in a stand's rotation.

Among the production stands, the older spruce stands had the highest average bird species richness, and largest total number of species recorded. We suggest the higher diversity can be explained by some of their stand characteristics. Most obvious is the high basal area and hence leaf biomass in the older stands, which increase the living space and number of niches provided by the trees (Fig. 1). Moreover, despite attempts during stand selection to reduce divergence in site fertility, the older spruce stands seem on average be slightly more fertile relative to the other stand types. A positive correlation between productivity and diversity has been shown in many studies and for many different organism groups (Begon et al. 2005; Helle and Mönkkönen 1990). In addition, the higher bird species diversity may also stem from the high proportion of broadleaves found in these stands (Fig. 1). Even a relatively small broadleaved component in coniferous stands has been found to boost levels of bird diversity in this region (Lindbladh et al. 2017). Moreover, the older Spruce stands also had higher volumes of dead wood, more large trees (≥ 40 cm DBH), and higher numbers of woody shrubs than the other production stand types—all of which are forest attributes demonstrated to increase bird diversity (Hewson et al. 2011). Finally, from a stand management and nature conservation perspective, the higher bird diversity in the Spruce80 stands may also indicate the potential benefits to bird diversity from the adoption of longer than normal rotation times (Felton et al. 2017; Roberge et al. 2018). Correspondingly, concerns can likewise be raised due to pressures to shorten the rotation lengths of Norway spruce stands in this region (Felton et al. 2016a).

Production forests and reserves

Collectively reserves supported a higher diversity of bird species than production forests, and five bird species were unique to the reserves, including the near threatened Black woodpecker. This indicates that the reserves are contributing to the γ-diversity at landscape level (Whittaker 1960), admittedly even if the occurrence of many of these species, including the black woodpecker, was limited to a few individuals only. The community composition of the reserves appeared to encompass a broader range of bird species than supported by Norway spruce or Scots pines either stands, and also included seven species otherwise limited to either Norway spruce or Scots pine production stands. We suggest that the higher bird species richness encountered in the reserves likely stemmed from their possession of trees in excess of 100 years old (according to management plans), higher amounts of deadwood, and a more balanced mix of Norway spruce and Scots pine (Table 3).

Nevertheless, the bird diversity found in the reserves in this study was lower than could potentially be expected when comparing highly managed with unmanaged forests (Rosenvald et al. 2011). Most importantly, the average species richness of reserves was not significantly different from either age category of Norway spruce stand. This may be explained by most of the reserves being newly established (1985–2014), and although they contained some old-growth features, many reserves differed little from the oldest Norway spruce stands and are not true "old-growth forests" (Nilsson et al. 2002). For example, the reserves contained very few trees above 50 cm in DBH, and had a low abundance of woody shrubs. In addition, much of the dead wood came from recently dead Norway spruce trees (personal observation), and the reserves only supported slightly more broadleaves than the older Norway spruce stands. Hence, the coniferous reserves in the region were the best available, but still limited examples of natural forest reference conditions. The limitation of these reserves is, however, likely to be temporary. Their diversity of forest birds and other forest taxa can be expected to increase over time as natural disturbance processes facilitate the development and availability of old-growth structures, and likewise increase opportunities for understory shrubs and broadleaf tree species.

A further indication that the reserves supported that a relatively limited bird diversity can be derived from assessing species defined as indicators of old-growth (structurally complex) forests in the government's environmental quality goals (www.sverigesmiljomal.se), which include the Crested tit, Treecreeper, Willow tit, Coal tit, and Bullfinch. Bullfinch was only recorded once, whereas the other four species were encountered relatively frequently. Of these, the Crested tit and Treecreeper behaved according to expectations, and occurred less frequently in the production stands compared to the reserves. However, both the Willow tit and Coal tit were, in contrast, more common in the Norway spruce stands than in the reserves. The conservation status of Willow tit has been of concern since decreases in the species populations began in the 1970s. These declines have been suggested to result from the frequent removal of understory vegetation, i.e., small trees, in production forests (Eggers and Low 2014). Interestingly, this bird species was most common in Spruce55 (6 out of 10 stands), despite this stand category being much lower in the number of woody shrubs, and less structurally complex than any of the other stand types. Goldcrest is another species that deserves to be mentioned in this regard. It was recently red-listed because of a continuous national population decline recorded since 1990 (Green et al. 2018). One suggested reason for these declines is the transformation of structurally complex Norway spruce forests to dense plantations (Gärdenfors 2015). Interestingly, our study does not support this suggestion either, as Goldcrest was common in all stand types, and in the Spruce55 stands, it was recorded in nine out of ten stands. For both of these species, our results indicate that additional drivers need to be considered when trying to account for current national level declines, and questions may be raised regarding the suitability of some of the avian indicators of old-growth forest being used in Sweden.

Conclusion

In summary, our results indicated that (i) Scots pine and Norway spruce support overlapping but nevertheless to some degree distinct bird communities, but with the caveat that few individuals were recorded of many of the species unique to either stand type; (ii) the conversion of Scots pine to Norway spruce is likely to increase the homogeneity of the bird communities in this region; and (iii) conifer-dominated reserves, though lacking in many old-growth features; nevertheless, positively contributed to γ-diversity at the landscape level. We emphasize that the habitats provided by these protected areas can be expected to improve over coming decades. In contrast, the contribution of Norway spruce stands to forest bird habitats can be expected to decline over coming decades, if rotation lengths are shortened as expected (Felton et al. 2017).

Finally, we want to emphasize that our results are confined to forests late in the rotation cycle and that they are most reliable in terms of the more common conifer-associated birds that are readily encountered using standard point count survey methodologies. We therefore cannot draw firm conclusions for bird species or guilds that need specifically designated survey techniques, such as irregular breeders (e.g., crossbills), and species with sparse populations (e.g., Capercaille and Black grouse), or large territories (e.g., birds of prey and woodpeckers). Due to this limitation, we cannot rule out the possibility that differences in the bird diversity supported by the two production forest types, and by the reserves and production forests, are in fact more pronounced than our results indicate. Conducting surveys of such bird species and their response to protected and production forest land alternatives is an important task for future studies, as are surveys in a wider range of stand ages.

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